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Optimal Foraging and Predator–Prey Dynamics

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A system consisting of a population of predators and two types of prey is considered. The dynamics of the system is described by differential equations with controls. The controls model how predators forage on each of the two types of prey. The choice of these controls is based on the standard assumption in the theory of optimal foraging which requires that each predator maximizes the net rate of energy intake during foraging. Since this choice depends on the densities of populations involved, this allows us to link the optimal behavior of an individual with the dynamics of the whole system. Simple qualitative analysis and some simulations show the qualitative behavior of such a system. The effect of the optimal diet choice on the stability of the system is discussed. © 1996 Academic Press, Inc.

INTRODUCTION

Since there is convincing experimental evidence that some animals can make decisions with respect to their foraging activities, many papers have been devoted to modeling optimal foraging behavior, for a review see Stephens and Krebs (1986), Mangel and Clark (1988). It is assumed that when foraging, these decisions lead to *optimal foraging* which maximizes some optimality criterion. Standard foraging models are based on the assumption of maximization of the net rate of energy intake during foraging which leads to maximization of

$$\frac{E}{T_{\mathrm{s}}+T_{\mathrm{h}}},$$

see Stephens and Krebs (1986). Here T_{s} stands for the total time spent by searching, T_{h} denotes the total time spent by handling, and E is the net amount of energy gained in the total time $T_{\mathrm{s}}+T_{\mathrm{h}}$. Assuming that encounters are linearly related to T_{s}, the above expression leads to maximization of

$$\frac{\lambda e}{1+\lambda h}, \tag{1}$$

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where λ denotes the encounter rate of a predator with a prey when searching, e is the average energy gained per encounter, and h is the average time spent by handling. Expression (1) was also generalized to the situation where many types of prey are present (Stephens and Krebs, 1986). In the case of two types of prey this leads to maximization of

$$R(p_1, p_2) = \frac{p_1 \lambda_1 e_1 + p_2 \lambda_2 e_2}{1 + p_1 \lambda_1 h_1 + p_2 \lambda_2 h_2}. \tag{2}$$

Here p_1 and p_2 denote the probability that a predator will attack prey type 1 or prey type 2, λ_i stands for the encounter rate of a predator with the ith type of prey when searching, e_i is the expected net energy gained from the ith type of prey, and h_i is the expected handling time spent with the ith type of prey.

Based on maximization of (2) one obtains a composition of the diet of a predator which depends on the ranking of different types of prey according to the ratios e_i/h_i. The main result of the optimal foraging theory which may be easily derived from (2) states that predators will always forage on the most profitable type of prey, i.e., the prey type with the highest ratio e_i/h_i. The other type of prey will be included into the diet only if the value of R will not decrease by doing so. Thus assuming that the first type of prey is more profitable than the second one, $p_1 = 1$ and p_2 is either zero or one depending on the parameters involved. This is the well-known result from the theory of optimal foraging which holds also for more types of prey, see Stephens and Krebs (1986). This basic model goes back to Charnov (1976) and many others who elaborated on it, including some other phenomena that may influence the decision of the predator. We refer to Stephens and Krebs (1986) and Mangel and Clarke (1988) for more detailed information and an extensive reference list. However, the above model is set into a static environment, where the densities of populations involved are fixed. Thus, for example, the encounter rate λ_i is taken as constant. Since these encounter rates must necessarily depend on the densities of populations of prey, this assumption holds as long as the densities of prey are fixed. Obviously, this is not so, since each population has its own dynamics which, in turn, will be influenced by the foraging behavior of predators. Thus, assuming that the dependence of the encounter rate on the density of prey is known allows us to link the behavior of an individual predator with the dynamics of populations of predator and prey. The control p_2 may be expressed as a function of the density of prey type 1. There is a critical density x_1^* of the first prey type such that if the density of the first prey type is below this threshold, then prey type 2 will be included into the optimal diet, i.e., $p_2 = 1$. If the density of the first prey type is larger than the threshold, the optimal diet will consist only of prey type 1. If the density of prey type 1 will equal x_1^*, then p_2 cannot be determined directly and it may be anywhere between 0 and 1. Thus p_2 as a function of the density of the more profitable prey type is a *step function*.

In order to construct a model of population dynamics we have to choose the functional response function. Since this function depends on the predator diet choice given by a step function we cannot uniquely define the value of the functional response at those points where *switching* occurs, i.e., where the diet of predators changes. One possible way to overcome this problem is to approximate the step function by a continuous function. This approach was used in Tansky (1978), Teramoto *et al.* (1979), Vance (1978), Murdoch and Stewart-Oaten (1975), Holt (1983), and Fryxell and Lundberg (1994). The main aim of these papers was to study the effect of switching on the stability of predator–prey systems. However, the resulting dynamics may depend crucially on the approximation of the step function describing the diet of the predator, since this approximation is strongly nonlinear. Thus the stability analysis will depend on the particular choice of the approximation. Another approach based on balancing costs and benefits related to the amount of time spent by foraging which alters the shape of Holling type II functional response was discussed in Abrams (1982, 1984, 1990). In the framework of optimal patch selection the effect of individual behavior on the stability of predator–prey (or host–parasite) systems was studied for example in Hassell and May (1973), van Baalen and Sabelis (1993), Colombo and Křivan (1993), and Křivan (1995).

The aim of this paper is to deal directly with the step function describing the diet choice. We will assume that the densities of populations involved may be described by a system of differential equations with controls that allow us to model selective foraging by predators. Together with this system we consider the optimality criterion (2) which allows us to specify *optimal foraging strategies* among all plausible controls. The optimal foraging strategy is not defined uniquely, and, in the last analysis, we get a differential inclusion instead of a differential equation. We show that, despite this ambiguity, solutions are uniquely defined. Then we consider a particular example where both populations of prey grow logistically with the same growth parameter. Under this assumption we study the qualitative behavior of the model. Mainly, we are interested in the effect of optimal diet choice on the stability of the system.

In this paper we follow Colombo and Křivan (1993), where a general dynamical framework for description of optimal foraging strategies was given in terms of control systems. For the sake of simplicity we consider only one type of predators foraging on two types of prey, although the present approach applies to more complex systems as well.

THE DYNAMICS

Let us consider a population of a predator foraging on two different populations of prey. The density of the population of the predator is described by x_3, while the densities of populations of prey are x_1, x_2. Following Holling (1959), see Appendix A, the dynamics of the system which corresponds to the optimality criterion (2) is described by

$$\begin{aligned} x_1' &= x_1\, g_1(x_1, x_2) - \frac{p_1 \lambda_1 x_3}{1 + p_1 h_1 \lambda_1 + p_2 h_2 \lambda_2} \\ x_2' &= x_2\, g_2(x_1, x_2) - \frac{p_2 \lambda_2 x_3}{1 + p_1 h_1 \lambda_1 + p_2 h_2 \lambda_2} \\ x_3' &= \frac{p_1 e_1 \lambda_1 x_3 + p_2 e_2 \lambda_2 x_3}{1 + p_1 h_1 \lambda_1 + p_2 h_2 \lambda_2} - m x_3. \end{aligned} \tag{3}$$

Let us stress that p_1, p_2 are taken as controls which change in time. In this equation functions g_i, $i = 1, 2$, are the growth rate functions for populations of prey. One possible form of these functions is

$$g_i(x_1, x_2) = a_i \left(1 - \frac{x_i}{K_i}\right), \qquad i = 1, 2. \tag{4}$$

To simplify subsequent analysis we will always assume that

$$e_1/h_1 > e_2/h_2, \tag{5}$$

and thus $e_1 h_2 - e_2 h_1 > 0$, i.e., the first prey is more convenient for the predator than the second one. Since λ_i denotes the encounter rate of a searching predator with a prey of the ith type, it depends on the density of the ith type of prey, i.e., $\lambda_i(x_i)$. Assuming this dependence is linear

$$\lambda_i(x_i) = l_i x_i, \qquad i = 1, 2, \tag{6}$$

where l_i is a positive parameter, gives the following dynamics with Holling type II trophic function:

$$\begin{aligned} x_1' &= x_1\, g_1(x_1, x_2) - \frac{p_1 l_1 x_1 x_3}{1 + p_1 h_1 l_1 x_1 + p_2 h_2 l_2 x_2} \\ x_2' &= x_2\, g_2(x_1, x_2) - \frac{p_2 l_2 x_2 x_3}{1 + p_1 h_1 l_1 x_1 + p_2 h_2 l_2 x_2} \\ x_3' &= \frac{p_1 e_1 l_1 x_1 x_3 + p_2 e_2 l_2 x_2 x_3}{1 + p_1 h_1 l_1 x_1 + p_2 h_2 l_2 x_2} - m x_3. \end{aligned} \tag{7}$$

All parameters in (7) are assumed to be nonnegative. Controls p_1, p_2 are interpreted as probabilities that a prey of the ith type will be attacked upon encounter with a predator, thus $(p_1, p_2) \in U$, where

$$U = \{(p_1, p_2) \mid 0 \leqslant p_1 \leqslant 1, 0 \leqslant p_2 \leqslant 1\}.$$

Solution of (7) is a couple $(x(t), p(t))$, where $x(t) = (x_1(t), x_2(t), x_3(t))$ is an absolutely continuous function (i.e., its derivative exists almost everywhere in the sense of Lebesgue measure) and $p(t) = (p_1(t), p_2(t))$ is a measurable function, such that (7) is satisfied for almost all t. Those readers who are not familiar with these concepts may think that "almost everwhere" means with an exception of "some" points. Due to (6) the optimality criterion (2) becomes

$$R(p_1, p_2) = \frac{p_1 e_1 l_1 x_1 + p_2 e_2 l_2 x_2}{1 + p_1 l_1 x_1 h_1 + p_2 l_2 x_2 h_2}. \tag{8}$$

Following standard theories of optimal foraging we consider (8) as a *fitness function* which is maximized. We see that this amounts to saying that the the growth rate of an average predator which is given by x_3'/x_3 is maximized. The optimal strategy thus depends on the densities of prey. For each pair of (x_1, x_2) we get a set of optimal controls $S(x_1, x_2)$ which we call *strategy map*

$$S(x_1, x_2) = \{(p_1, p_2) \in U \mid R(p_1, p_2) = \max_{(u_1, u_2) \in U} R(u_1, u_2)\}.$$

Let us note that the above-defined strategy is *myopic*, i.e., the choice of (p_1, p_2) is based only upon the knowledge of the present situation by predators, and no insight into the future is assumed.

Thus our general model for one population of predators feeding on two different types of prey assuming optimal behavior of predators has the form

$$\begin{aligned} x_1' &= x_1 g_1(x_1, x_2) - \frac{p_1 l_1 x_1 x_3}{1 + p_1 h_1 l_1 x_1 + p_2 h_2 l_2 x_2} \\ x_2' &= x_2 g_2(x_1, x_2) - \frac{p_2 l_2 x_2 x_3}{1 + p_1 h_1 l_1 x_1 + p_2 h_2 l_2 x_2} \\ x_3' &= \frac{p_1 e_1 l_1 x_1 x_3 + p_2 e_2 l_2 x_2 x_3}{1 + p_1 h_1 l_1 x_1 + p_2 h_2 l_2 x_2} - m x_3 \\ &(p_1, p_2) \in S(x_1, x_2). \end{aligned} \tag{9}$$

This is a control system in which the actual value of control (p_1, p_2) depends on the state of the system. We see that dynamics of (9) is not uniquely determined at those points where the strategy map $S(x_1, x_2)$ is multivalued. Therefore (9) is not a differential equation, but it is equivalent to a differential inclusion, see Aubin and Cellina (1984), or to Filippov regularization of a dynamics with discontinuous right-hand side, Filippov (1988), and Colombo and Křivan (1993).

OPTIMAL STRATEGY

Now we look for those controls which belong to the set $S(x_1, x_2)$. Computing derivatives of the map $R(p_1, p_2)$ allows us to deduce the maximizing controls p_1, p_2. This is a standard way of deriving the optimal behavior of a predator in the foraging theory. Due to (5) it turns out, see Appendix B, that

$$\frac{\partial R}{\partial p_1} > 0.$$

Thus $p_1 = 1$. Since the sign of $\partial R/\partial p_2$ does not depend on p_2 it follows that if

$$\frac{\partial R}{\partial p_2} \neq 0,$$

then the maximum is achieved for either $p_2 = 0$ or $p_2 = 1$, depending on the sign of the derivative, see Appendix B. This is a well-known result from the optimal foraging theory which says that the optimal control is of the *bang-bang* (or *zero–one*) type, i.e., the more profitable prey is always included in the diet and the less profitable prey is either included or excluded depending on the sign of $\partial R/\partial p_2$. Thus *partial preferences* (i.e., $0 < p_2 < 1$) do not arise in the classical model of optimal foraging. However, standard theory of optimal foraging which considers all parameters involved as constants does not take into account the case when

$$\frac{\partial R}{\partial p_2} = 0. \tag{10}$$

This is a legitimate simplification, since such a case may be excluded by a negligible change in parameters. Thus from a practical point of view this cannot happen. However, in the present dynamic setting the encounter rates $\lambda_1(x_1)$, $\lambda_2(x_2)$ depend on the densities of prey populations, see (6), and we cannot exclude from our considerations the case when (10) holds. This is due to the fact that it may well happen that $\lambda_1(x_1)$, $\lambda_2(x_2)$, will change in such a way that (10) will be reached after some time and consequently, optimal decision will lead to partial preferences. After some algebra, see Appendix B, we get that the strategy map S has the values

$$S(x_1, x_2) = \begin{cases} (1, 1) & \text{if} \quad x_1 < \dfrac{e_2}{l_1(e_1 h_2 - e_2 h_1)} \\ (1, 0) & \text{if} \quad x_1 > \dfrac{e_2}{l_1(e_1 h_2 - e_2 h_1)} \\ (1, p_2), 0 \leqslant p_2 \leqslant 1 & \text{if} \quad x_1 = \dfrac{e_2}{l_1(e_1 h_2 - e_2 h_1)}. \end{cases} \tag{11}$$

We see that the strategy map S is not singlevalued but multivalued for

$$x_1^* = \frac{e_2}{l_1(e_1 h_2 - e_2 h_1)}. \tag{12}$$

Consequently, the strategy of a predator when it encounters a prey is:

(a) If it encounters a prey of the most profitable type, i.e., prey 1, it will always attack it.

(b) If it encounters a prey of the less profitable type, then there are three possibilities:

(i) it should attack it provided that the gain from eating is larger than the gain from rejection and searching for a more profitable prey, i.e., if

$$x_1 < x_1^*;$$

(ii) it should reject it if

$$x_1 > x_1^*;$$

(iii) the strategy is not fully determined (i.e., $p_2 \in [0, 1]$) if

$$x_1 = x_1^*.$$

We want to stress here that in case (iii) it may still be possible to determine uniquely values of p_2 if we take into account the dynamics of the system, see below. Rewriting (7) together with the above strategy map we get

$$\begin{aligned} x_1' &= x_1 g_1(x_1, x_2) - \frac{l_1 x_1 x_3}{1 + h_1 l_1 x_1 + p_2 h_2 l_2 x_2} \\ x_2' &= x_2 g_2(x_1, x_2) - \frac{p_2 l_2 x_2 x_3}{1 + h_1 l_1 x_1 + p_2 h_2 l_2 x_2} \\ x_3' &= \frac{e_1 l_1 x_1 x_3 + p_2 e_2 l_2 x_2 x_3}{1 + h_1 l_1 x_1 + p_2 h_2 l_2 x_2} - m x_3 \\ &\quad (1, p_2) \in S(x_1, x_2). \end{aligned} \tag{13}$$

The dynamics of (13) is not uniquely determined at those points where $x_1 = x_1^*$. Despite this nonuniqueness in the dynamics, the existence and uniqueness of solutions of (13) for every initial condition follows from Appendix C. Let us denote

$$G^1 = \left\{ x \in \mathbf{R}^3_+ \mid x_1 < \frac{e_2}{l_1(e_1 h_2 - e_2 h_1)} \right\},$$

$$G^2 = \left\{ x \in \mathbf{R}^3_+ \mid x_1 > \frac{e_2}{l_1(e_1 h_2 - e_2 h_1)} \right\},$$

$$G^0 = \left\{ x \in \mathbf{R}^3_+ \mid x_1 = \frac{e_2}{l_1(e_1 h_2 - e_2 h_1)} \right\},$$

see Fig. 1. For a better understanding we rewrite (13) on each of the above defined sets. In the region G^1 the dynamics of (13) is given by

$$\begin{aligned} x_1' &= x_1\, g_1(x_1, x_2) - \frac{l_1 x_1 x_3}{1 + h_1 l_1 x_1 + h_2 l_2 x_2} \\ x_2' &= x_2\, g_2(x_1, x_2) - \frac{l_2 x_2 x_3}{1 + h_1 l_1 x_1 + h_2 l_2 x_2} \\ x_3' &= \frac{e_1 l_1 x_1 x_3 + e_2 l_2 x_2 x_3}{1 + h_1 l_1 x_1 + h_2 l_2 x_2} - m x_3, \end{aligned} \tag{14}$$

in G^2 by

$$\begin{aligned} x_1' &= x_1\, g_1(x_1, x_2) - \frac{l_1 x_1 x_3}{1 + h_1 l_1 x_1} \\ x_2' &= x_2\, g_2(x_1, x_2) \\ x_3' &= \frac{e_1 l_1 x_1 x_3}{1 + h_1 l_1 x_1} - m x_3, \end{aligned} \tag{15}$$

and in G^0 by

$$\begin{aligned} x_1' &= x_1\, g_1(x_1, x_2) - \frac{l_1 x_1 x_3}{1 + h_1 l_1 x_1 + p_2 h_2 l_2 x_2} \\ x_2' &= x_2\, g_2(x_1, x_2) - \frac{p_2 l_2 x_2 x_3}{1 + h_1 l_1 x_1 + p_2 h_2 l_2 x_2} \\ x_3' &= \frac{e_1 l_1 x_1 x_3 + p_2 e_2 l_2 x_2 x_3}{1 + h_1 l_1 x_1 + p_2 h_2 l_2 x_2} - m x_3 \\ & p_2 \in [0, 1]. \end{aligned} \tag{16}$$

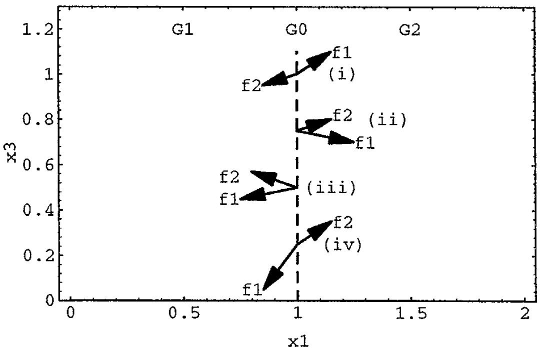

FIG. 1. Four possible types of behavior of the right-hand side of (13) in G^0.

In other words, the dynamics of (13) is uniquely determined in G^1 and in G^2, where it is described by a differential equation, while in G^0 it is not, since p_2 may take any value in $[0, 1]$.

ANALYSIS OF SWITCHING

Now we focus on the qualitative analysis of (13) in G^0. Let $n = (1, 0, 0)$ denote the normal vector to G^0, oriented from G^1 toward G^2. We denote by $f_1(x_1, x_2, x_3)$ the right-hand side of (14) and by $f_2(x_1, x_2, x_3)$ the right-hand side of (15). Since in G^1 and in G^2 the dynamics is described by a system of differential equations, we have to study the behavior of a solution when it falls on G^0 where switching occurs. This behavior is given by projections of vector fields f_1 and f_2 on the normal vector n. We have to distinguish four possible cases ($\langle \cdot, \cdot \rangle$ stands for the scalar product):

(i) $\langle n, f_1 \rangle > 0$, $\langle n, f_2 \rangle < 0$, which means that trajectories of (13) will stay in G^0

(ii) $\langle n, f_1 \rangle > 0$, $\langle n, f_2 \rangle > 0$, which means that trajectories of (13) will pass through G^0 in direction from G^1 to G^2

(iii) $\langle n, f_1 \rangle < 0$, $\langle n, f_2 \rangle < 0$, which means that trajectories of (13) will pass through G^0 in direction from G^2 to G^1

(iv) $\langle n, f_1 \rangle < 0$, $\langle n, f_2 \rangle > 0$, which means that trajectories of (13) which start on G^0 will move either to G^1 or to G^2,

see Fig. 1. From Appendix C it follows that the case (iv) cannot happen. Under condition (i), a trajectory which hits G^0 stays there as long as (i) holds. Such behavior is called *sliding regime* in the theory of discontinuous differential equations. This means that *partial preferences* arise, i.e., the probability of attacking the second type of prey is strictly between zero and one. This has one important consequence; namely, it allows us to derive uniquely value of p_2 along G^0. Let us assume that a solution of (13) is in the part of G^0 where the sliding regime occurs. Since in this case it cannot leave G^0 it must hold

$$x_1'(t)=0.$$

This allows us to compute explicitly p_2 at those points where $g_1(x_1^*, x_2)\neq 0$. Namely, we get

$$p_2(x_1^*, x_2, x_3)=\frac{l_1x_3-(1+h_1l_1x_1^*)\,g_1(x_1^*, x_2)}{h_2l_2x_2\,g_1(x_1^*, x_2)}. \tag{17}$$

From (i) it follows that partial preferences arise at those points of G^0 where

$$\frac{g_1(x_1^*, x_2)(1+h_1l_1x_1^*)}{l_1}<x_3<\frac{g_1(x_1^*, x_2)(1+h_1l_1x_1^*+h_2l_2x_2)}{l_1}. \tag{18}$$

Thus we see that partial preferences do not arise if $g_1(x_1^*, x_2)<0$. In this case $\langle n, f_1(x_1^*, x_2, x_3)\rangle<0$, $\langle n, f_2(x_1^*, x_2, x_3)\rangle<0$ for all positive x_2, x_3, and trajectories of (13) cross G^0 transversally in direction from G^2 to G^1.

AN EXAMPLE

We consider (13) with the growth rate functions given by (4), i.e.,

$$\begin{aligned}
x_1'&=a_1x_1\left(1-\frac{x_1}{K_1}\right)-\frac{l_1x_1x_3}{1+h_1l_1x_1+p_2h_2l_2x_2}\\
x_2'&=a_2x_2\left(1-\frac{x_2}{K_2}\right)-\frac{p_2l_2x_2x_3}{1+h_1l_1x_1+p_2h_2l_2x_2}\\
x_3'&=\frac{e_1l_1x_1x_3+p_2e_2l_2x_2x_3}{1+h_1l_1x_1+p_2h_2l_2x_2}-mx_3\\
&(1, p_2)\in S(x_1, x_2).
\end{aligned} \tag{19}$$

First we will study qualitative behavior of (19) in G^1 and in G^2 separately. In order to make the analysis possible we will assume $a_1=a_2$ and $l_1=l_2$. For $p_2=1$ there exists one equilibrium $E^1=(x_1^1, x_2^1, x_3^1)$ of (19) with all nonzero components

$$x_1^1 = \frac{mK_1}{l_2(e_1K_1 + e_2K_2 - m(h_1K_1 + h_2K_2))}$$

$$x_2^1 = \frac{mK_2}{l_2(e_1K_1 + e_2K_2 - m(h_1K_1 + h_2K_2))}$$

$$x_3^1 = \frac{a_2(e_1K_1 + e_2K_2)(e_1K_1l_2 + e_2K_2l_2 - m(1 + h_1K_1l_2 + h_2K_2l_2))}{l_2^2(m(h_1K_1 + h_2K_2) - e_1K_1 - e_2K_2)^2}.$$

This equilibrium is *strictly positive* (i.e., $x_1^1 > 0, x_2^1 > 0, x_3^1 > 0$) if

$$m < \frac{e_1K_1l_2 + e_2K_2l_2}{1 + h_1K_1l_2 + h_2K_2l_2}. \tag{20}$$

Since we are able to compute eigenvalues for E^1, see Appendix D, we can study local stability of E^1. From Appendix D it follows that E^1 is locally stable if

$$\frac{(e_1K_1 + e_2K_2)(h_1K_1l_2 + h_2K_2l_2 - 1)}{(h_1K_1 + h_2K_2)(h_1K_1l_2 + h_2K_2l_2 + 1)} < m < \frac{e_1K_1l_2 + e_2K_2l_2}{1 + h_1K_1l_2 + h_2K_2l_2}. \tag{21}$$

If

$$m \leqslant \frac{(e_1K_1 + e_2K_2)(h_1K_1l_2 + h_2K_2l_2 - 1)}{(h_1K_1 + h_2K_2)(h_1K_1l_2 + h_2K_2l_2 + 1)},$$

then a stable limit cycle around E^1 may appear via Hopf bifurcation. If

$$m > \frac{e_1K_1l_2 + e_2K_2l_2}{1 + h_1K_1l_2 + h_2K_2l_2}, \tag{22}$$

then equilibrium $(K_1, K_2, 0)$ is locally stable, see Appendix D.

For $p_2 = 0$ the nontrivial equilibrium $E^2 = (x_1^2, x_2^2, x_3^2)$ of (19) is

$$x_1^2 = \frac{m}{l_1(e_1 - h_1m)}$$

$$x_2^2 = K_2$$

$$x_3^2 = \frac{a_1e_1(e_1K_1l_1 - m - h_1K_1l_1m)}{K_1l_1^2(h_1m - e_1)^2}.$$

This equilibrium is strictly positive provided

$$m < \frac{e_1K_1l_1}{1 + h_1K_1l_1}.$$

The equilibrium E^2 is globally stable if

$$\frac{e_1(K_1 l_1 h_1 - 1)}{h_1(K_1 l_1 h_1 + 1)} < m < \frac{e_1 K_1 l_1}{1 + h_1 K_1 l_1}.$$

If

$$m \leqslant \frac{e_1(K_1 l_1 h_1 - 1)}{h_1(K_1 l_1 h_1 + 1)}, \tag{23}$$

then there exists a stable limit cycle around the fixed point E^2, see Hofbauer and Sigmund (1988). If either

$$m > \frac{e_1 K_1 l_1}{1 + h_1 K_1 l_1} \tag{24}$$

or

$$m > \frac{e_1}{h_1}, \tag{25}$$

then the equilibrium $(K_1, K_2, 0)$ of (19) is globally stable, see Hofbauer and Sigmund (1988).

Equilibrium E^2 belongs to G^2 if it is strictly positive and

$$x_1^* < x_1^2,$$

which gives

$$\frac{e_2}{h_2} < m < \frac{e_1 K_1 l_1}{1 + h_1 K_1 l_1}. \tag{26}$$

Similarly, $E^1 \in G^1$ if (20) holds and

$$m < \frac{e_2}{h_2}. \tag{27}$$

Thus we see that the situation where $E^1 \in G^1$, $E^2 \in G^2$ cannot occur, i.e., either $E^1, E^2 \in G^1$ or $E^1, E^2 \in G^2$. We do not consider the case when $E^1, E^2 \in G^0$ since by a negligible change in parameters this situation may be excluded.

Now we study the behavior of a trajectory of (19) when it falls on G^0. On G^0

$$\langle n, f_1 \rangle > 0 \qquad \text{if} \quad x_3 < \frac{a_1}{l_1}(1 + h_1 l_1 x_1^* + h_2 l_2 x_2)\left(1 - \frac{x_1^*}{K_1}\right)$$

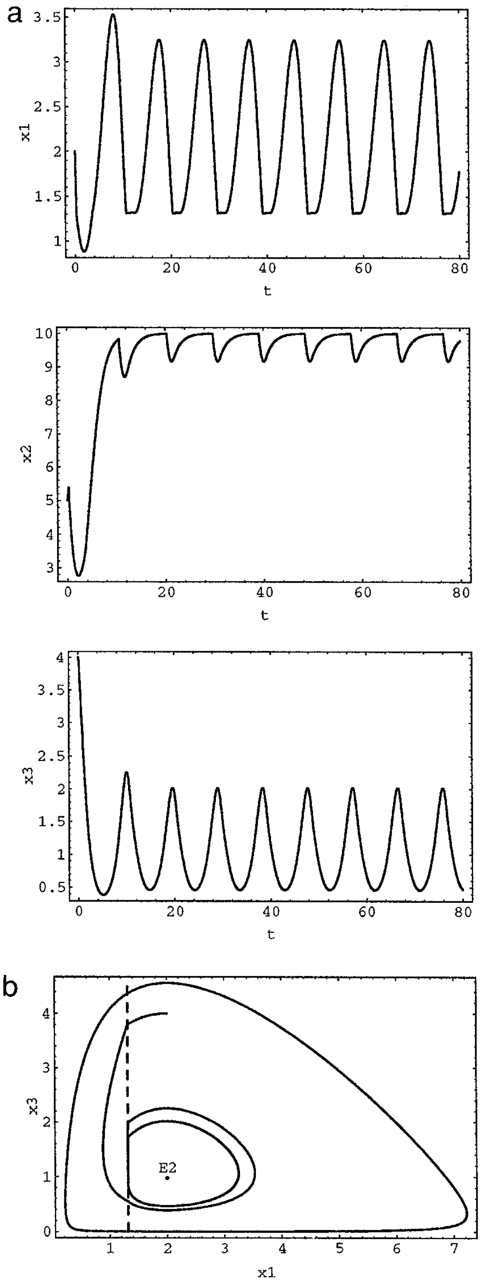

FIG. 2. A solution of (19) plotted in time domain (a) and in the (x_1, x_3) plane (b). Predators follow the optimal diet choice and partial preferences do appear when the solution moves in G^0 (denoted by the dashed line). The large cycle in (b) is the limit cycle for system described by (31). Thus optimal diet choice may reduce fluctuations in population densities. Parameters: $a_1 = 1$, $a_2 = 1$, $e_1 = 2.6$, $e_2 = 1$, $h_1 = 0.4$, $h_2 = 0.3$, $l_1 = 2$, $l_2 = 2$, $K_1 = 8$, $K_2 = 10$, $m = 4$.

and

$$\langle n, f_2 \rangle > 0 \qquad \text{if} \quad x_3 < \frac{a_1}{l_1}(1 + h_1 l_1 x_1^*)\left(1 - \frac{x_1^*}{K_1}\right).$$

Thus we see that if $K_1 < x_1^*$, then $\langle n, f_1 \rangle < 0$ and $\langle n, f_2 \rangle < 0$. Under this assumption trajectories cross G^0 only in direction from G^2 to G^1. Once a trajectory enters G^1, it will stay there forever. The diet of a predator will consists of both prey types, and the probability of attacking the second prey upon encounter will be 1.

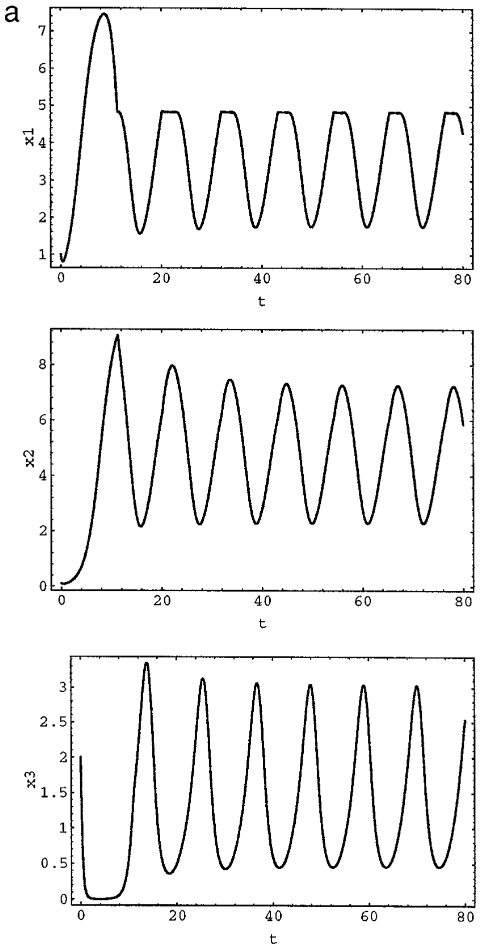

FIG. 3. In this figure the optimal diet choice destabilizes population dynamics. If predators feed only on the more profitable prey type (b), system (31) has a stable equilibrium. However, if predators follow the optimal diet choice described by (19) (a) (c), a limit cycle appears. Partial preferences do appear when the solution moves along G^0 (denoted by the dashed line). Parameters: $a_1 = 1$, $a_2 = 1$, $e_1 = 2.6$, $e_2 = 3$, $h_1 = 0.2$, $h_2 = 0.35$, $l_1 = 2$, $l_2 = 2$, $K_1 = 8$, $K_2 = 10$, $m = 8$.

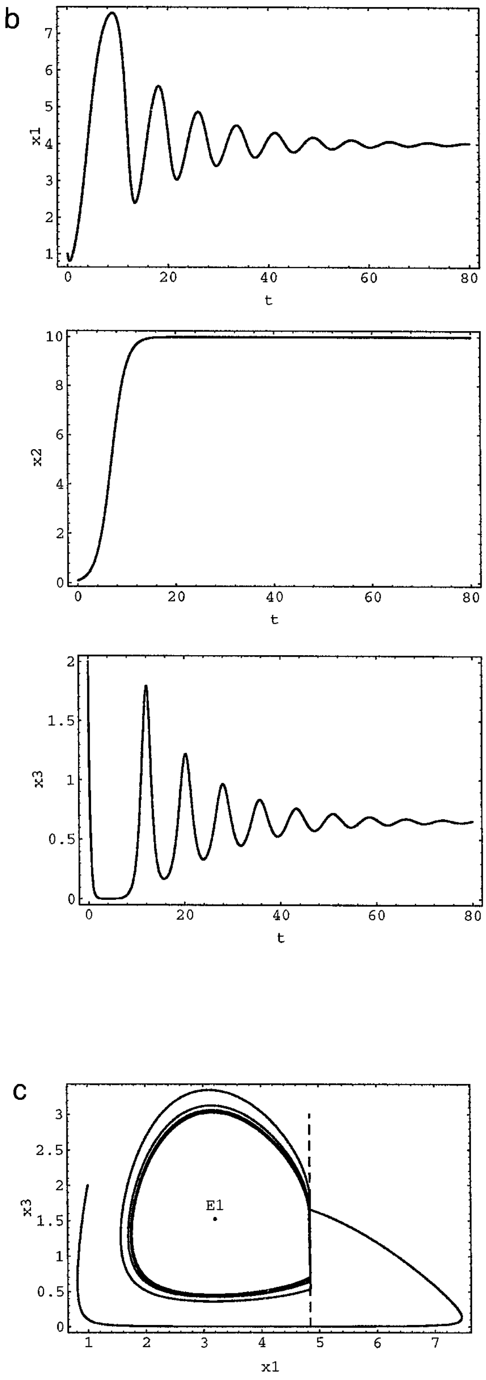

FIG. 3—*Continued*

In what follows we assume $x_1^* < K_1$. Then following (18) we get that if

$$\frac{a_1}{l_1}(1+h_1l_1x_1^*)\left(1-\frac{x_1^*}{K_1}\right) < x_3 < \frac{a_1}{l_1}(1+h_1l_1x_1^*+h_2l_2x_2)\left(1-\frac{x_1^*}{K_1}\right), \tag{28}$$

then the trajectory will move along G^0 and partial preferences do arise. If

$$x_3 > \frac{a_1}{l_1}(1+h_1l_1x_1^*+h_2l_2x_2)\left(1-\frac{x_1^*}{K_1}\right), \tag{29}$$

then the trajectory will cross G^0 in direction from G^2 to G^1, and if

$$x_3 < \frac{a_1}{l_1}(1+h_1l_1x_1^*)\left(1-\frac{x_1^*}{K_1}\right), \tag{30}$$

then it will cross G^0 in direction from G^1 to G^2.

In order to study the qualitative behavior of (19) let us consider the case when $E^2 \in G^2$. Let us consider a system in which predators specialize on the more profitable prey type only, i.e.,

$$\begin{aligned} x_1' &= a_1x_1\left(1-\frac{x_1}{K_1}\right) - \frac{l_1x_1x_3}{1+h_1l_1x_1} \\ x_2' &= a_2x_2\left(1-\frac{x_2}{K_2}\right) \\ x_3' &= \frac{e_1l_1x_1x_3}{1+h_1l_1x_1} - mx_3. \end{aligned} \tag{31}$$

If E^2 is stable for differential equation (31), then also every solution of (19) which starts in G^2 close to E^2 will converge to E^2 since (19) coincides with (31) in G^2. If E^2 is unstable for (31) and a stable limit cycle exists for (31), then the behavior of (19) depends on the position of this limit cycle with respect to G^0. If the limit cycle intersects G^0, then partial preferences may appear, see Fig. 2. In Fig. 2b the large cycle is the limit cycle of (31), while the smaller cycle corresponds to (19). In fact, the amplitude of the limit cycle of (19) decreases as the distance of E^2 from G^0 decreases. In Fig. 2b we see the qualitative behavior of solutions of (19) on G^0. At the first moment when the solution of (19) falls on G^0 the density of the population of predators is high, i.e., (29) holds and the system moves from G^2 to G^1, i.e., predators include the less convenient prey into their diet. When the solution falls on G^0 for the second time, the density of predators is low, (30) holds, and the predators will switch to feed only on the more convenient prey type. However, when the trajectory falls the next time on G^0, (28) is satisfied and for a predator the optimal strategy is to include the second prey into its diet only with a certain probability which is strictly between zero and one. This corresponds to the movement of the system along G^0 where partial preferences arise. However, after some time, condition (30) will be satisfied and the system will leave G^0 to G^2. A new limit cycle appears. Since this limit cycles is smaller than the limit cycle for predators feeding only on the more convenient prey, we may say that the optimal diet choice may lead to partial stabilization of the system.

Now we consider the case when $E^2 \in G^1$. Although E^2 still may be the stable equilibrium for (31), see Fig. 3b, it may not be stable for (19), see Figs. 3a and 3c. In this case optimal foraging destabilizes the system, which would be stable for specialized predators feeding only on the more profitable prey. In Fig. 3c we see that the limit cycle belongs partly to G^0 and partial preferences do appear. It may also happen that for some other parameters the limit cycle belongs to G^1 only, i.e., there may be no partial preferences or E^1 may be a stable equilibrium.

We may also be interested if the optimal diet choice may stabilize an unstable system. Namely, assuming that E^2 is un unstable equilibrium for (31) we may be interested if, when foraging optimally, this equilibrium will belong to G^1 and E^1 will be stable. In Appendix E we prove that this cannot happen.

Another question we may address is that of whether optimal foraging may lead to the coexistence of both prey and predator populations, and thus to *permanence*, see Hofbauer and Sigmund (1988). We show that this is indeed so. Let us consider predators which specialize on the most profitable prey type. The dynamics of such a system is described by (31). Let us assume that (24) holds, which means that (31) has a stable

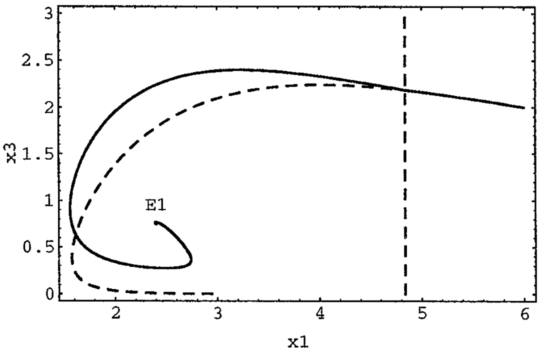

Fig. 4. Solutions of (19) (thick line) and of (31) (dashed line) plotted in the (x_1, x_3) plane. In this figure, (19) has a stable equilibrium with all components positive, whereas (31) has the stable equilibrium $(K_1, K_2, 0)$. Thus optimal foraging may lead to permanence of predator–prey systems. Parameters: $a_1 = 1$, $a_2 = 1$, $e_1 = 2.6$, $e_2 = 3$, $h_1 = 0.2$, $h_2 = 0.3$, $l_1 = 2$, $l_2 = 2$, $K_1 = 3$, $K_2 = 10$, $m = 8$.

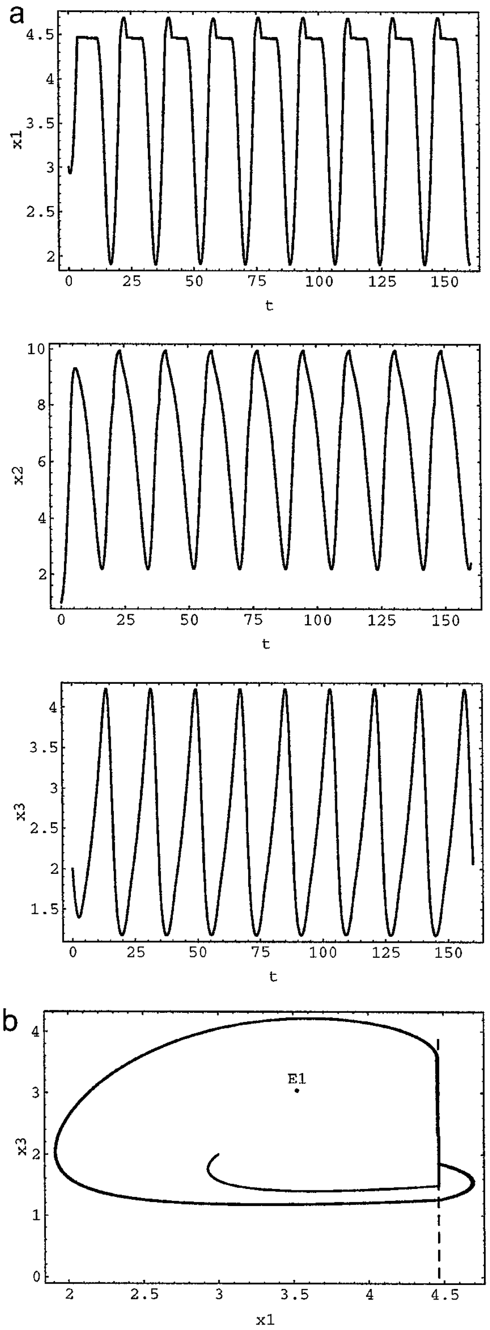

FIG. 5. A solution of (19) plotted in time domain (a) and in (x_1, x_3) space (b). Following the optimal diet choice, predators switch periodically between being specialists or generalists. Moreover, partial preferences do appear. Parameters: $a_1 = 0.7$, $a_2 = 2.2$, $e_1 = 2.6$, $e_2 = 1.25$, $h_1 = 0.4$, $h_2 = 0.3$, $l_1 = 1$, $l_2 = 2$, $K_1 = 20$, $K_2 = 10$, $m = 4$.

equilibrium $(K_1, K_2, 0)$. Moreover, let $K_1 < x_1^*$. We showed that under this condition every solution of (19) will reach G^1 and it will stay there. If $E^1 \in G^1$ is a stable equilibrium for (19) in G^1 or, more generally, if dynamics (19) in G^1 is permanent we get permanence of the whole system, see Fig. 4.

In general (i.e., $a_1 \neq a_2$, $l_1 \neq l_2$), the dynamics of (19) may be quite complex; one simulation is given in Fig. 5, where we see that the limit cycle belongs both to G^1 and G^2, and partial preferences do arise. Let us note that if partial preferences do appear we may compute p_2 using (17):

$$p_2(x_1^*, x_2, x_3) = \frac{e_1}{l_2 x_2(e_2 h_1 - e_1 h_2)} + \frac{K_1 l_1^2 x_3(e_2 h_1 - e_1 h_2)}{a_1 l_2 h_2 x_2(e_2 + l_1 K_1(e_2 h_1 - e_1 h_2))}. \tag{32}$$

DISCUSSION

In this paper we linked the theory of optimal foraging for a single individual with the population dynamics. The densities of populations are described by a control system where the meaning of controls is to model preferences of predators to feed on various types of prey. The controls were chosen in order to maximize energy gain of a single average predator. We saw that, in addition to the strategies which are given by zero–one rule (i.e., either to include second prey in diet or not), partial preferences may arise. This means that the more profitable prey is always included in a diet but the probability of feeding on the less profitable prey may be strictly between zero and one.

It is easy to see that in the present dynamic setting, simplistic statements concerning *generalist* or *specialist* behavior of foragers may be misleading. We saw that depending on the parameters of the model and on the initial condition predators may behave either as generalists or as specialists, or they may periodically switch between being generalists or specialists.

The effect of optimal foraging on stability of predator–prey system (19) is quite complex. We saw that a system consisting of predators which specialize on the more profitable prey only may be stable, while the same system with predators following the rule of the optimal diet choice may not have a stable equilibrium, see Fig. 3. Moreover, we proved that if the growth rate of prey populations is same and $l_1 = l_2$, then an unstable system consisting of predators which specialize on the more profitable prey only cannot be stabilized by including the second prey into the diet. However, we saw that the optimal diet choice may have a partially stabilizing effect, in the sense that the large fluctuations in the system where predators specialize only on the more profitable prey are reduced in the system where predators follow the optimal diet rule, see Fig. 2. If the distance of E^2 from G^0 is small, then the resulting fluctuations will also be small; thus from the practical point of view the system may be considered to be stabilized. We also showed that optimal foraging may lead to permanence of the predator–prey system, i.e., to coexistence of both prey and predator populations, see Fig. 4.

The formula for partial preferences (32) also gives some clue as to how any reasonable approximation of the step function p_2 should be constructed. Namely, any approximation should agree with (32) on the part of the set G^0 where partial preferences do occur. However, this is often not so, since typically the approximations chosen depend only on x_1, x_2 (Murdoch and Stewart-Oaten, 1975; Holt, 1983; Fryxell and Lundberg, 1994) and not on x_3 as formula (32) suggests. In general, we may study the effect of optimal foraging on the response function to prey 1 and prey 2. In classical models of predator–prey interactions where predators are assumed to attack both types of prey at random, the response to prey i is

$$\frac{c_i x_i}{1 + c_1 h_1 x_1 + c_2 h_2 x_2}, \tag{33}$$

see Abrams (1990). The constants c_i are called *attack rates*. The above functional response is obtained from (7) if the probability that a predator will attack prey type i upon an encouter is constant and $c_i = p_i l_i$. When predators forage optimally, it turns out that the attack rate $c_1 = l_1$ is constant, since probability of attacking the more profitable prey type is one, but c_2 becomes a function of densities of both prey types and predators. If the density of the first prey type x_1 is below the threshold x_1^* given by (12), then $c_2 = l_2$, and if $x_1 > x_1^*$, then $c_2 = 0$. Thus in G^1 and G^2 the attack rate c_2 depends only on the density of the more profitable prey and the general shape of the Holling second type functional response is kept. However, if partial preferences appear, then due to (32) the attack rate c_2 depends not only on the densities of prey types but also on the density of the population of predators. This leads to *higher order interactions*, see Werner (1992), which alter the shape of the response function. Thus along G^0 where partial preferences do appear the response function (33) to prey 1 becomes

$$\frac{a_1 e_2(-e_2 + K_1 l_1(e_1 h_2 - e_2 h_1))}{K_1 \lambda_1^2 x_3 (e_1 h_2 - e_2 h_1)^2},$$

and the response function to prey 2 is

$$\frac{a_1 e_1 h_2(e_2 + (e_2 h_1 - e_1 h_2)\, K_1 l_1) + x_3 K_1 l_1^2 (e_2 h_1 - e_1 h_2)^2}{h_2 K_1 l_1^2 x_3 (e_1 h_2 - e_2 h_1)^2}$$

The above response functions are not of Holling second type. The effect of various aspects of the optimal foraging on the shape of the response function was studied in Abrams (1982, 1984, 1990), where it was argued that optimal foraging changes the shape of the Holling second type response function. The results contained in the present paper support this idea. The approach used by Abrams is based on maximization of a fitness function with respect to attack rates. However, we saw that in the case when fitness function is given by the instantaneous growth rate, the point at which fitness function is maximized may not be uniquely determined. This nonuniqueness occurs when $x_1 = x_1^*$. Nevertheless, the present approach still allows to derive the shape of the response function.

The above-presented model is, of course, an idealization of real systems. First, working with average predators we neglect variance between individuals. Second, we assumed that the system is at each instant in an optimal state, i.e., there was no delay in decision of predators which would appear necessarily in real systems.

APPENDIX A: DERIVATION OF DYNAMICS (3)

Let us consider a predator during a given time T units of time. We denote by T_s the searching time and by T_h the handling time. We have $T = T_s + T_h$. Since

$$T_h = h_1 \lambda_1 p_1 T_s + h_2 \lambda_2 p_2 T_s$$

it follows that

$$T_s = \frac{T}{1 + h_1 \lambda_1 p_1 + h_2 \lambda_2 p_2}. \tag{34}$$

Thus

$$\begin{aligned}
x_1(t+T) - x_1(t) &= x_1(t)\, g_1(x_1(t), x_2(t))\, T - \lambda_1 p_1(t)\, x_3(t)\, T_s \\
x_2(t+T) - x_2(t) &= x_2(t)\, g_2(x_1(t), x_2(t))\, T - \lambda_2 p_2(t)\, x_3(t)\, T_s \\
x_3(t+T) - x_3(t) &= e_1 \lambda_1 p_1(t)\, x_3(t)\, T_s + e_2 \lambda_2 p_2(t)\, x_3(t)\, T_s - m x_3(t)\, T.
\end{aligned}$$

Using (34), dividing by T, and taking the limit for $T \to 0$ gives system (3).

APPENDIX B: DERIVATION OF OPTIMAL STRATEGY

Deriving function R we get

$$\frac{\partial R}{\partial p_1} = \frac{l_1 x_1 (e_1 + p_2 l_2 x_2 (e_1 h_2 - e_2 h_1))}{(1 + p_1 l_1 x_1 h_1 + p_2 l_2 x_2 h_2)^2},$$

and

$$\frac{\partial R}{\partial p_2}=\frac{l_2x_2(e_2-p_1l_1x_1(e_1h_2-e_2h_1))}{(1+p_1l_1x_1h_1+p_2l_2x_2h_2)^2}.$$

Thus we see that the sign of $\partial R/\partial p_1$ does not depend on p_2 and similarly for $\partial R/\partial p_2$. We assume that $e_1/h_1>e_2/h_2$, and thus $e_1h_2-e_2h_1>0$. Since p_2 is always nonnegative, we see that for all p_1, p_2

$$\frac{\partial R}{\partial p_1}>0.$$

Thus R is maximized for $p_1=1$ and, consequently, the predator will always forage on the first prey. Similarly, $\partial R/\partial p_2>0$ if

$$p_1<\frac{e_2}{l_1x_1(e_1h_2-e_2h_1)}.$$

Since $p_1=1$, this means that $p_2=1$ if

$$x_1<\frac{e_2}{l_1(e_1h_2-e_2h_1)}$$

and $p_2=0$ if

$$x_1>\frac{e_2}{l_1(e_1h_2-e_2h_1)}.$$

If

$$x_1=\frac{e_2}{l_1(e_1h_2-e_2h_1)},$$

then $\partial R/\partial p_2=0$ and p_2 cannot be determined. Thus p_2 as a function of x_1 is a step function.

APPENDIX C: EXISTENCE AND UNIQUENESS OF SOLUTIONS OF (13)

Let $n=(1,0,0)$ denote the normal vector to G^0, oriented from G^1 toward G^2. Denoting by $f_1(x_1,x_2,x_3)$ the right-hand side of (14) and by $f_2(x_1,x_2,x_3)$ the right-hand side of (15) we get

$$\langle n, f_1(x_1^*,x_2,x_3)\rangle=\langle n, f_2(x_1^*,x_2,x_3)\rangle+\frac{l_1l_2h_2x_1^*x_2x_3}{(1+l_1h_1x_1^*+l_2h_2x_2)(1+l_1h_1x_1^*)}.$$

Since $e_1h_2 > e_2h_1$ it follows $x_1^* > 0$ and either

$$\langle n, f_2 \rangle \geqslant 0$$

and consequently $\langle n, f_1 \rangle > 0$ or

$$\langle n, f_2 \rangle < 0.$$

We see that either $\langle n, f_1 \rangle > 0$ or $\langle n, f_2 \rangle < 0$. Let f denote the right-hand side of (13). Then for every $p_2 \in S(x_1, x_2)$,

$$\frac{d}{dp_2}\langle n, f(x) \rangle = \frac{l_1 l_2 h_2 x_1 x_2 x_3}{(1 + h_1 l_1 x_1 + h_2 l_2 p_2 x_2)^2} \neq 0.$$

These are the conditions that ensure existence and uniqueness of trajectories of (13), see Theorem 3, p. 113 in Filippov (1988).

APPENDIX D: Stability Analysis of E^1

The eigenvalues for E^1 are

$$\begin{aligned}
\lambda_1 &= \frac{a_2 m}{l_2(m(h_1K_1 + h_2K_2) - e_1K_1 - e_2K_2)} \\
\lambda_2 &= \frac{a_2B - \sqrt{(a_2B)^2 + 4a_2AC}}{2A} \\
\lambda_3 &= \frac{a_2B + \sqrt{(a_2B)^2 + 4a_2AC}}{2A},
\end{aligned}$$

where

$$\begin{aligned}
A &= l_2(e_1K_1 + e_2K_2)(e_1K_1 + e_2K_2 - mh_1K_1 - mh_2K_2) \\
B &= -m((e_1K_1 + e_2K_2)(1 - h_1K_1l_2 - h_2K_2l_2) \\
&\quad + m(h_1K_1 + h_2K_2)(1 + h_1K_1l_2 + h_2K_2l_2)) \\
C &= m(-e_1K_1l_2 - e_2K_2l_2 + m + h_1K_1l_2m + h_2K_2l_2m) \\
&\quad \times (e_1K_1 + e_2K_2 - mh_1K_1 - mh_2K_2).
\end{aligned}$$

Equilibrium E^1 is locally asymptotically stable if all real parts of its eigenvalues are negative. Thus $\lambda_1 < 0$ if

$$m < \frac{e_1K_1 + e_2K_2}{h_1K_1 + h_2K_2}. \tag{35}$$

Let us assume that $(a_2 B)^2 + 4a_2 AC < 0$, i.e., λ_2, λ_3 are complex conjugates. This happens if

$$a_2 < -\frac{4AC}{B^2}. \tag{36}$$

Since we assume $a_2 > 0$ the above condition can be satisfied only if $AC < 0$, i.e.,

$$m < \frac{e_1 K_1 l_2 + e_2 K_2 l_2}{1 + h_1 K_1 l_2 + h_2 K_2 l_2}.$$

Due to (35), $A > 0$, and thus $B/(2A) < 0$ if $B < 0$, i.e.,

$$m > \frac{(e_1 K_1 + e_2 K_2)(h_1 K_1 l_2 + h_2 K_2 l_2 - 1)}{(h_1 K_1 + h_2 K_2)(h_1 K_1 l_2 + h_2 K_2 l_2 + 1)}.$$

Since

$$\frac{e_1 K_1 + e_2 K_2}{h_1 K_1 + h_2 K_2} > \frac{e_1 K_1 l_2 + e_2 K_2 l_2}{1 + h_1 K_1 l_2 + h_2 K_2 l_2}$$

and

$$\frac{e_1 K_1 l_2 + e_2 K_2 l_2}{1 + h_1 K_1 l_2 + h_2 K_2 l_2} > \frac{(e_1 K_1 + e_2 K_2)(h_1 K_1 l_2 + h_2 K_2 l_2 - 1)}{(h_1 K_1 + h_2 K_2)(h_1 K_1 l_2 + h_2 K_2 l_2 + 1)},$$

we get that if

$$\frac{(h_1 K_1 l_2 + h_2 K_2 l_2 - 1)(e_1 K_1 + e_2 K_2)}{(h_1 K_1 l_2 + h_2 K_2 l_2 + 1)(h_1 K_1 + h_2 K_2)} < m < \frac{e_1 K_1 l_2 + e_2 K_2 l_2}{1 + h_1 K_1 l_2 + h_2 K_2 l_2} \tag{37}$$

and (36) holds then the real parts of eigenvalues are negative.

Now let us consider the case when $(a_2 B)^2 + 4a_2 AC \geqslant 0$. This happens if

$$a_2 \geqslant -\frac{4AC}{B^2}. \tag{38}$$

Under the condition (35), $\lambda_3 \geqslant \lambda_2$. Then $\lambda_3 < 0$ if

$$a_2 B + \sqrt{(a_2 B)^2 + 4a_2 AC} < 0.$$

This may happen if $B < 0$ and $AC < 0$. It follows that all eigenvalues are negative if (38) together with (37) is satisfied. Thus for all $a_2 > 0$ we get that E^1 is locally stable if (37) holds.

The eigenvalues corresponding to equilibrium $(K_1, K_2, 0)$ of (19) are

$$\left\{-a_1, -a_2, \frac{e_1K_1l_2+e_2K_2l_2-m(1+h_1K_1l_2+h_2K_2l_2)}{1+h_1K_1l_2+h_2K_2l_2}\right\}.$$

This equilibrium is locally stable if

$$m>\frac{e_1K_1l_2+e_2K_2l_2}{1+h_1K_1l_2+h_2K_2l_2}.$$

APPENDIX E: STABILITY OF E^1 WHEN E^2 IS UNSTABLE

We prove that if E^2 is unstable for (31) and there exists a limit cycle around E^2, then E^1 cannot be stable for (19) if it belongs to G^1. The existence of a limit cycle for (31) is equivalent to (23) and the local stability of $E^1 \in G^1$ is equivalent to (21). Since $E^1 \in G^1$, it follows from (21) and (27)

$$\frac{(e_1K_1+e_2K_2)(h_1K_1l_2+h_2K_2l_2-1)}{(h_1K_1+h_2K_2)(h_1K_1l_2+h_2K_2l_2+1)}<\frac{e_2}{h_2},$$

which is equivalent to

$$l_2<\frac{e_2h_1K_1+e_1h_2K_1+2e_2h_2K_2}{K_1(e_1h_2-e_2h_1)(h_1K_1+h_2K_2)}. \tag{39}$$

From (23) and (21) we get

$$\frac{(e_1K_1+e_2K_2)(h_1K_1l_2+h_2K_2l_2-1)}{(h_1K_1+h_2K_2)(h_1K_1l_2+h_2K_2l_2+1)}<\frac{e_1(K_1h_1l_2-1)}{h_1(K_1l_2h_1+1)}.$$

Since we assume $l_2>0$ this gives

$$l_2>\frac{D+\sqrt{4h_1K_1(e_1h_2-e_2h_1)^2\,(h_1K_1+h_2K_2)+D^2}}{2h_1K_1(e_1h_2-e_2h_1)(h_1K_1+h_2K_2)}, \tag{40}$$

where

$$D=2e_1h_1h_2K_1+e_1h_2^2K_2+e_2h_1h_2K_2.$$

After some algebra we get that (39), (40) cannot hold simultaneously and E^1 cannot be stable.

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