Predators feeding on behaviourally responsive prey: some implications for classical models of optimal diet choice

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ABSTRACT

Hundreds of studies exist on predator foraging behaviour, and the same holds for anti-predator behaviour in prey. However, despite these many studies, almost nothing is known about diet choice by predators that feed on prey with anti-predator behaviour. We addressed this problem theoretically by incorporating anti-predator vigilance into two classical models of diet choice by predators. Vigilance allows prey to detect attack and escape, and prey become more vigilant as the predator focuses more of its attention on a specific prey type. We considered diet models in which predators encounter two types of prey either simultaneously (in mixed-type groups) or sequentially (solitary, randomly distributed prey). In both cases, anti-predator behaviour in prey causes predators to adopt a more generalized diet than one might predict on the basis of classical theory. When prey are encountered simultaneously, increased dietary generalization by predators often reflects broad 'partial prey preferences'. Here, predators tend to attack both prey types some of the time rather than attack only one prey type all of the time (as suggested by classical theory). When prey are encountered sequentially, increased dietary generalization reflects mainly an increase in the threshold encounter rate necessary to cause the predator to drop the less profitable prey from the diet. However, when sequentially encountered prey require an investment in stalking time (which will be lost to the predator if the prey detects attack), partial preferences may hold over a large part of parameter space. Also possible under this stalking-time scenario is the reversal of prey preferences, in which the inherently less profitable prey is always preferred by the predator. These general deviations from the expectations of classical diet theory reflect, in part, the fact that predators faced with behaviourally responsive prey will often benefit from 'managing' the anti-predator responses of those prey.

Keywords: anti-predator behaviour, diet models, foraging theory, partial preferences, predator–prey interactions, prey management, vigilance.

INTRODUCTION

Models of optimal diet choice address the reasons why a predator might include only a subset of available prey in its diet – that is, why some prey types are attacked when

encountered while others are ignored (Stephens and Krebs, 1986). These models trace their roots back to the model of diet choice developed by MacArthur and Pianka (1966). This model was born of a desire to better understand the behavioural mechanisms underlying trophic interactions, and many researchers are still involved with this endeavour (see Schmitz, 1997, and papers therein). MacArthur and Pianka's model also introduced optimality modelling into the study of behaviour (see also Stephens and Krebs, 1986; Mitchell and Valone, 1990), which provided a focal point for many conceptual developments in behavioural ecology (e.g. Maynard Smith, 1982; Mangel and Clark, 1988; Giraldeau and Caraco, 2000).

The basic model of diet choice was cast into its present form by Schoener (1971), Pulliam (1974) and Charnov (1976). The basic idea behind this model is that predators have been 'designed' by natural selection (*sensu* Stephens and Krebs, 1986) to attack only that subset of available prey (the optimal diet) that will maximize their rate of energy intake. A key insight of this classical model is that a predator may actually benefit by ignoring certain prey in favour of attacking others, even if the former are abundant in the environment. Furthermore, prey in the optimal diet are always attacked upon encounter, and those not in the diet are never attacked (the '0,1 rule').

Basic diet theory has been extended to include a variety of issues that might be faced by predators. For instance, 'partial preferences' for prey (a violation of the 0,1 rule in which a given prey type is not always attacked upon encounter) may result from difficulties in discriminating among prey types (Rechten *et al.*, 1983; Glaizot and Arditi, 1998) or constraints imposed by nutrients or toxins (Hirakawa, 1995). When prey are encountered simultaneously in mixed-type groups (Stephens *et al.*, 1986), apparently profitable prey may be ignored in favour of less profitable prey. Constraints imposed by gut capacity or processing can also alter classical expectations (Belovsky, 1978; Abrams and Schmitz, 1999), as will prey depletion (Mitchell, 1990; Visser, 1991) and the risk of starvation (Stephens and Charnov, 1982).

Diet theory in its many forms has a proven ability to predict the basics of predator behaviour in many circumstances. Under controlled experimental conditions, in which the assumptions of theory can be better met, diet theory has a good record of predicting and explaining prey choice by a variety of animals (see Stephens and Krebs, 1986). The application of diet theory to field conditions has proven somewhat more difficult and controversial. A recent review, however, suggests that diet theory is able to explain at least the basic aspects of diet choice by many types of predators, although perhaps not in circumstances in which predators are feeding on mobile prey (Sih and Christensen, 2001).

Research on prey decision making under the risk of predation also traces its roots directly back to MacArthur and Pianka (1966) and classical foraging theory (see Dill, 1987; Sih, 1987; Mangel and Clark, 1988; Lima and Dill, 1990). However, despite these origins and well over one thousand papers devoted to such decision making, only a few models have considered the effects of predation risk on diet choice *per se* (Lima, 1998). These models assume that the predation risk is experienced by the forager, and that available prey differ in ways that influence the forager's risk of predation (Lima, 1988; Gilliam, 1990; Godin, 1990; but see Abrams and Schmitz, 1999). Under this scenario, prey choice should be influenced not only by the energetic characteristics of the prey, but also by the ambient risk of predation experienced by the forager. Empirical tests of these classically inspired ideas are few (see Lima, 1998; but see also Brown and Morgan, 1995; Abrams and Schmitz, 1999).

Our aim here is to extend classical diet theory to consider a common situation that has received virtually no attention: predators feeding on prey that respond to the risk of predation. The lack of work devoted to this topic is remarkable, given the fact that the study of anti-predator decision making is fundamentally about prey responsiveness to the risk of predation. However, this reflects a long-standing tradition in the study of behavioural predator–prey interactions in which only one party – predator or prey – is actually allowed to behave (Lima, 2002). In the study of diet choice, this tradition expresses itself in the form of prey that are assumed (explicitly or implicitly) to be behaviourally inert, immobile or otherwise lacking in any anti-predator behaviour. Only a few studies of habitat choice (Schwinning and Rosenweig, 1990; Hugie and Dill, 1994; Heithaus, 2001; see also Lima, 2002) and some recent models of predator–prey activity patterns (Brown *et al.*, 2001; Kotler *et al.*, 2002) have broken with this tradition.

In the simple models that we develop below, we allow for an explicit interplay between predator and prey. Our models deal with circumstances in which a predator encounters prey either simultaneously (in groups) or sequentially (one at a time). For comparative purposes, we confine our models to the classical modelling paradigm as much as possible. In all cases, diet choice by a predator is influenced by prey responses to its dietary options. As we will show, this interaction between predator and prey may change both the quantitative and qualitative nature of classical expectations.

PREDATION RISK AND PREY BEHAVIOUR

Before addressing specific models of diet choice, we first consider the nature of risk experienced by prey and the way in which they will respond to that risk.

Prey responsiveness to risk

The anti-predator behaviours that are most relevant to classical diet theory are those that influence the probability of prey capture upon encounter with a predator. We chose to focus on one such behaviour that is particularly well studied: anti-predator vigilance (for reviews, see Elgar, 1989; Roberts, 1996; Bednekoff and Lima, 1998; Treves, 2000). Vigilance is a form of alertness that usually involves a cessation of feeding. Hence an increase in vigilance always leads to a greater likelihood of detecting predatory attack, but at the expense of energy intake.

We modelled vigilance using a simple formulation developed by Parker and Hammerstein (1985) as modified by Lima (1990). This simple and tractable formulation assumes that prey fitness is akin to survival, and that the probability of survival for ith prey type is given by

$$P\,(\text{surv}) = [1 - a_i\,(1 - v_i)]\,(1 - v_i^{\beta_i}) \tag{1}$$

where v_i is the proportion of time spent vigilant and a_i is the probability of attack. The parameter β_i represents the foraging-related cost of being vigilant: vigilance becomes less costly as β_i increases. The first bracketed factor in equation (1) represents the probability of escaping attack, and the second factor represents the probability of avoiding starvation. This formulation assumes that a prey animal must be vigilant at the time of attack in order to escape. Relatively complex models of vigilance show that a scan initiated after the start of attack may still allow for effective escape (McNamara and Houston, 1992). Allowing for such an effect would accentuate the results presented below, hence the formulation in

equation (1) is not only tractable but also conservative in many ways. Modifications for grouped prey are considered later.

In the basic predator–prey interaction that we envision, a_i is determined by the choices made by the predator. The more attacks that the predator chooses to direct towards prey type i, the greater the likelihood of attack (a_i) on a given individual of prey type i (see also next section). The value of β_i determines how responsive prey vigilance will be to an increase in the likelihood of attack. As β_i increases (i.e. as the cost of vigilance declines), prey vigilance becomes more responsive to increased risk. In general, prey types may differ in a_i as a result of predator choice, and in β_i as a result of their particular feeding situations.

Equation (1) must usually be solved numerically for optimal vigilance (v_i^*) as a function of a_i and β_i. Lima (1990) considers the form of these optimal solutions in some detail. We note here that optimal vigilance (v_i^*) always increases with increasing a_i, but eventually levels off ($\partial^2 v_i^*/\partial a_i^2 < 0$ for large a_i). Optimal vigilance is always non-zero for $\beta_i > 1$. For $0 < \beta_i < 1$, $v_i^* = 0$ up to some threshold probability of attack beyond which $v_i^* > 0$. For $\beta_i = 0$, optimal vigilance is always zero. As mentioned above, v_i^* increases with β_i ($\partial v_i^*/\partial \beta_i > 0$).

Predatory environment and risk experienced by prey

Our modelling scenario requires us to specify more about the predatory environment than one usually does in models of diet choice. First, we allow a predator to make a total of A_{tot} attacks on the prey in its territory. As implied in classical theory, we assume that the prey in a predator's territory are not available to other predators. This territory contains a population of N_1 type 1 prey and N_2 type 2 prey. These prey are distributed uniformly across the predator's territory. The predator distributes its A_{tot} attacks such that A_1 and A_2 attacks are directed towards prey types 1 and 2, respectively ($A_{\text{tot}} = A_1 + A_2$). The predator's goal is to distribute its attacks across the two prey types such that its rate of energy intake is maximized.

For simplicity, we place some restrictions on the number of attacks. First, we assume that a given prey individual is attacked at most only once (this essentially assumes systematic search by the predator over its territory), and that $A_i \leq N_i$. Thus the risk of attack experienced by an individual prey of type i is $a_i = A_i/N_i$. We also require that $A_{\text{tot}} \leq \min(A_1, A_2)$ in order to avoid forcing the predator to attack both prey types when a generalized diet will not maximize the predator's rate of energy intake.

The need to specify prey population sizes leads to complications in the relationships among prey encounter rates, prey population sizes and risk experienced by prey. For instance, if one envisions a predator with a territory that does not vary in size with prey abundance (see Newton, 1998, for examples), then an increase in encounter rates implies an increase in prey population sizes within its territory. This, in turn, implies that the risk experienced by prey declines as encounter rates increase (for a given A_{tot}). Since our models focus on the interaction between predator diet choice and prey response to risk, allowing risk to vary with encounter rate is undesirable. We thus take the approach of varying encounter rates for fixed prey population sizes. In this scenario, changing encounter rates implies a change in the predator's territory size, which would happen when a predator regulates its territory size in relation to its energetic needs (Newton, 1998). We note that the qualitative conclusions reached below are not dependent upon which risk scenario is used.

DIET SELECTION BY PREDATORS

We consider two important cases of classical diet theory in which the predator encounters prey simultaneously (in groups) or sequentially (as solitary individuals). For the case of simultaneous encounters of grouped prey, we modify the classic model to consider cases in which vigilant prey may or may not share collective detection of predators. For the sequential encounter of prey, we consider cases in which vigilant prey may or may not require the predator to invest time in stalking prey.

Simultaneous encounter of grouped prey

A great deal of work on anti-predator decision making revolves around sociality as a defence against predators (Krause, 1994; Roberts, 1996; Lima, 1998). However, there are very few models of diet choice in which predators encounter grouped prey. Once again, this lack of a consideration of prey behaviour reflects the tendency to consider only behaviourally inert prey in models of diet choice by predators.

We base our simple models on that of Stephens *et al.* (1986), who provide an insightful exception to the rule of ignoring grouped prey in the classical modelling paradigm. Their 'flock' model considers two prey types that occur in mixed-type pairs. The predator can capture only one member of a given pair; during an attack, the other member of the group escapes, but is allowed no other form of anti-predator behaviour before an attack.

The predator's energy intake rate (E/T), as developed by Stephens *et al.* (1986), is

$$\frac{E}{T} = \frac{p_1 e_1 + p_2 e_2}{\dfrac{1}{\lambda_p} + p_1 h_1 + p_2 h_2} \tag{2}$$

where e_i is the energy content in prey type i, p_i is the proportion of encountered prey of type i that are actually attacked and consumed, and h_i is the handling time necessary to capture and consume prey type i. Prey abundance is represented by λ_p, which is the encounter rate between predator and the pairs/flocks of prey. The diet maximizing the predator's rate of energy intake follows the 0,1 rule: a prey item is either always attacked ($p_i = 1$) or it is never attacked ($p_i = 0$) given optimal behaviour. Intuitively, one might expect that the predator should simply take the item with the higher profitability (defined as e_i/h_i), but Stephens and co-workers' key insight is that this simple rule holds only when $e_1 > e_2$ When $e_2 > e_1$, there exists a critical λ_p above which only prey 1 is taken and below which prey 2 is taken. Stephens *et al.* (1986) show that this diet choice problem is analogous to a simple patch-departure decision.

In our model, we deal with predation risk and prey vigilance as described earlier. We also maintain the simple flock structure of Stephens *et al.* (1986) in which prey occur in two types (1 and 2) and always in mixed-type pairs (one of each type). There are N_p pairs of prey uniformly spread over the predator's territory, and thus $N_1 = N_2 = N_p$. The predator distributes A_{tot} attacks such that A_1 and A_2 attacks are directed towards prey types 1 and 2, respectively ($A_{tot} = A_1 + A_2$). No pair/flock is attacked more than once, thus $A_{tot} \leq N_p$. The predator's 'goal' is to distribute its attacks across the two prey types such that its rate of energy intake is maximized.

During an encounter with a flock, the predator can target only one individual for attack; the other flock member always escapes. For the present case, in keeping with Stephens *et al.*

(1986), we do not allow for strong collective detection of attack between flock members. Thus, if a given flock member is targeted for attack, and it is not vigilant at the point of attack, then it cannot be 'rescued' if the attack is detected by its flockmate. Both members of the flock are on their own when it comes to detecting an attack. Such a situation may occur when flock members are isolated by visual obstructions or are distantly separated (see Lima and Zollner, 1996). However, the fracas during an attack will always alert all flock members to an attack after it happens. We consider the implications of strong collective detection between prey in a later section.

Prey respond to the risk of attack via greater vigilance (v_i) as described earlier (see equation 1), where the probability of attack experienced by an individual of prey type i is $a_i = A_i/N_p$. As outlined earlier, v_i increases with increasing a_i and increasing β_i (or decreasing cost of vigilance). Prey may differ in a_i as a result of predator choice, and β_i as a result of their particular feeding situation.

Given this risk structure, the predator's rate of energy intake is a straightforward modification of equation (2), which accounts for the probability of prey capture ($1 - v_i$):

$$\frac{E}{T} = \frac{(1 - v_1)\, p_1 e_1 + (1 - v_2)\, p_2 e_2}{\dfrac{1}{\lambda_p} + (1 - v_1)\, p_1 h_1 + (1 - v_2)\, p_2 h_2} \tag{3}$$

All variables are as defined earlier. The value of p_i, or the probability that prey type i is attacked when encountered, can be better interpreted as the probability that prey type i is targeted during a given encounter with a flock. As such, $p_1 = A_1/(A_1 + A_2)$, and $p_2 = 1 - p_1$.

We express optimal diet choice in terms of p_2^* ($0 \le p_2^* \le 1$) as a function of the encounter rate λ_p. Note that for the case of simultaneous encounters, $p_1^* = 1 - p_2^*$. Optimal diet choice (or p_i^* values) must be determined numerically, which we did using a simple algorithm that systemically considered the entire state space of A_i values subject to the constraint that $A_1 = A_{\text{tot}} - A_2$. Fractional (rather than simply integer) A_i values are allowed. Baseline parameter values are as follows: $e_1 = 1$, $e_2 = 2$, $h_1 = 1$, $h_2 = 4$, $N_1 = N_2 = N_p = 100$, $A_{\text{tot}} = 50$. Note that prey type 1 is more profitable than prey 2 ($e_1/h_1 > e_2/h_2$), and that $e_2 > e_1$. These values hold throughout unless otherwise stated.

Results and discussion

Standard theory with behaviourally inert prey predicts (for baseline conditions) that for $\lambda_p < 0.5$, the optimal diet consists solely of prey 2 ($p_1^* = 0$, $p_2^* = 1$), and that the diet consists solely of prey 1 for $\lambda_p > 0.5$ ($p_1^* = 1$, $p_2^* = 0$). When prey are vigilant but experience no collective detection of attack, a general feature of diet choice (Fig. 1) is a gradual transition (involving partial preferences) from a diet dominated by prey type 2 to one consisting solely of prey type 1 ($p_1^* = 1$, $p_2^* = 0$; recall that $p_1^* = 1 - p_2^*$ for simultaneous prey encounters). These trends hold whether both prey types are moderately (Fig. 1a) or very responsive to increasing risk (Fig. 1b). When overall risk (A_{tot}/N_p, shown as a percentage in the figures) is relatively high, this transition may involve a broad range of encounter rates over which both prey are in the diet. Furthermore, as overall risk increases, one may never obtain a diet focused solely on prey type 2 ($p_2^* = 1$), even at very low encounter rates (Fig. 1).

The general existence of partial preferences in this simultaneous encounter paradigm (see also below) reflects a sort of 'prey management' by predators (Kotler *et al.*, 2002; Lima,
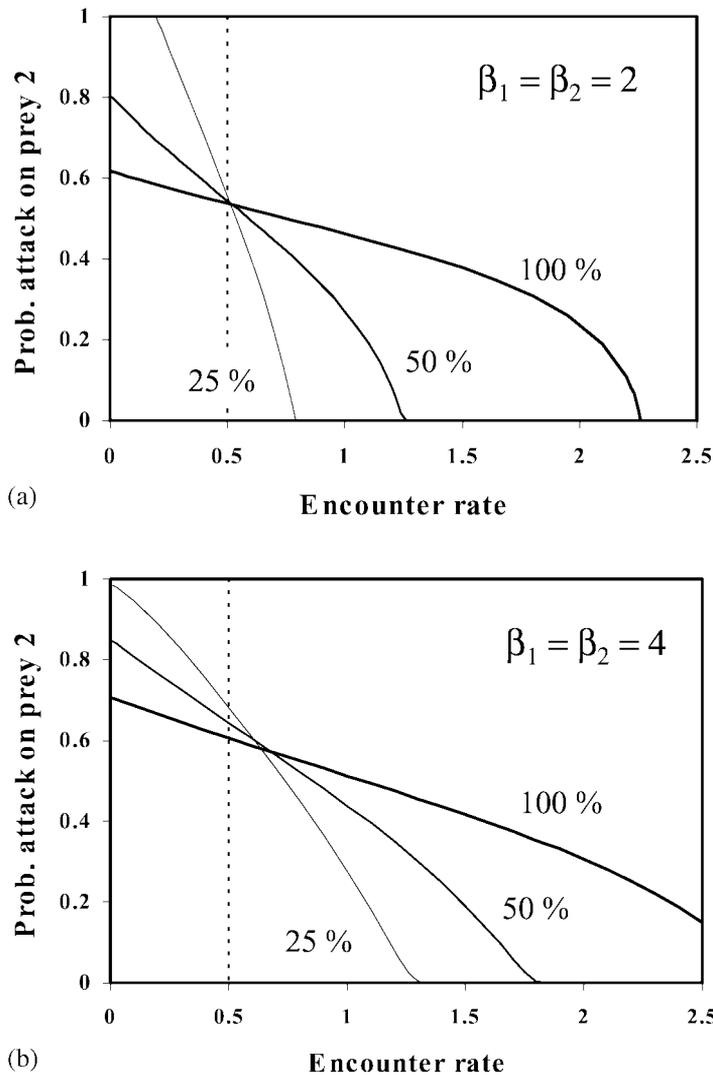
Fig. 1. Optimal predator diet choice for different overall levels of risk (25, 50 or 100% of available flocks attacked, determined as A_{tot}/N_p) when prey are encountered simultaneously in mixed-type 'flocks'. Both prey types are moderately responsive (a) or strongly responsive (b) to increasing risk (increasing β_i indicates greater responsiveness). There is no collective detection of attack within flocks. Shown is the optimal probability of attacking prey type 2 (when encountered) as a function of the encounter rate with flocks. The optimal probability of attacking prey type 1 is $p_1^* = 1 - p_2^*$. The dashed line represents optimal predator behaviour with unresponsive prey. All parameters are as specified in the baseline set (see text).

2002). Because prey respond directly to an increase in risk, a given prey type will exhibit maximal vigilance if the predator focuses all of its attention on that type. At lower encounter rates, it is generally better for a predator to 'spread the risk' over both prey types

than to attack only one type or the other. Eventually, however, the encounter rate with pairs will reach the point where focusing only on prey 1 is the best choice for the predator (as suggested by classical theory).

Accordingly, the relative strength of vigilance responsiveness across prey types can exhibit a strong effect on diet choice in the simultaneous encounter paradigm (Fig. 2). When
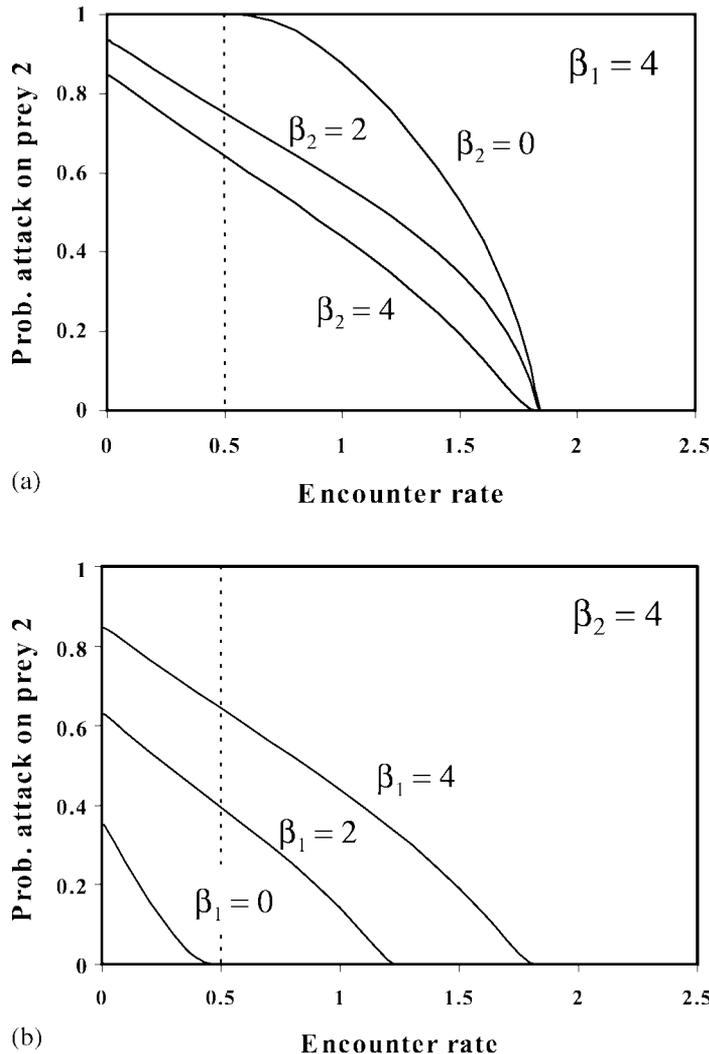

Fig. 2. Optimal predator diet choice when prey types differ in responsiveness to risk. Predators encounter prey simultaneously in mixed-type 'flocks' in which there is no collective detection of attack. Shown is the optimal probability of attacking prey type 2 (when encountered) as a function of encounter rate with flocks when the more responsive prey is type 1 (a) and type 2 (b). The optimal probability of attacking prey type 1 is $p_1^* = 1 - p_2^*$. The dashed line represents optimal predator behaviour with unresponsive prey. All parameters are as specified in the baseline set (see text).

prey type 2 is very responsive, a progressive drop in prey 1 responsiveness (decreasing β_1) leads to the near exclusion of prey 2 from the diet under all encounter rates (Fig. 2b). Conversely, when prey type 1 is the more responsive prey type, prey type 2 is more prominently represented in the diet (compare Fig. 2a and 2b). These results reflect the intuitive idea that, everything else being equal, unresponsive prey types are in a sense more valuable than those that respond strongly to increasing risk.

Finally, classical theory (unresponsive prey) suggests that prey type 2 may be taken by the predator only when $e_2 > e_1$ (assuming $e_1/h_1 > e_2/h_2$). This criterion does not generally hold when considering behaviourally responsive prey. As shown in Fig. 3, predators may show substantial partial preferences for prey even when $e_2 < e_1$. This result illustrates the value of 'prey management' to the predator. Consider the special case in which the two prey types are identical: $e_1 = e_2$, $h_1 = h_2$ and $\beta_1 = \beta_2$, $p_1^* = p_2^* = 0.5$ for all λ_p (line c, Fig. 3). If such prey were unresponsive, then any value of p_1 or p_2 would be acceptable (assuming $p_1 + p_2 = 1$). However, with behaviourally responsive prey, spreading the risk equally among these prey types leads to a greater long-term energy intake rate: risk spreading makes prey maximally catchable. The value of this prey management also holds even when e_2 begins to drop a bit below e_1, hence the partial preferences observed with $e_2 < e_1$. However, when $e_2 \ll e_1$, prey type 2 will usually be a minimal or non-existent part of the predator's diet.

Simultaneous encounter of grouped prey: collective detection of predators

One of the most widespread benefits of grouping is the collective detection of predators enjoyed by socially vigilant prey (Elgar, 1989; Roberts, 1996; Bednekoff and Lima, 1998; Treves, 2000). The basic idea behind collective detection is that all group members are somehow alerted to an attack, even if most members did not actually detect the attack themselves. The existence of collective detection allows individual group members to focus
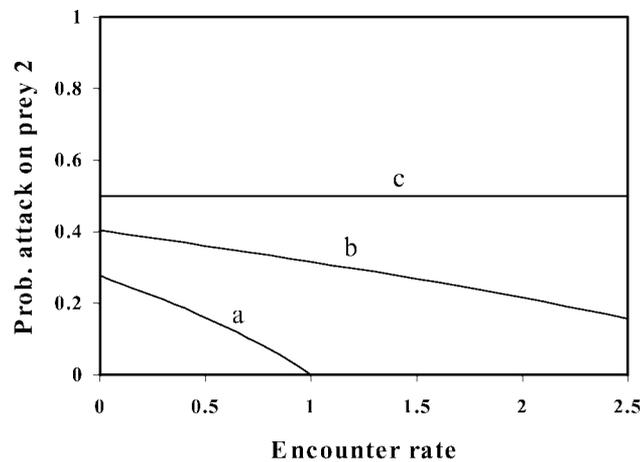

Fig. 3. Optimal predator diet choice, when prey are encountered simultaneously in mixed-type 'flocks', for three cases in which $e_2 \leq e_1$. Line a: $e_1/h_1 = 1/1$, $e_2/h_2 = 0.6/1$; line b: $e_1/h_1 = 1/1$, $e_2/h_2 = 0.8/1$; line c: $e_1/h_1 = e_2/h_2 = 1/1$. All other parameters are as specified in the baseline set (see text).

more on feeding and less on vigilance as group size increases. Here, we modify the basic simultaneous encounter model to include collective detection.

We maintain the simple mixed-pair flock structure assumed in the theoretical template of Stephens *et al.* (1986). The basic risk structure of the previous section also applies to the present case. As before, there are N_p pairs of prey uniformly spread over the predator's territory, and they are encountered by the predator at rate λ_p. The predator distributes $A_{\text{tot}} \leq N_p$ attacks such that A_1 and A_2 attacks are directed towards prey types 1 and 2, respectively ($A_{\text{tot}} = A_1 + A_2$). During an encounter with a flock, the predator can target only one individual for attack with probability $p_1 = A_1/(A_1 + A_2)$, and $p_2 = 1 - p_1$. The probability of attack experienced by an individual of prey type i is $a_i = A_i/N_p$.

With collective detection, however, equation (1) will no longer suffice to determine optimal prey vigilance. In fact, there exists no formal theory of optimal vigilance in mixed-species flocks despite the many studies devoted to this topic (e.g. Sullivan, 1984; Cimprich and Grubb, 1994; Dolby and Grubb, 1998). To proceed, we first assume a simple form of 'perfect' collective detection in which both members of a flock escape attack as long as at least one member detects attack. A given attack by the predator will be successful only when both flock members are not vigilant at the time of attack, which occurs with probability $(1 - v_1)(1 - v_2)$. Thus the probability of survival for a given individual of prey type i can be derived from a simple modification of equation (1):

$$P_i(\text{surv}) = [1 - a_i(1 - v_i)(1 - v_j)(1 - v_i^{\beta_i})] \tag{4}$$

Here, the subscript j represents the other flock member. Since flock members will generally differ in a_i as a result of predator targeting and β_i as a result of their particular feeding situation, determining optimal vigilance for both members is not as straightforward as in the previous case.

To determine optimal vigilance, we used a simple representation of game theory (Heithaus, 2001; Grand, 2002) in which the evolutionarily stable level of vigilance is determined by locating the intersection of the 'best response curves' of the two flock members. The best vigilance response of flock member 1 to a given value of v_2 can be determined by fixing v_2 in equation (4) and then solving for v_1^* as per the algorithm used to find the maximum in equation (1). The curve formed by the best responses to all v_2 in the interval [0,1] defines the best response curve for flock member 1. We similarly determined the best response of flock member 2 to the range of vigilance options available to member 1. The intersection of these two curves represents the best response to each other's vigilance, and thus the evolutionarily stable level of vigilance. Our numerical algorithm, in effect, locates this intersection.

Under the scenario of collective detection, the vigilance of flock members still increases with increasing probability of attack. However, for any given a_i, vigilance with collective detection is always lower than that determined using equation (1) (in which prey are on their own). The success rate for the predator nevertheless declines relative to previous cases due to collective detection itself. Furthermore, when $a_i > a_j$ and/or $\beta_i > \beta_j$, flock member i will be more vigilant than member j and thus carry the greater burden of collective detection. When $a_i = a_j$ and $\beta_i = \beta_j$, both flock members exhibit the same level of vigilance (as per Lima, 1990).

Given this risk structure, the predator's rate of energy intake is a straightforward modification of equation (3), which accounts for the probability of prey capture under collective detection:

$$\frac{E}{T} = \frac{(1 - v_1)(1 - v_2)\, p_1 e_1 + (1 - v_1)(1 - v_2)\, p_2 e_2}{\dfrac{1}{\lambda_p} + (1 - v_1)(1 - v_2)\, p_1 h_1 + (1 - v_1)(1 - v_2) p_2 h_2}$$

All variables are as defined in the previous section. The predator's goal is to distribute its attacks across the two prey types such that its rate of energy intake is maximized. We once again express optimal diet choice in terms of p_2^* ($0 \le p_2^* \le 1$, $p_1^* = 1 - p_2^*$) as a function of the encounter rate λ_p. Baseline parameter values are those used in the previous section; recall that prey type 1 is more profitable than prey 2, and $e_2 > e_1$.

Results and discussion

The prospect of collective detection provides a more complex view of prey vigilance, but it sometimes leads to a simple 0,1 rule of diet choice for the predator (Fig. 4). This is particularly true when both prey are very responsive to the risk of attack (e.g. $\beta_1 = \beta_2 = 4$; Fig. 4b). Here, at low λ_p, the diet consists solely of prey 2 ($p_1^* = 0$, $p_2^* = 1$), and the diet shifts abruptly to prey type 1 ($p_1^* = 1$, $p_2^* = 0$) at a threshold value of λ_p. However, this threshold λ_p is not the risk-invariant value of standard theory, but rather one that increases with overall risk. The reason for the re-emergence of the 0,1 rule reflects the difficulty of a successful attack on a flock in which both prey members are very vigilant and share collective detection. The best option for the predator is to focus all of its attention on a given prey type rather than deal with two types of very vigilant prey. This result is reminiscent of solutions to the problem of detecting multiple predator types, in which it is sometimes best to focus on only a given predator type rather than try to detect all types simultaneously (Matsuda *et al.*, 1993).

When prey are less responsive to risk (e.g. $\beta_1 = \beta_2 = 2$; Fig. 4a), partial preferences are again apparent at dietary shifts. As in the case without collective detection (see Fig. 1), partial preferences are more extensive with an increase in overall risk. With these less responsive prey (and thus an overall lower degree of collective detection), the predator once again can benefit from spreading risk across prey types rather than focusing solely on one or the other prey type. Finally, partial preferences can also occur when $e_2 < e_1$ under much the same circumstances discussed earlier in the case without collective detection (no figure is shown).

As in the case with no collective detection, there are no empirical data available with which to test these ideas. Studies on anti-predator sociality usually focus on the prey rather than the predator (Lima, 2002), hence little information is available on predatory aspects of the interaction. However, there are some limited data on predator targeting of prey types within mixed groups. FitzGibbon (1990) found that cheetahs feeding on mixed-species groups of Grant's and Thompson's gazelles tend to target the latter when in mixed groups. Chimpanzees attacking mixed groups of red colobus and diana monkeys focus exclusively on the former (Noe and Bshary, 1997).

Sequential encounter of prey

The classic model with the sequential encounter of solitary prey (Stephens and Krebs, 1986) depicts the predator's energy intake rate (*E*/*T*) (assuming two prey types, 1 and 2) as

$$\frac{E}{T} = \frac{\lambda_1 p_1 e_1 + \lambda_2 p_2 e_2}{1 + \lambda_1 p_1 h_1 + \lambda_2 p_2 h_2}$$
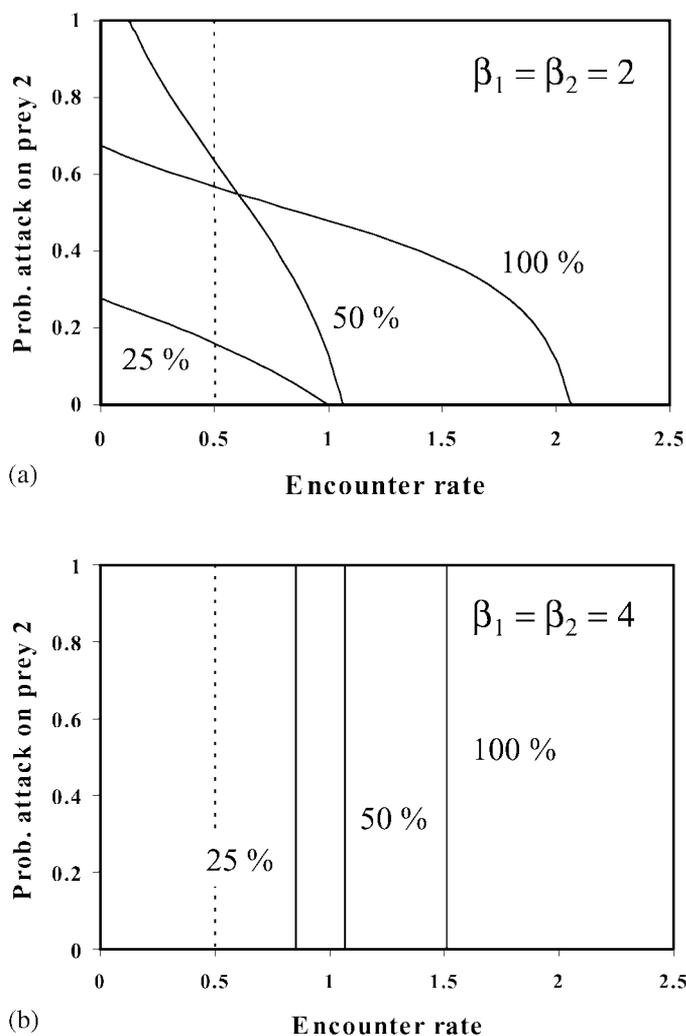
Fig. 4. Optimal predator diet choice for different overall levels of risk (25, 50 or 100% of available flocks attacked) when prey are encountered simultaneously in mixed-type 'flocks' in which there is complete collective detection. Both prey types are moderately responsive (a) or strongly responsive (b) to increasing risk. All else is as in Fig. 1.

As before, e_i is the energy content of prey type i, p_i is the proportion of encountered prey of type i that are actually attacked and consumed, and h_i is the handling time necessary to capture and consume prey type i. Prey abundance is represented by λ_i, which is the number of prey of type i that are encountered per unit search time. In this model, prey are ranked according to their profitability e_i/h_i, and added to the diet in deceasing order of profitability until E/T is maximized (see Stephens and Krebs, 1986). The optimal p_i values follow the 0,1 rule much as in other simple diet theories.

The classic model can be modified to include prey vigilance as follows:

$$\frac{E}{T} = \frac{(1 - v_1)\,\lambda_1 p_1 e_1 + (1 - v_2)\,\lambda_2 p_2 e_2}{1 + (1 - v_1)\,\lambda_1 p_1 h_1 + (1 - v_2)\,\lambda_2 p_2 h_2} \tag{5}$$

where $1 - v_i$ is the probability that an individual of type i will be captured (i.e. non-vigilant) when attacked. As outlined earlier, the predator maximizes E/T by allocating A_{tot} attacks to A_1 attacks on prey type 1 and A_2 attacks on prey type 2. The vigilance of prey type i (v_i) is determined as per equation (1), and increases with increasing A_i.

The p_i values are also functions of the attack allocation (A_1 and A_2), and could fall into one of three cases depending on the relative magnitude of A_i/λ_i:

$$\frac{A_1}{\lambda_1} > \frac{A_2}{\lambda_2}, \quad p_1 = 1, \quad p_2 = \frac{A_2\lambda_1}{A_1\lambda_2} \leq 1$$

$$\frac{A_2}{\lambda_2} > \frac{A_1}{\lambda_1}, \quad p_1 = \frac{A_1\lambda_2}{A_2\lambda_1} \leq 1, \quad p_2 = 1$$

$$\frac{A_1}{\lambda_1} = \frac{A_2}{\lambda_2}, \quad p_1 = p_2 = 1$$

These cases follow from the facts that (i) A_i/λ_i represents the search time devoted to locating the requisite A_i individuals of type i, and (ii) the predator searches for both prey types simultaneously. For instance, considering the first case shown above, if $A_1/\lambda_1 > A_2/\lambda_2$, then all prey of type 1 encountered will be attacked. However, the A_1/λ_1 time units that must be devoted to searching for A_1 type 1 prey are more than is needed to encounter and attack all A_2 type 2 prey. Hence only a portion of the encountered prey of type 2 will be attacked ($p_2 < 1$). Similar reasoning applies to the second and third cases. Note that a given attack allocation can lead to partial preferences for prey 1 (second case) or prey 2 (first case). For the 0,1 rule to hold, one A_i value must be 0 or, if both prey are in the diet, then A_i values must be allocated such that $A_1/A_2 = \lambda_1/\lambda_2$ (third case above).

We express optimal diet choice in terms of the optimal proportion of prey type 2 that should be attacked when encountered (p_2^*, $0 \leq p_2^* \leq 1$) as a function of encounter rate with prey 1. Optimal behaviour was determined numerically as described earlier. Baseline parameter values are $e_1 = 1$, $e_2 = 2$, $h_1 = 1$, $h_2 = 4$, $N_1 = N_2 = 50$, $A_{\text{tot}} = 50$. Note that prey type 1 is more profitable than prey type 2 ($e_1/h_1 > e_2/h_2$).

Results and discussion

With no vigilance response to risk (i.e. behaviourally inert prey) and baseline parameter values, the optimal proportion of prey type 2 to be attacked when encountered (p_2^*) shows the 0,1 rule with a step-function drop from 1 to 0 at a threshold of $\lambda_1 = 1$. A near step-function drop in p_2^* also occurs when both prey are allowed a moderate ($\beta_1 = \beta_2 = 2$) or major ($\beta_1 = \beta_2 = 4$) vigilance response to an increasing probability of attack (Fig. 5). However, the threshold of diet shift occurs at a larger λ_1 value as (i) the overall level of risk increases, and (ii) as prey vigilance becomes more responsive to risk. As per classical theory, $p_1^* = 1$ holds throughout; that is, the more profitable prey is always included in the diet.

Overall, the predictions of the classical and vigilance-modified models share many of the same qualitative characteristics. However, when the available prey may be vigilant for
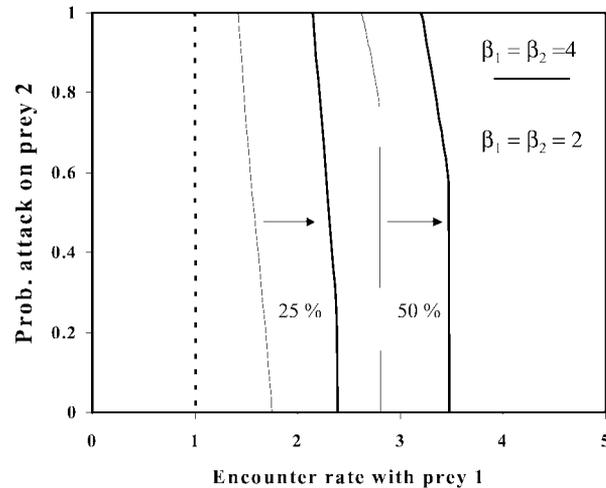
Fig. 5. Optimal predator diet choice for different levels of prey responsiveness to risk (β_i) and overall level of risk (25 or 50% of available prey attacked, determined as $A_{tot}/[N_1 + N_2]$) when prey are encountered sequentially. Shown is the optimal probability of attacking prey type 2 (when encountered) as a function of the encounter rate with prey type 1. Prey type 1 is the more profitable prey type and should always be attacked when encountered ($p_1^* = 1$). Thin and bold lines correspond, respectively, to prey whose vigilance is moderately ($\beta_1 = \beta_2 = 2$) or strongly responsive ($\beta_1 = \beta_2 = 4$) to predation risk. Arrows indicate the effect of increasing β_i (prey responsiveness) for a given overall level of risk. The dashed line represents optimal predator behaviour with unresponsive prey. All other parameters are as in the baseline set (see text).

attack, the predator will require a larger encounter rate with prey 1 before dropping prey 2 from the diet. In other words, prey vigilance favours a more generalized predator diet. The vigilance-modified model also suggests that partial preferences may be observed at dietary transitions (see Fig. 5), but such preferences are not very extensive. Hence distinguishing between the classical and vigilance-modified diet models would require a quantitative rather than qualitative test. No such test currently exists.

   The general correspondence in qualitative predictions between the two models reflects a key assumption implicit to this point: that no time is lost to the predator in the interaction with prey. In essence, attack and prey escape occur instantaneously. Hence, the main effect of vigilance is to lower the effective encounter rate with a given prey item to $(1 - v_i)\lambda_i$; vigilance has no effect on prey profitability. As a result, larger absolute encounter rates are necessary to effect changes in diet than one might expect if anti-predator behaviour is ignored. When the interaction between predator and prey involves a time cost to the predator, however, expectations regarding diet choice can change considerably.

Sequential encounter of prey: mandatory stalking of prey

Stalking time is an important part of the attack process for many types of predators, and reflects the simple reality that prey are vigilant for attack (Scannell *et al.*, 2001; Bednekoff and Lima, 2002). In other words, a predator must get close to its prey before launching an attack. Stalking might take the classic form of a cheetah stalking a gazelle, in which the

cheetah creeps up on its prey while it is not vigilant, and then initiates its final attack when the prey lowers its head (e.g. FitzGibbon, 1989). Alternatively, stalking time might represent the time necessary for the predator to position itself relative to some visual obstruction, as in attacks by *Accipiter* hawks on avian prey (T.C. Roth and S.L. Lima, personal observations). For simplicity, we assume that predators do not time attacks relative to prey vigilance (as per accipiters). The important point is that time is lost to the predator when prey detect attack.

We include a mandatory stalking time in the vigilance-modified standard model (equation 5) by assuming that a proportion ρ_i of the handling time of prey type i must be devoted to stalking before an attack is even possible. The predator pays this portion of handling time even when prey escape. The remaining handling time, $h_i(1 - \rho_i)$, is paid only when a prey item is captured (with probability $1 - v_i$). The variable H_i is the average handling time for prey type i, and is given by

$$H_i = (1 - v_i)h_i(1 - \rho_i) + h_i\rho_i$$

The predator's rate of energy intake is thus modified from equation (5) as

$$\frac{E}{T} = \frac{(1 - v_1)\lambda_1 p_1 e_1 + (1 - v_2)\lambda_2 p_2 e_2}{1 + \lambda_1 p_1 H_1 + \lambda_2 p_2 H_2}$$

All other aspects of the previous model apply in this case. Accordingly, the predator maximizes E/T by allocating A_{tot} attacks into A_1 attacks on prey 1 and A_2 attacks on prey 2. The vigilance of prey type i (v_i) increases with increasing A_i. We express optimal diet choice in terms of the optimal proportion of prey type 2 that should be attacked when encountered (p_2^*, $0 \leq p_2^* \leq 1$) as a function of increasing λ_1. The previous set of baseline parameter values also applies here.

Results and discussion

The main effect of mandatory stalking time is a broad range of partial preferences associated with dietary shifts. Figure 6 shows some examples of this effect for baseline conditions and relatively responsive prey ($\beta_1 = \beta_2 = 4$) and values of ρ_i such that the two prey types require differing degrees of investment in stalking time. Typically, as with the standard model, both prey are included in the diet ($p_1^* = p_2^* = 1$) when prey are sparse (note that $p_1^* = 1$ for all conditions considered in Fig. 6). Beyond some encounter rate, the predator should begin to drop prey 2 from the diet. Prey 2 may be dropped relatively quickly to very low levels, or it may never fully disappear from the predator's diet. Note also that the prediction of the classical diet model (dotted line in Fig. 6) is unaffected by stalking time, since behaviourally inert prey can never escape.

The degree to which prey 2 is dropped from the diet with increasing prey abundance depends on which of the two prey requires the greater investment in stalking time. If prey type 2 (the inherently less profitable item) requires relatively more stalking time than prey type 1 (bottom curve in Fig. 6), then prey 2 may be dropped from the diet relatively quickly to the point where $p_2^* = 0$. When the situation is reversed (top curve in Fig. 6), prey 2 remains in the diet to a significant degree; in this case, prey type 2 is always in the diet as p_2^* asymptotes at a non-zero value with increasing λ_1. These patterns in partial preferences reflect a key distinction of the stalking time model: the profitability of a given prey type is a function of its vigilance. When a prey item requires much mandatory stalking time, even
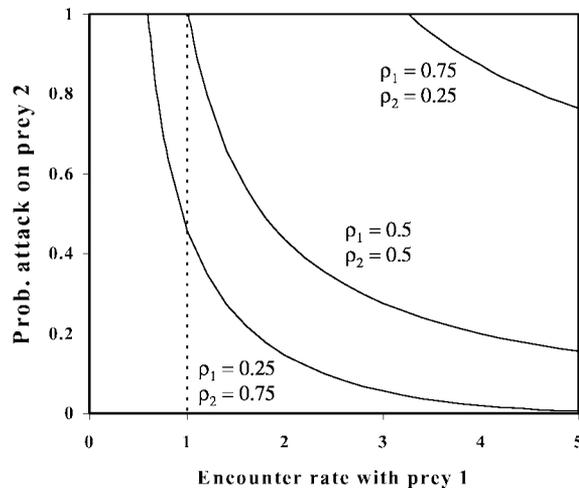
Fig. 6. Optimal predator diet choice when prey types differ in relative stalking time, and are encountered sequentially. The value of ρ_i indicates the proportion of the overall handling time of prey type i that the predator must devote to stalking. Shown is the probability of attacking prey type 2 (when encountered) as a function of the encounter rate with prey type 1, for three cases: prey 1 requires relatively more stalking than prey 2 (top line), prey 2 requires relatively more stalking (bottom line), and both require the same degree of stalking (middle line). Prey type 1 is the inherently more profitable prey type and should always be attacked when encountered ($p_1^* = 1$) for the cases shown. The dashed line represents optimal predator behaviour with unresponsive prey. $\beta_1 = \beta_2 = 4$, and all other parameters are as specified as in the baseline set (see text).

a small amount of vigilance can reduce its effective profitability. When that prey is the inherently less profitable item, its value to the predator can decline relatively quickly as vigilance increases.

A notable consequence of the variable profitability of prey types is the possibility of a reversal in overall preference ranking for prey. Under baseline conditions, such reversals occur when prey type 2 is behaviourally inert ($\beta_2 = 0$) and prey type 1 responds strongly to risk (e.g. $\beta_1 = 4$). Such cases correspond, for instance, to a common situation in which a hawk may prey on both adult birds and nestlings (the latter effectively have no defences against predators). For baseline conditions, $\beta_2 = 0$ and $\beta_1 = 4$, there exists a critical value of $\rho_1 = 0.555$ above which $p_1^* < 1$ and $p_2^* = 1$, and below which $p_1^* = 1$ and $p_2^* < 1$; when $\rho_1 = 0.555$, $p_1^* = p_2^* = 1$ regardless of prey abundance.

There are no standard models of optimal diet selection that include stalking time, since it is of no consequence to differentiate between handling time and stalking if prey cannot escape an attack. However, Anholt *et al.* (1987) developed a model of optimal pursuit time by predators, which considers the point at which to break-off a pursuit once initiated (although a time investment by prey in detecting attack is not considered). The prey in their model always detect an attack and pursuit time is a random variable. As in our stalking time model, the time spent in unsuccessful pursuit is lost to the predator. Similarly, Anholt *et al.* (1987) found that broad partial preferences are possible under this scenario.

There are no empirical studies that address the specifics of our predictions. However, a study on diet selection in the presence of kleptoparasites (Thompson and Barnard, 1984)

is perhaps most relevant to our model. This study considers a situation in which feeding shorebirds often lose large worms to kleptoparasitic gulls. Large worms require considerable time to be extracted, and this time cost is paid whether or not the worm is lost to a gull. The loss of large worms to gulls is analogous to escape by prey after much time spent stalking it. Accordingly, the shorebirds appeared to avoid large worms because such prey are likely to be lost.

GENERAL DISCUSSION

Classical optimal diet theory provides important insights into the reasons why predators might attack some prey and ignore others. In the case of sequentially encountered prey, classical models suggest that predators should choose generalized diets when prey are relatively scarce (Stephens and Krebs, 1986). For simultaneously encountered prey, classical models suggest that predators may not always prefer the most profitable prey available (Stephens *et al.*, 1986). Our explicit consideration of the interaction between predator and responsive prey does not (for the most part) radically change these general expectations.

Our results suggest, however, that the transition between general and relatively specialized diets will be influenced by the interaction between predator and responsive prey. Generally speaking, for sequential encounters with prey, predator diets should tend towards greater generalization with an increase in the risk experienced by prey. This greater generalization reflects mainly a shift in prey abundance thresholds at which diet shifts occur. However, when handling times involve significant time spent stalking prey, a more generalized diet might reflect extensive partial preferences for prey. Furthermore, when profitable prey types also require much stalking time, apparent rankings of prey preferences may not reflect simple prey profitability.

Extensive partial preferences (at dietary transitions) are common in our versions of classical theory with the simultaneous encounter of grouped prey. These partial preferences become more marked as overall risk to prey increases. However, if grouped prey share strong collective detection, then partial preferences may disappear at transitions in diet choice. We note that partial preferences are not unique to our modelling approach. Such predator preferences can occur with behaviourally inert prey for a variety of reasons, such as errors in prey recognition (Rechten *et al.*, 1983; Glaizot and Arditi, 1998). With responsive prey, however, partial preferences reflect 'prey management' by predators, and tend to be much more extensive than in other modelling scenarios.

Our results may ultimately shed light on the apparent failure of classical diet theory to predict predator behaviour when prey are mobile (i.e. responsive; see Sih and Christensen, 2001). However, as outlined earlier, few data exist with which to test even the most basic aspects of our models' predictions (see also Lima, 2002). In fact, there is little information on whether animals act very differently when their prey type is included in, or excluded from, their predators' current diet (Sih and Krupa, 1996, provide a notable exception). More encouraging, however, is recent work which suggests that many types of animals (mainly aquatic) can chemically detect the current nature of predator diets (Chivers and Mirza, 2001). There is a clear need for additional empirical work in this general area.

Further elaboration of our simple models may also prove insightful. For comparative purposes, we confined our models to the classical modelling paradigm as much as possible. For instance, we assumed that both predator and prey have perfect information about each other. In reality, however, a predator's diet may change over time as prey gain experience

with their local predator (see also Luttbeg and Schmitz, 2000). Furthermore, prey will probably be forced to contend with multiple types of predators (Soluk and Collins, 1988; Sih *et al.*, 1998; McIntosh and Peckarsky, 1999), and thus may be engaged in more anti-predator behaviour than our model would suggest; such an effect would probably accentuate our results. Diet models with more realistically grouped prey would also be useful. Finally, it may be insightful to consider the diet-related effects that competitive interactions among predators (e.g. Yamamura and Tsuji, 1987) might have when they feed on the same general population of responsive prey.

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