

State-dependent habitat selection games between predators and prey: the importance of behavioural interactions and expected lifetime reproductive success

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ABSTRACT

The fitness of both prey and predators will be affected by the behaviour of conspecifics and other (predator or prey) species. However, little theory has considered the case where predators and prey respond to one another simultaneously. I present a framework that examines the impact of the predator–prey behavioural interactions (within and between species) in a state-dependent life-history context. I use multiple linked dynamic state variable game equations to predict the patch selection of prey and predators as a function of their energy reserves. When prey are expected to maximize their probability of survival, the individual predators and prey that are not at risk of starvation are predicted to be uniformly distributed among patches independent of the difference in resource input rates among sites. However, individuals near starvation cause more prey and predators to be found in high resource sites. In contrast, when predators and prey both maximize reproduction, predators and prey are predicted to show imperfect resource matching. The proportion of individuals at risk of starvation causes deviations from the perfect resource matching predicted by previous predator–prey games. The predicted patterns clearly illustrate the importance of recognizing that predators and prey will both respond concurrently to one another's distributions. However, the models also illustrate that an organism's state, competition among conspecifics and the life-history pattern of both predators and prey are key to understanding their distribution and behaviour. We can increase our understanding of these interactions and the distribution of predators and prey in space and time by combining the consideration of interactions within and between the species with knowledge of how foraging relates to lifetime expected reproductive success of both predators and prey.

Keywords: dynamic state variable model, game theory, habitat selection, life history, predator–prey interactions.

INTRODUCTION

Interactions between species are at the heart of many important ecological and evolutionary processes. Predator–prey dynamics are a classic and relatively well-studied example of

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interactions between individuals that have population- and community-level consequences. Two main approaches have been used to examine predator–prey interactions. The population dynamics approach has generally focused on interactions at the species level, while optimal foraging and habitat selection research has concentrated mainly on individual behaviour. In general, however, we would expect both predators and prey to respond to the behaviour and abundance of the other species while concurrently being affected by and responding to competition from individuals within the same species. Thus, individual behaviour will affect and be affected by interactions within and between predator and prey species. In a recent review, Lima (2002) argued for the need to put ‘predators back into behavioral predator–prey interactions’. In this paper, I examine the impact of interactions within and between species on the predicted habitat selection behaviour of both predators and prey within the context of expected lifetime fitness.

Extensive theoretical and empirical ecological research has focused on understanding the population dynamics of predator and prey populations (e.g. Turner and Mittelbach, 1990; Hixon and Menge, 1991; Brown and Vincent, 1992; Kacelnik *et al.*, 1992; Kennedy and Gray, 1993; Marrow and Cannings, 1993; McCauley *et al.*, 1993; van der Laan and Hogeweg, 1995; Marrow *et al.*, 1996; Fischer and Frost, 1997; Kendall *et al.*, 1999). Although many population dynamic models exist (e.g. May, 1973; Kingsland, 1985; Kerfoot and Sih, 1987; Kacelnik *et al.*, 1992; Marrow and Cannings, 1993; Marrow *et al.*, 1996; Fryxell and Lundberg, 1998; Kendall *et al.*, 1999; Sait *et al.*, 2000; Hanski *et al.*, 2001), these models tend to assume fixed or extremely simple predator and prey behaviours while focusing on predicting population dynamics. If these models consider individual behaviour at all, the focus has generally been on understanding the consequences of specific behaviour patterns rather than predicting behavioural responses to predator–prey interactions.

Related empirical studies have documented links between predator and prey population growth rates as well as population size using both experimental and observational approaches (e.g. Sih *et al.*, 1985; Kerfoot and Sih, 1987; Turner and Mittelbach, 1990; Hixon and Menge, 1991; Fischer and Frost, 1997). However, these studies have tended to ignore or even exclude the possibility of predator and prey behaviour. Predator and prey population sizes are inherently linked, but behavioural responses to predation risk and prey availability will impact these links and their effect on birth and death rates in both prey and predator populations. As a result, both predators and prey will affect the fitness and evolution of individual behaviours within a population.

In contrast, other research has focused on individual foraging behaviour and habitat selection (e.g. Fretwell, 1972; Krebs *et al.*, 1977, 1978; Parker and Sutherland, 1986; Schoener, 1987; Mangel and Clark, 1988; Licht, 1989; Barkan, 1990; Roitberg, 1990; Milinski and Parker, 1991; Rosenzweig, 1991; Travers and Sih, 1991; Giske and Aksnes, 1992; Giske *et al.*, 1992, 1994, 1997; Kacelnik *et al.*, 1992; Mangel and Roitberg, 1992; Roitberg *et al.*, 1992; Sutherland, 1992; Horat and Semlitsch, 1994; Hugie and Dill, 1994; Fiksen, 1997; Houston and McNamara, 1997; Rosenzweig and Abramsky, 1997; Brown, 1998; Fiksen and Carlotti, 1998; Sih, 1998; Clark and Mangel, 2000) while mainly ignoring interactions between species. Theoretical and empirical studies of foraging behaviour and habitat selection have clearly documented the importance of differences in mortality risk (and refuge from predation) among habitats, competition among conspecifics, the abundance of the prey or resource, lifetime fitness effects of foraging, and variation between individuals in state and experience. Few theoretical and no empirical studies have examined prey and predator behaviour concurrently (Lima, 2002).

Although an extensive body of theory exists on foraging behaviour and habitat selection in the presence of predation risk, only a few theoretical examples have considered the behaviour of both predators and prey (e.g. Iwasa, 1982; van Baalen and Sabelis, 1993, 1999; Hugie and Dill, 1994; Bouskila, 1995, 2001; Sih, 1998; Huse *et al.*, 1999; Lima, 2002). Although these models clearly illustrate the potential importance of such an approach, they do not consider the impact of an organism's state (such as energy reserves or individual experience) or life-history effects on foraging behaviour. Yet, one of the important lessons of the extensive research on foraging and habitat selection is the need to consider the impact of individual dynamics and expected lifetime reproductive success on foraging and habitat selection (e.g. Houston and McNamara, 1988, 1997; Mangel, 1989, 1990, 1992; McNamara and Houston, 1990; McNamara *et al.*, 1991; Kulling and Milinski, 1992; Litvak and Leggett, 1992; Houston *et al.*, 1993; Merad and McNamara, 1994; Bouskila *et al.*, 1998).

If individual state and life-history affect foraging behaviour, then they will also impact interactions within and between species. However, state-dependent life-history models have generally assumed fixed predation risk and most have ignored competition between conspecifics (e.g. Houston and McNamara, 1988, 1997; Mangel, 1989, 1990, 1992; McNamara and Houston, 1990; McNamara *et al.*, 1991; Houston *et al.*, 1993; Merad and McNamara, 1994; Nonacs *et al.*, 1994, 1998; Lima, 2002). As a result, the models tend to predict that prey aggregate in safer patches unless reproductive needs or risk of starvation requires prey to use riskier habitats. But we would expect predators to respond to these aggregations of prey and, in turn, prey to respond to predation risk. However, it is not sufficient to focus only on interactions between species. Any individual will simultaneously experience interactions with both conspecifics and the other (prey or predator) species. No current theory exists to predict how prey will distribute themselves among habitats when foraging behaviour depends on state, competition with conspecifics and predation risk that is not fixed. At the same time, predators may experience trade-offs between survival, foraging and reproduction that affect their interactions with prey. A more complete understanding of predator-prey behavioural interactions must consider interactions within and between species within a context of lifetime expected reproductive success. Lifetime fitness associated with realistic behaviours will depend on individual state, the behaviour of predators or prey and competition with conspecifics. Dynamic state-variable models that use expected reproductive success as the measure of fitness (e.g. Houston and McNamara, 1987, 1992, 1999; Houston *et al.*, 1988; Mangel and Clark, 1988; Mangel, 1989; McNamara and Houston, 1990, 1992; Clark and Mangel, 2000) have greatly increased our understanding of patch selection and foraging behaviour. However, when predicting habitat selection, one must also consider how the behaviour of other individuals in the population affects fitness, which is usually accomplished using game theoretical models (e.g. Brown and Vincent, 1987, 1992; Brown, 1990, 1998; Mangel, 1990; Bouskila *et al.*, 1998; Lima, 2002). It would be ideal to consider a model that simultaneously considers the impact of interactions within and between predator and prey species on the lifetime reproductive success of individual prey and predators.

Until recently, no methods existed for examining these kinds of games between species in space and time. In this paper, I use a method developed to examine multi-player state-dependent games within a species (Alonzo and Warner, 2000a,b) and recently extended to between-species games (S.H. Alonzo, P. Switzer and M. Mangel, submitted) to examine the state-dependent habitat selection of predators and prey simultaneously. Using this new method, it is possible to predict predator and prey distributions in space and time as a

function of their individual state and interactions within and between species. I focus on two important comparisons. First, how do predictions that assume fixed predation risk differ from those made when prey and predators respond to interactions within and between species? Second, how does the relationship between foraging success and expected lifetime reproductive success impact the predicted behaviour of predators and prey?

THE PREDATOR–PREY BEHAVIOURAL GAME

In this model, individuals select among patches that may differ in the input rate of resources (Lessells, 1995), competition from conspecifics and risk of mortality. I assume that prey forage on a fixed resource and experience mortality risk due to the presence of predators (Fig. 1). Predators forage for prey and experience a fixed risk of mortality; the amount of food for predators in each patch depends on prey behaviour and competition from other predators (Fig. 1). Thus, both predators and prey experience competition from conspecifics, depending on the distribution of other individuals among the patches. The model predicts the spatial and temporal distribution of prey and predators. I use one dynamic programming equation to predict prey patch selection and another to predict predator behaviour. These two equations are linked by prey behaviour that determines the food available to predators and predator behaviour that determines prey mortality risk (Figs 1 and 2). I also assume that both predators and prey have complete information about the available patches. In future models, I will explore the impact of incomplete information and learning on predator–prey interactions.

Although I use this structure to focus on interactions between predators and prey in space and time, this method could be adapted to almost any situation where multiple groups interact in ways that influence the fitness of behaviours or life histories. Examples include competition among species, co-evolution between mutualists and host–parasite interactions. Dynamic state-variable games are solved using a best response method (Houston and McNamara, 1987; Mangel, 1990; Mangel and Roitberg, 1994; McNamara *et al.*, 1997; Clark and Mangel, 2000). The algorithm finds the best response, π_n , to the strategy adopted by the population, π_{n-1} , and iterates until $\pi_n = \pi_{n-1}$. [For more details on extending dynamic programming games to multi-player situations within a species, see Alonzo and Warner (2000a,b), and for between species, see Alonzo *et al.* (submitted).] To implement the

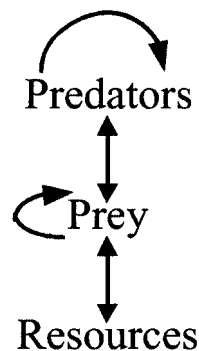


Fig. 1. Trophic structure of the model: interactions within and between predators.

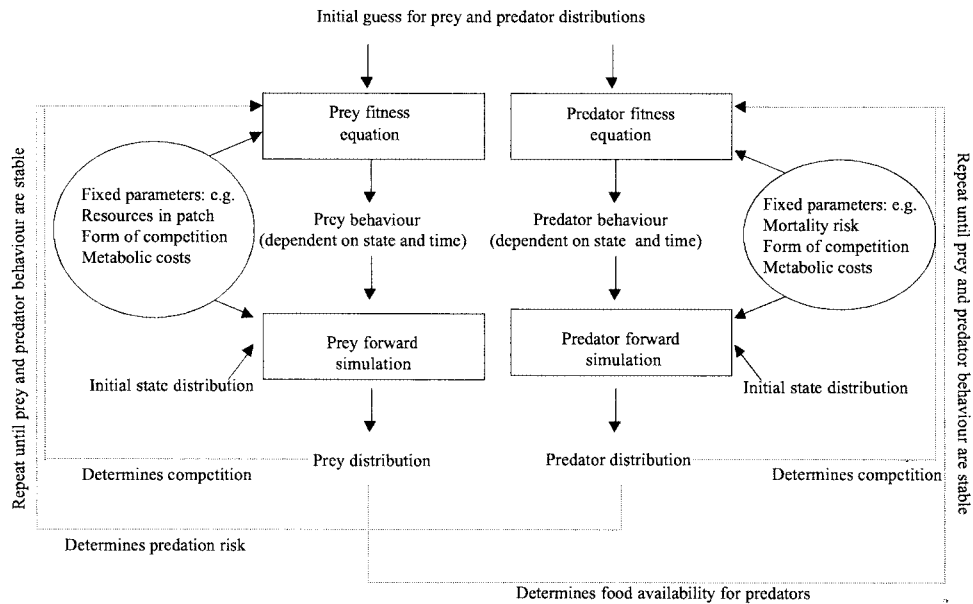


Fig. 2. The computer algorithm used to solve the dynamic state-variable predator–prey game. See text for more details.

algorithm, one first makes an initial approximation for both prey and predator population strategies ($\pi_v(n-1)$, $\pi_p(n-1)$) and generates as a result of those strategies the environment any mutant would experience. One then finds the best response to these initial strategies ($\pi_v(n)$, $\pi_p(n)$) and calculates the new prey and predator distributions. These two steps are repeated until the stable predator and prey strategies are found that satisfy $\pi_v(n) = \pi_v(n-1)$ and $\pi_p(n) = \pi_p(n-1)$ (i.e. they are the best response to themselves; Fig. 2).

For both predators and prey, I examine two possible measure of fitness. I first examine the case where fitness during a period of time is measured as their probability of surviving throughout that time (T). This measure is relevant in cases where animals are overwintering and the state of the animal at the end of the time period does not affect future reproduction (Mangel and Clark, 1988; Clark and Mangel, 2000). For the second case, I measure fitness as expected reproductive success during the entire time under consideration. I assume that animals are ‘income breeders’ where their current reproduction is based on the food they consume in the present time period. This fitness measure is relevant when animals are reproducing during the time period under consideration and their reproductive value at the end of that time is zero.

Prey habitat selection

Patches vary in their relative input rate of resources R_i (measured as the fraction of available resources), the proportion of prey $N_i(t)$ and the proportion of predators $P_i(t)$ in each patch i during time period t . Individual prey will differ in energy reserves (state) and their behaviour may depend on their energy reserves x and time in the season t . Let m_i represent

total prey mortality per fraction of predators in patch i per time period (or an individual predator's feeding rate). Then, the probability of individual prey survival $\sigma_i(t)$ in patch i from time t to $t + 1$ will be:

$$\sigma_i(t) = \max \left\{ 1 - \frac{m_i P_i}{N_i}, 0 \right\} \quad (1)$$

Case 1: maximizing survival

Assume that, at some level of energy reserves $x_{\min}$, prey will not survive to the next time period (i.e. they starve). However, if prey exceed the minimum energy level, then the probability of surviving to the next time period will be $\sigma_i(t)$ given in equation (1). Also assume that there is a maximum amount of energy reserves that can be stored $x_{\max}$ and, therefore, $x_{\min} < x \leq x_{\max}$. $F(x, t)$ represents the prey maximum probability of survival from the current time period t to the final time period T with energy reserves x at time t . Then, the probability of survival in the final time period (the terminal fitness) $F(x, T) = 1$ if $x > x_{\min}$. Fitness is zero if prey starve or $F(x_{\min}, t) = 0$ for all t .

Prey fitness depends on the combined need to avoid starvation and predation. Assume that the amount of food obtained when successful at foraging depends on the proportion of total resources in the patch R_i and competition from the proportion of other prey in the patch $N_i(t)$. Assume the risk of finding no food r_i in patch i during the time period decreases linearly with the fraction of resources in the patch, so that $r_i = 1 - R_i$. The amount of energy reserves a prey will have in the next time period depends on current state, foraging success and the cost of foraging in the patch α_i during the current time period t given $x(t) = x$. If x'_i represents the energy reserves in the next time period if successful while foraging, or x''_i if unsuccessful, then

$$x'_i = x + \kappa(R_i/N_i(t)^\chi) - \alpha_i \quad \text{and} \quad x''_i = x - \alpha_i \quad (2)$$

where χ determines the form of competition with other prey and κ represents a conversion rate of food intake into stored energy. $\chi = 1$ represents ideal competition, while $\chi > 1$ represents interference competition, $\chi < 1$ weak competition and $\chi = 0$ no competition. For the results presented here, I assume ideal competition ($\chi = 1$). If $V_i(x, t)$ represents the expected future reproductive value or reproductive success of foraging in patch i at time t (Mangel and Clark, 1988; Houston and McNamara, 1999; Clark and Mangel, 2000), then

$$V_i(x, t) = \sigma_i(t) [(1 - r_i) F(x'_i, t + 1) + r_i F(x''_i, t + 1)] \quad (3)$$

Prey patch selection behaviour is given by the patch i which leads to the maximum expected fitness or

$$F(x, t) = \max_i \{ V_i(x, t) \} \quad (4)$$

Case 2: maximizing reproduction

For this case, I assume that prey are at the end of their reproductive life span after the final time period T , so that $F(x, T) = 0$. In this case, prey do not store energy and thus starve if they fail to find any food in the current time period. I assume that prey reproduction is

food-limited and, therefore, current reproduction is a linear function of their food intake with conversion rate ϕ . Once again, if x' represents the state in the next time period if prey are successful at gaining food, and x'' if unsuccessful, then

$$x'_i = x \quad \text{and} \quad x''_i = x_{\min} \quad (5)$$

and equation (3) is replaced by

$$V_i(x, t) = (1 - r_i) \left[\phi \frac{R_i}{N_i(t)^{\alpha}} - \alpha_i + \sigma_i(t) F(x'_i, t + 1) \right] \quad (6)$$

Equation (4) is still used to find the patch selection that maximizes prey fitness.

Solving the prey equations

Given $P_i(t)$ and $N_i(t)$, equations (1–6) are solved with backward iteration using dynamic programming (Mangel and Clark, 1988; Houston and McNamara, 1999; Clark and Mangel, 2000). Then the game is solved using the best response method as described by Houston and McNamara (1987), McNamara *et al.* (1997) and Clark and Mangel (2000). For the model described here, I used the ‘error’ method described in Clark and Mangel (2000) and a damping method adapted from McNamara *et al.* (1997). This method assumes that the probability an individual will adopt a specific behaviour depends on the difference between the expected fitness associated with that behaviour and the behaviour with the highest expected fitness. Therefore, we assume that animals make errors and that the probability of the error depends on the fitness consequences of adopting the ‘wrong’ behaviour. When the ‘tolerance’ for making errors is low, this method results in predicting the probability of adopting one of two behaviours at which an individual’s fitness will not increase if either behaviour is adopted with a higher probability. The ‘behaviour’ being predicted becomes the probability of selecting a patch rather than a discrete patch choice.

It is only possible to find a stable solution to this kind of model if the behaviour being predicted is the probability of selecting a patch. To understand this, consider the case where individual prey distribute themselves in the absence of predators between two patches with equal resources. Assuming patches differ only in competition with other prey, one would intuitively expect prey to distribute themselves evenly among the patches. However, if the entire population adopts the behaviour ‘forage in patch 1’, the best response to that behaviour is ‘forage in patch 2’. The best response to a population of individuals foraging in patch 2 is, of course, to forage in patch 1. Thus, a stable solution will not be found. However, if one examines the probability of choosing patch 1, the best response to ‘forage in patch 1 with probability 0.5’ is to adopt the same behaviour. Thus, it is necessary to consider patch selection preference rather than a discrete behaviour choice when using the best response method. However, it is possible that the stable probability of selecting a patch will be zero or 1 depending on the expected fitness difference among the patches. The need to use this method to find a stable solution to a best response game is not limited to patch selection.

$F(x, t)$ represents the expected reproductive value of adopting the habitat choice that leads to the greatest fitness (found by solving equation 4 using equation 3 or 6). If an individual of state x at a time t has expected fitness associated with patch i , $V_i(x, t)$, then let $C_i(x, t)$ represent the cost of selecting patch i :

$$C_i(x, t) = F(x, t) - V_i(x, t) \quad (7)$$

The probability that prey will select patch i is

$$s_i(x, t) = \frac{E}{E + C_i(x, t)} \bigg/ \sum_r \frac{E}{E + C_i(x, t)} \quad (8)$$

where E is a shape parameter that determines the relative chance of an error.

To solve these equations, however, one must know the distribution of predators and prey among habitats. (This makes it a game theoretical model.) To find the stable solution to the game, we start with an initial approximation of the distribution of prey and predators and then find the prey behaviour (and predator behaviour described below) that is the best response to the initial distribution of prey and predators. Then, given an initial state-distribution of prey, the predicted behaviour $s_i(x, t)$ and state dynamics (equation 2 or 5) can be used to calculate the distribution of prey among patches $N_i(t)$. Changes in the state and spatial distribution of prey depend on their foraging success and patch selection behaviour and determine the food available to predators. It is necessary to assume a starting state distribution of prey. For this model, I assume there is a uniform distribution of prey among energy reserves at $t = 1$. This assumption has no effect on the qualitative patterns. Allow $D_i(x, t)$ to represent the proportion of prey of state x that are in patch i at time t . If $s_i(x, t)$ is the probability a prey with state x at time t will select patch i and $g_{i,t}(x, x_{\text{new}})$ represents the probability ($1 - r_i$, r_i or 0) that a prey of state x selecting patch i will change from state x to x_{new} , then the distribution of prey in the next time period is given by

$$D_i(x_{\text{new}}, t + 1) = \sum_x s_i(x, t) D_i(x, t) g_{i,t}(x, x_{\text{new}}) \quad (9)$$

And the proportion of prey in each patch is

$$N_i(t) = \sum_x D_i(x) \quad (10)$$

This number is used to solve the best response behaviour of prey (and predators as described below). The model then searches for the stable distribution behaviour of prey and predators. It is still possible for some cases to cycle even when using these methods. For example, if prey fitness is measured as energy reserves at time T , the predator–prey model cycles. The need to predict behaviour as a function of a discrete state when using dynamic programming may drive these cycles. However, these cycles (unlike cycles in predator–prey population dynamic models) are not biologically meaningful, as illustrated by the simple prey patch selection example described above.

Predator habitat selection

Predators distribute themselves among patches that vary in the proportion of prey $N_i(t)$, the cost of foraging for prey β_i , and competition from (and proportion of) other predators $P_i(t)$. Let μ_i represent a predator's mortality rate in patch i per time period. For the results presented here, predator survival is assumed to be independent of the proportion of predators and prey in the patch. However, it would be possible to examine the case where predator survival is a decreasing function of the frequency of other predators in the patch (e.g. $u_i = u_0 + u_1 P_i(t)$). For simplicity, I also assume predators exhibit a linear functional response to prey (Luttbeg and Schmitz, 2000). Alternatives are easily included. Let y represent the predator's energy reserves. As with prey, I assume that predators starve if $y = y_{\min}$ and that $y_{\min} < y < y_{\max}$ and predation is deterministic.

Case 1: maximizing survival

If $G(x, t)$ represents the maximum probability of survival during the non-breeding season for predators, then $G(y, T) = 1$ if $y > y_{\min}$ and $G(y_{\min}, t) = 0$ for all t . Let β_i represent the cost of foraging in patch i and c_i represent the fraction of prey taken by predators. Then, predator energy reserves in the next time period y'_i will be

$$y'_i = y + \lambda \frac{c_i N_i(t)}{P_i(t)^v} - \beta_i \quad (11)$$

where λ represents the conversion rate of food into stored energy and v is the form of competition between predators. For the results presented here, I assume ideal competition ($v = 1$). For consistency, the predator feeding rate in the patch is equal to the total prey mortality per predators in the patch ($m_i = c_i N_i(t) / P_i(t)^v$). Let $W_i(x, t)$ represent a predator's expected reproductive value of foraging in patch i and

$$W_i(y, t) = \exp(-\mu_i) G(y'_i, t + 1) \quad (12)$$

and

$$G(y, t) = \max_i \{W_i(y, t)\} \quad (13)$$

Case 2: maximizing reproduction

If predators breed based on the current food intake, then equation (12) changes and the expected reproductive value of selecting a patch i will be:

$$W_i(y, t) = \Phi \frac{\mu_i N_i(t)}{P_i(t)^v} - \beta_i + \exp(-\mu_i) G(y'_i, t + 1) \quad (14)$$

where Φ represents the conversion rate of food into reproduction and predator state in the next time period if foraging in patch i will be:

$$y'_i = y \quad \text{if} \quad \frac{\mu_i N_i(t)}{P_i(t)^v} - \beta_i > 0 \quad \text{otherwise} \quad y = y_{\min} \quad (15)$$

Equations (14) and (15) thus replace equations (11) and (12) when finding the patch selection that maximizes expected reproductive success for predators (by solving equation 13).

Solving the predator equations

I also assume a uniform state distribution of predators at $t = 1$ and calculate the distribution of predators among patches in the same way as described for prey in detail above. The model then iterates until the stable response of both predators and prey is found. For the predators, I used the same damping and error methods described above in detail for the prey equations.

RESULTS

I focus on the case where patches differ only in the relative input rate of resources to the patch but do not differ in the risk of mortality to predators or the vulnerability of prey to predation. Imagine there are two types of sites (i.e. high and low resource) that differ in the

input rate of resources to the patch. Here I concentrate on whether the distribution of prey and predators matches the resources in the patch. I also compare the model's predictions to the predictions that would be made if one ignored the fact that both predators and prey are simultaneously selecting among patches. It would, of course, be interesting and relevant to consider cases where prey trade-off high resource patches with higher vulnerability of predation or if predators must trade-off prey availability and their own risk of predation; I will explore these scenarios in future papers. However, at present, it is useful to focus on how the addition of state dependence and concurrent interactions within and between predator and prey species is predicted to affect their distribution in space and time with respect to resources in the patch. The parameter values used for the results presented here are given in Table 1.

When both predators and prey maximize their probability of survival

Prey and predators might interact during a part of their life cycle where neither species is reproducing but instead both are simply trying to survive. Both species might be selected to maximize their probability of surviving the time period during which they overlap if both species are overwintering and will reproduce later in time. This case also assumes that the level of energy reserves at the end of the period of interaction does not affect future

Table 1. Parameters in the model

Parameter	Description
General	
T	final time period (10 , 100)
R_i	fractions of resources in patch i (all combinations in 0.1 increments)
E	error curve shape parameter (0.1 , 0.05)
Prey	
$x_{\min}$	minimum energy reserves for prey at which starvation occurs (1)
$x_{\max}$	maximum energy reserves for prey (5 or 10)
α_i	cost of foraging for prey in patch i (0.5 , 0–2 in 0.5 increments)
κ	conversion rate of food to energy reserves for prey (1)
χ	strength of competition among prey (1)
ϕ	conversion rate of food into reproduction for prey (1)
Predators	
$y_{\min}$	minimum energy reserves for predators at which starvation occurs (1)
$y_{\max}$	maximum energy reserves for prey (5 or 10)
μ_i	total individual mortality rate for predators per time period (0.02 , 0.1)
β_i	cost of foraging for prey in patch i (0.5 , 0–2 in 0.5 increments)
c_i	fraction of prey taken by predators per predator in the patch (0.1 , 0.2)
λ	conversion rate of food to energy reserves for prey (1)
v	strength of competition among predators (1)
Φ	conversion rate of food into reproduction for predators (1)

Note: Baseline parameters values are given in **bold** followed by the sensitivity analyses conducted where applicable.

fitness. This would be true in organisms for which the allocation to reproduction or future fecundity is determined by their size or energy reserves earlier in their life history.

When both predators and prey respond simultaneously to one another and prey respond to the abundance of resources in the patch, the model predicts that individuals not at risk of starvation (with high energy reserves) will be uniformly distributed among the patches. However, the prey or predators that are at risk of starvation are predicted to prefer the high resource patch. Furthermore, the extent to which the predicted distribution of predators and prey differs from uniform is determined by the proportion of individuals that have low energy reserves and the risk of starvation rather than only the difference in resources among patches (Fig. 3a). Metabolic costs, the risk of foraging unsuccessfully and the amount of resources and competition in the patch all influence the risk of starvation for individuals with low energy reserves (Fig. 4). Similarly, when prey and predators are at higher risk of starvation (because food is not abundant, conversion to stored energy is inefficient, foraging is costly or the risk of not finding food is high), then more individuals will be found in the high resource site than in good conditions. The need to avoid starvation and maximize survival makes both predators and prey mainly indifferent to the resources as long as they are not at risk of starvation, and thus the predicted distribution of predators and prey is largely independent of the difference in input rate of resources to the patch. In this case, one would not find a close match between the relative abundance of resources in patches and the distribution of either prey or predators (Fig. 3a). However, the model does predict that more prey and predators would be found in the higher resource site (Fig. 3a).

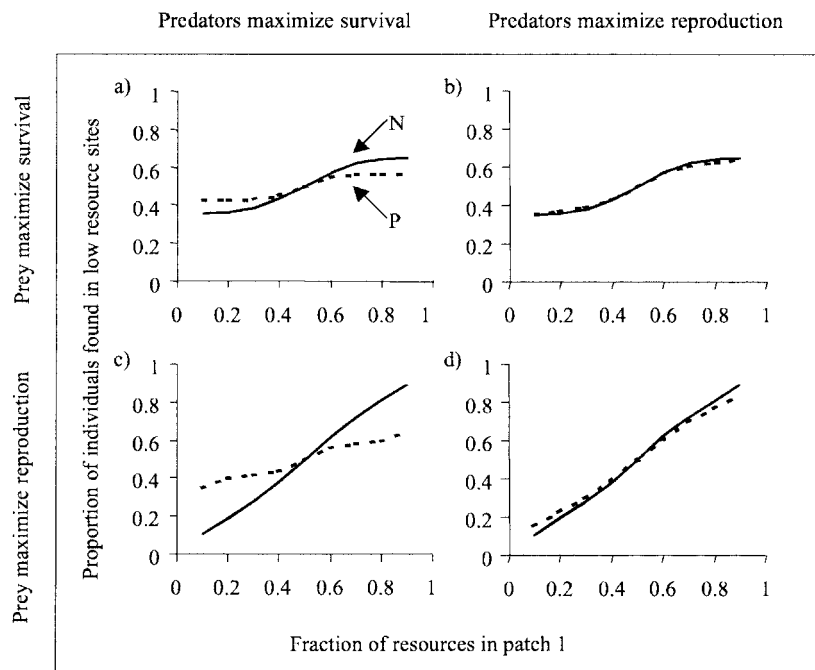


Fig. 3. Prey (solid lines) and predator (dashed lines) distributions with respect to resources as a function of how foraging affects lifetime expected reproductive success (assumes 20% of predators and prey are at risk of starvation using baseline conditions at $t = 1$ (see Table 1)).

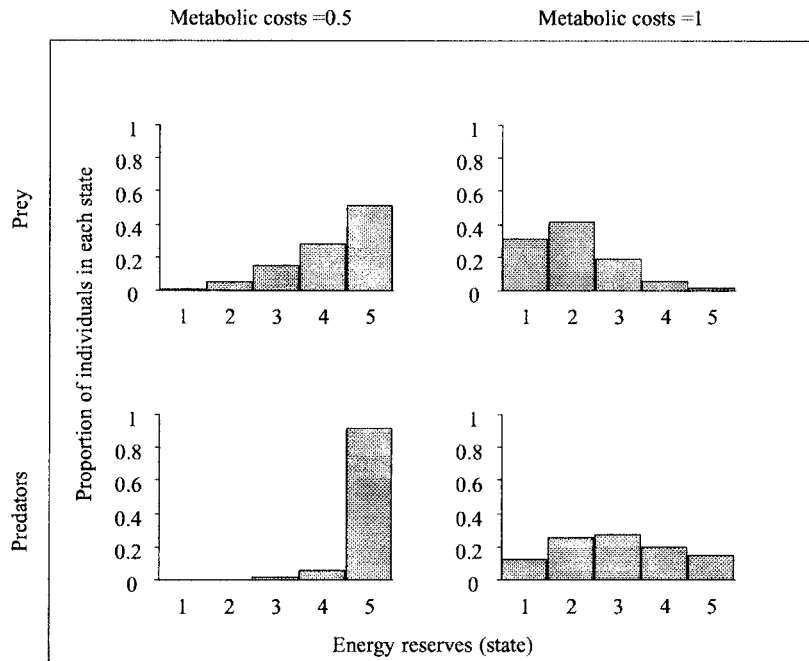


Fig. 4. The distribution of prey and predators among energy reserves (for baseline conditions at $t = T$) with lower and higher metabolic costs. Results are shown for the case where both predator and prey are maximizing survival, $R_1 = 0.1$ and $R_2 = 0.9$. A higher proportion of individuals are at risk of starvation (and are predicted to prefer the high resource site) when metabolic costs are high.

In contrast, when predation risk is fixed and there is a high resource but also high risk site, prey that are not at risk of starvation are predicted to prefer the safer patch (Table 2). However, unlike in previous optimization models of patch selection, prey with high energy reserves are not predicted to be found only in the safe sites. Due to intraspecific competition, a proportion of the prey with high energy reserves, as well as the prey that are close to starving, are expected to be found in the high risk (but high resource) patch. Only if food is sufficiently abundant that there is no risk of starvation would all prey be predicted to aggregate in the safe patch. However, as long as competition is sufficient to put some individuals at risk of starvation, then prey must balance competition (and the risk of starvation) with the risk of predation. When predation is fixed and uniform among patches, then prey are predicted to be uniformly distributed among the patches, except the individuals at risk of starvation would be found in the high resource patch. However, if no predators are at risk of starvation (i.e. prey are abundant), then predators are predicted to be distributed evenly among the sites and the skew in the prey distribution towards the high resource site will be determined by the proportion of prey at risk of starvation.

If we contrast the case where predation risk is fixed and differs among sites with the predictions when predators respond to prey, we do not get prey aggregating in a safer patch (Table 2). Instead, when predators respond to prey, individual predation rates will be equalized among the sites. However, if we compare the case where predation rate is fixed but equal across sites, then the prey distribution is the same as predicted for the model where

Table 2. Summary of the comparison of different model predictions for prey behaviour

	Predators maximize survival	Predators maximize reproduction
Prey maximize survival		
Full model: predators respond and state-dependence	high energy reserves → no preference low energy reserves → prefer high resource site	high energy reserves → no preference low energy reserves → prefer high resource site
Fixed predation risk: state-dependence	more in safe site high energy reserves → prefer safe site (depends on relative risk)	more in safe site high energy reserves → prefer safe site (depends on relative risk)
State-independent: predators responding	uniform	uniform
Prey maximize reproduction		
Full model: predators respond and state-dependence	resource matching with deviations caused by starving prey	resource matching with deviations caused by starving prey
Fixed predation risk: state-dependence	resource matching with deviations caused by risk	resource matching with deviation caused by risk
State-independent: predators responding	perfect matching	perfect matching

Note: Fixed predation risk assumes the high resource site is riskier than the low resource site. See text for more details.

predators respond to prey. Yet, the two predicted distributions differ in their underlying dynamics of whether predators are fixed or responding to prey.

If predators distribute themselves among patches that differ in the fixed amount of prey, then predators are predicted to be unresponsive to the total amount of prey in each site unless they are at risk of starvation. In contrast to when both prey and predators respond, the fixed-prey model would not predict that predators match the prey distribution unless prey were uniformly distributed among the sites. However, the model of both predators and prey predicts that even though both predators and prey are not matching the resources they will partially match one another, as predators and prey avoid the risk of starvation.

It is also important to realize that minimizing the risk of mortality as a function of current state is different from minimizing the risk of mortality without considering state. If patches simply differ in a fixed predation risk, then a model without state dynamics predicts that all prey (or predators) would be found in the safer site. If we did not consider starvation but allow both predators and prey to respond to one another in a state-independent game, then a completely uniform distribution of predators and prey would be predicted. In contrast, this model leads to the interesting prediction that there will be more predators and prey in the higher resource site and that the extent to which the distribution is skewed will not match the difference in resources. Instead, it is driven by the percentage of individuals that are at risk of starvation. The predictions differ qualitatively from models that ignore

either the state-dependence of foraging behaviour or the simultaneous interactions within and between predators and prey (Table 2).

When prey maximize survival and predators are income breeders

In some cases, prey might not be reproducing while the predators are feeding on the prey during the predator's reproductive period (Luttbeg and Schmitz, 2000). Then prey fitness is the minimum risk of mortality (due to starvation and predation) and predator fitness is expected reproductive success.

In this case, the predictions are very similar to the case when fitness for both predators and prey is survival (Fig. 3b). This occurs because prey distributions are driven mainly by avoiding starvation (the skew among sites is determined by the proportion of individuals at risk of starvation). Predators maximize their food intake by responding directly to the distribution of prey. This leads to the basic pattern that prey and predators are not distributed with respect to the relative difference in resources. The extent to which more predators and prey are found in the high resource sites is now determined by the proportion of prey at risk of starvation rather than the proportion of predators at risk of starvation. The dynamics are driven by the prey. Predators mainly map onto the distribution of prey because predators achieve higher fitness if they find more prey. More prey and predators will be found in the higher resource site, but the relative difference in resources among the sites will not correspond directly to the prey or predator distribution.

If one were to focus on predators alone (and not allow prey to respond), the prediction is that predators would respond to the distribution of prey among sites. However, understanding the predator distribution with respect to the resources for prey is not intuitive without an understanding of prey behaviour and how it responds to predators and resources. If we fix predation and only allow prey to respond, the predictions would be the same as described in the previous section. Thus the predictions of the model that allows predators and prey to respond clearly differ from those of fixed predation (or fixed prey) that differs among sites (Table 2).

When prey are income breeders and predators avoid starvation

If prey are reproductive but predators are not reproducing during the period of interaction, the predictions of the model that considers both species differ greatly from the previously described patterns (Fig. 3c). Prey respond to the resources at the site and competition from conspecifics, whereas predators respond only weakly to the difference in prey among patches and, as above, the difference in the distribution of predators among patches is determined by the proportion of predators that are at risk of starvation. Prey are predicted to match roughly the difference in resources at the site. For example, if the resources at the high resource site were three times higher than at the low resource site, approximately one-quarter of the prey would be found in the low resource site. In contrast, predators are predicted to match neither the resources nor the prey. These predictions can only be understood by knowing the effect of food intake on lifetime reproductive success, the effect of individual state on behaviour and the interactions within and between the predator and prey species.

Models with fixed predation rates cannot predict these patterns of prey distribution (Table 2). For example, when there is no difference in the fixed predation risk among sites,

prey are predicted to respond only to the difference in resources at the site, and even the proportion of individuals near starvation will not cause deviations from resource matching. Fixed-predation or fixed-prey models will only predict the same predator and prey distributions if the assumed fixed rates match the stable pattern described above.

When both prey and predators are income breeders

In the case where both prey and predators are reproducing based on the amount of energy gained during the present time period, then both predators and prey are mainly predicted to match the underlying difference in the input rate of resources among patches (Fig. 3d). More prey are predicted to be found in the higher resource patch and the difference in the distribution of prey among sites will increase as the relative abundance of resources increases between the patches. Predators are, in turn, predicted to respond to the distribution of prey and correspondingly more predators are predicted to be found in the higher resource sites. However, neither predators nor prey will exhibit perfect resource matching. Prey that are at risk of starvation cause deviations from a perfect matching of resources.

Although fixing either predation rate or prey behaviour will lead to similar predictions of resource matching mediated by differences in predation risk or prey matching on the part of predators, the exact distribution of prey with respect to resources and predators with respect to prey can only be understood by considering how both predators and prey concurrently respond to one another (Table 2). For example, if patches are assumed to be equal in their fixed predation rate, the prey are predicted to match the resources exactly. Solutions of the model without state-dependence also predict perfect resource matching (Table 2). In contrast, models where predators respond to prey distributions and include state-dependence predict deviations from perfect resource matching that depend on the distribution of both prey and predators among energy reserve levels.

DISCUSSION

Previous patch selection models have focused mainly on cases where prey experience fixed predation risk and no direct competition with conspecifics (Mangel and Clark, 1986, 1988; Houston and McNamara, 1988, 1997; Mangel, 1989, 1990, 1992; McNamara and Houston, 1990; McNamara *et al.*, 1991; Houston *et al.*, 1993; Merad and McNamara, 1994). These models tend to predict that prey at risk of starvation will be found in the high risk and high resource sites, while all other prey will aggregate in safer patches. By adding competition among prey, we first find that, even independent of predator responses, prey will no longer only aggregate in safe patches. Instead, competition and the risk of starvation drive some prey (even if they have higher energy reserves) into risky habitats. When predation is no longer fixed, we find that prey move among patches and predators respond to prey in a way that usually equilibrates the risk of predation among patches. This assumes, however, that predators do not experience their own trade-off among patches and that patches are equal in the refuge they offer prey. However, predictions of a model that includes both competition with conspecifics and predator responses differ from the predictions of previous patch choice models (Table 2).

It is also clear that considering the state-dependence of behaviour and its effects on fitness leads to predictions that differ from state-independent models (Table 2) (Hugie and Dill, 1994; Sih, 1998). These models predict, in the case of ideal competition, that predators and

prey match resources. However, variation among individuals with respect to their state cause deviations from resource matching. Furthermore, the life history of the animal and the relationship between foraging and lifetime reproductive success can alter the pattern further. Animals for which survival is equal to fitness will not match resources, and even animals for which fitness is determined by current reproduction may deviate from perfect resource matching when in danger of starvation.

Empirically, the next step is to examine predator and prey distributions either observationally or experimentally when both species can respond to the distribution of conspecifics and predator or prey species (Lima, 2002). It is also clear that we need to understand the state dynamics of both predators and prey and how individual behaviour and condition varies within populations. We also need to have a clear picture of how foraging is related to fitness in both predators and prey. The general patterns of predator–prey distributions are predicted to depend on the life history of both species. When predators and prey experience similar circumstances (i.e. both maximizing survival), their distributions are expected to closely match one another. However, whether they match underlying differences in the resources at sites will depend mainly on prey fitness as a function of foraging. In general, we would predict that animals in low condition would be found together in high resource sites independent of the rest of the population's distribution. We would also predict that the proportion of individuals that are near starvation should explain deviations from either resource matching or uniform distributions among sites. It is clear that some of these patterns (e.g. individual condition or fitness) may be difficult to measure in the field. However, observational and experimental studies have yet to examine predator and prey responses concurrently in any system and simple studies in known systems would be a positive step towards understanding predatory–prey interactions.

The predicted distributions of predators and prey described above clearly illustrate the importance of considering the response of predators to one another's distributions. However, the models also illustrate the impact of an organism's state and individual variation on the predicted behaviour. Similarly, competition among conspecifics and the life-history pattern of both predators and prey are key to understanding their distribution and behaviour. Through a combined understanding of interactions within and between the species with knowledge of how foraging relates to lifetime expected reproductive success of both predators and prey, we can increase our understanding of these interactions and the distribution of predators and prey in space and time.

Clearly, the models presented here are relatively simple and do not begin to explore the multitude of potential interactions between predators and prey, behavioural responses to predation and prey behaviour, or patterns of competition within species. Both predators and prey were assumed here to have perfect information. Future models will address the impact of learning and individual experience on prey and predator behaviour. More complex prey and predator behaviours could also be considered. This approach can also be used to ask how the predicted behaviours will depend on and influence population dynamics, thus linking the two mainly separate approaches to predator–prey interactions. Using the same basic framework, the expected reproductive success and survival of predators and prey could be used to predict population dynamics. This would also allow prey and predator population density to vary in the model. Models could examine further species interactions either through additional top predators or additional competitors for a given resource or prey species. Finally, predator–prey models often cycle

and these models are no exception. For example, the model described above cycles for the case where predators or prey are 'capital breeders' and reproduction is state-dependent at the end of the time period. Future analyses will include individual-based models to examine whether these cycles are biologically interesting or merely an outcome of the approach.

ACKNOWLEDGEMENTS

Many thanks to Marc Mangel without whom this research would not have been possible. I also thank John McNamara and Alisdair Houston for helpful discussions during the early stages of the research. This research was supported by National Science Foundation grant OPP-9714983 to Marc Mangel, a National Science Foundation Postdoctoral Fellowship to S.H.A. and the Center for Stock Assessment Research (CSTAR), UCSC.

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