

# A Mechanistic Model for Partial Preferences

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**Classic prey optimal foraging model assumes that individual predators are globally omniscient; that is, they have exact knowledge of prey population densities in the environment. This study examines a spatially explicit individual-based model of a one-predator two-prey system where individual predators are assumed to be omniscient only locally, i.e., to know prey population densities only in the range of their perception. Due to local variations in prey numbers, the probability of acceptance of less profitable prey shifts from the zero–one rule to a gradually decreasing function, for which an explicit formula is derived, giving way to partial preferences. A corresponding predator functional response to more profitable prey is shown to have a sigmoid-like form.** © 2000 Academic Press

**Key Words:** diet composition; functional response; individual-based model; limited perception; optimal foraging.

## 1. INTRODUCTION

Optimal foraging theory (MacArthur and Pianka, 1966; Emlen, 1966; Schoener, 1971; Pulliam, 1974; Werner and Hall, 1974; Charnov, 1976; Stephens and Krebs, 1986; Schmitz, 1997) aims to explain diet composition of animals from a behavioural perspective. It assumes that foraging behaviour plays a considerable role in predator fitness and, in its classic formulation, that this fitness is proportional to the average rate of net energy gain during foraging. In fine-grained environments, one important prediction is the so called “zero–one rule”: a prey type should be either always attacked or always ignored upon encounter with a predator.

In experiments on diet composition by consumers, however, partial preferences for prey are typically observed; that is, a prey type is sometimes attacked and sometimes ignored when encountered (Werner and Hall, 1974; Davies, 1977; Goss-Custard, 1977; Krebs *et al.*, 1977; Mittelbach, 1981; Rechten *et al.*, 1983; Jones, 1990). Partial preferences may be seen by instantly observing food decisions of a group of predators (partial preferences of a population of individuals) and/or by observing a

single predator’s behaviour in a series of its food decisions (partial preferences of individuals). Various mechanisms have been proposed to explain partial preferences within the energy rate maximization models. They range from incorrect classification of prey and sampling by predators (Krebs *et al.*, 1977; Rechten *et al.*, 1983), through prey crypsis (Ericksen *et al.*, 1980), estimation of encounter rates with prey by predators (McNamara and Houston, 1987; Hirvonen *et al.*, 1999), to a limited memory capacity of predators (Mangel and Roitberg, 1989; Bélisle and Cresswell, 1997); see McNamara and Houston (1987), Mitchell (1989), and Bélisle and Cresswell (1997) for more detailed lists.

The classic prey optimal foraging model (Pulliam, 1974; Werner and Hall, 1974; Charnov, 1976) assumes, among other things, that predators are omniscient; that is, they have exact knowledge of prey densities in the environment at each time instant, a feature that is quite unrealistic. McNamara and Houston (1987) and Hirvonen *et al.* (1999) replaced this assumption by the ability of predators to estimate prey densities from the actual prey encounter histories of individual predators. Mangel and Roitberg (1989) addressed the issue of partial preferences in the host–parasite framework and

assumed that parasites assessed the densities of parasitized and unparasitized hosts by the time since last oviposition and the fraction of parasitized hosts in a number of previous encounters. In this article, we replace the assumption of predator omniscience by a weaker assumption of local omniscience: we suppose that any predator has exact knowledge of prey densities only in an immediate neighbourhood of its spatial location. This local omniscience can be due to perceptual limitations of predators, e.g., a limited detection range of pheromones released by prey, or limited visual or auditory ranges of predators (Rice, 1983; Kindvall *et al.*, 1998); it results in partial preferences for which an analytical formula can be derived. The change from the zero–one rule to partial preferences is rather important from the viewpoint of population dynamics because it modifies the predator functional response which, in turn, may have a strong impact on dynamical properties of the one-predator two-prey system (Fryxell and Lundberg, 1994; Křivan, 1996; Křivan and Sikder, 1999).

In the following section we formulate a spatially explicit individual-based model (IBM) of predators foraging on two prey types, using the methodology introduced by de Roos *et al.* (1991), McCauley *et al.* (1993), and Wilson *et al.* (1993). We then re-derive the classic prey choice rule in the IBM framework and derive a new prey choice rule incorporating a mechanism of limited perception by predators. The main advantage of the spatially explicit individual-based approach is that the model tracks every single individual's location in the environment, thus enabling us to define perception neighbourhoods readily for individual predators. We show that under such perceptual limitations, the classic zero–one rule describing the foraging strategy of predators for less profitable prey shifts to a gradually decreasing function, giving way to partial preferences.

## 2. MODEL

We begin with a formulation of a spatially explicit, one-predator two-prey, individual-based model, using the methodology introduced by de Roos *et al.* (1991), McCauley *et al.* (1993), and Wilson *et al.* (1993). The spatially homogeneous environment is modelled as a lattice of square sites. Population abundances are limited by the lattice size as we allow at most one prey individual (regardless of its type) and one predator individual to occupy any single site. Let time run in discrete steps. We assume that the numbers of prey 1 individuals ( $x_1$ ), prey 2 individuals ( $x_2$ ), and predators ( $y$ ) do not change with

time. This is the standard assumption “when we want to look at the instantaneous behaviour under a range of conditions” (Murdoch and Oaten, 1975). Moreover, we assume that prey are randomly distributed on the lattice at each time step, respecting the above constraint.

At each time step, the lattice sites are updated simultaneously according to the following rules. We assume that any predator is either searching for prey or handling prey. At the beginning of each time step any single predator may find itself in one of three situations: it can share the lattice site with a prey 1 individual or with a prey 2 individual or the site can be free of prey. For either of the first two cases, predator behaviour with respect to attacking prey has to be specified: if the predator encounters (i.e., shares the site with) a prey  $i = 1, 2$  individual, it decides to attack that prey with a probability  $p_i$ , which may vary with time. If the predator decides to attack the prey  $i$  individual, the attack is successful with a probability  $P_a^i$ . Following a successful attack, the predator handles prey  $i$  for  $T_h^i$  time steps. The handled prey cannot be attacked by another predator. When handling a prey item, the predator can neither attack another prey individual nor move. There is no interference between predators in our model.

Before we address optimal foraging issues, we derive the predator diet composition and functional response induced by the individual-based model just defined. Consider a single predator in a sufficiently large series of food decisions. The fraction of prey  $i$  individuals from all prey it captures in the series can be well approximated by the formula

$$\frac{x_i}{S} p_i P_a^i \bigg/ \left( \frac{x_1}{S} p_1 P_a^1 + \frac{x_2}{S} p_2 P_a^2 \right), \quad (1)$$

where  $S$  is the number of lattice sites; see Appendix for a detailed derivation. The predator functional response to prey  $i$ , defined here as the number of captured prey  $i$  individuals per predator per time step, can be analogously shown to approach

$$y_s \frac{x_i}{S} p_i P_a^i \bigg/ y \quad (2)$$

with the number of food decisions, where  $y_s$  the mean number of searching predators and  $y$  the total (fixed) number of predators. Following Wilson (1998), the ratio  $y_s/y$  can be approximated sufficiently by the expression  $1/(1 + T_h^{1/x_1} p_1 P_a^1 + T_h^{2/x_2} p_2 P_a^2)$ . The (approximate)

predator functional response to prey  $i = 1, 2$  thus turns out to be

$$\frac{\frac{x_i}{S} p_i P_a^i}{1 + T_h^1 \frac{x_1}{S} p_1 P_a^1 + T_h^2 \frac{x_2}{S} p_2 P_a^2}. \quad (3)$$

We note that the expressions (1) and (3) can also be derived from the point of view of a number of predators considered in a single time step; see Appendix. In the following section, plausible values for the decision probabilities  $p_i$  are derived.

### 3. OPTIMAL FORAGING

For two prey types, the classic prey optimal foraging model (Pulliam, 1974; Werner and Hall, 1974; Charnov, 1976) predicts that more profitable prey should always be attacked by predators upon encounter. Less profitable prey should be attacked upon each encounter, provided that the density of more profitable prey is below a certain threshold density. Above this threshold density, less profitable prey should be completely excluded from the predator optimal diet. This result was termed the “zero-one rule” by Stephens and Krebs (1986) and the “none-or-all” rule by McNamara and Houston (1987). In this section, we first re-derive this rule in the adopted IBM framework. We then derive a new prey choice rule that stems from the assumption that predators are able to perceive prey numbers only locally.

#### Exact Knowledge by Predators

According to evolutionary biology, every individual is supposed to maximize its fitness. Classic optimal foraging theory assumes that the fitness of predators is proportional to the average rate of net energy gain during foraging,

$$\frac{E}{T_s + T_h}, \quad (4)$$

where  $T_s$  is, in the context of our IBM formulation, the number of time steps spent searching,  $T_h$  stands for the number of time steps spent handling prey items, and  $E$  is the net amount of energy gained by the predator during the total foraging time  $T_s + T_h$ . Given the stochastic character of the IBM, the rate (4) is clearly a random

variable. For a sufficiently large number of consumed prey items (hence large foraging time) and a sufficiently large lattice size, the mean value of (4) approaches

$$R(p_1, p_2) = \frac{E_1 \frac{x_1}{S} p_1 P_a^1 + E_2 \frac{x_2}{S} p_2 P_a^2}{1 + T_h^1 \frac{x_1}{S} p_1 P_a^1 + T_h^2 \frac{x_2}{S} p_2 P_a^2}, \quad (5)$$

whereas its variance tends to zero (Stephens and Charnov, 1982; Stephens and Krebs, 1986).  $E_i$  is the net amount of energy predators gain from ingesting one prey  $i = 1, 2$  item. Therefore, we adopt the function (5) as the quantity predators tend to maximize with respect to the decision probabilities  $p_1$  and  $p_2$ . Assuming that prey 1 is more profitable than prey 2 (that is,  $E_1/T_h^1 > E_2/T_h^2$ ), the optimal strategy of a predator is to always attack prey 1 upon encounter ( $p_1 = 1$ ), independent of prey 1 and prey 2 population numbers, and to decide as

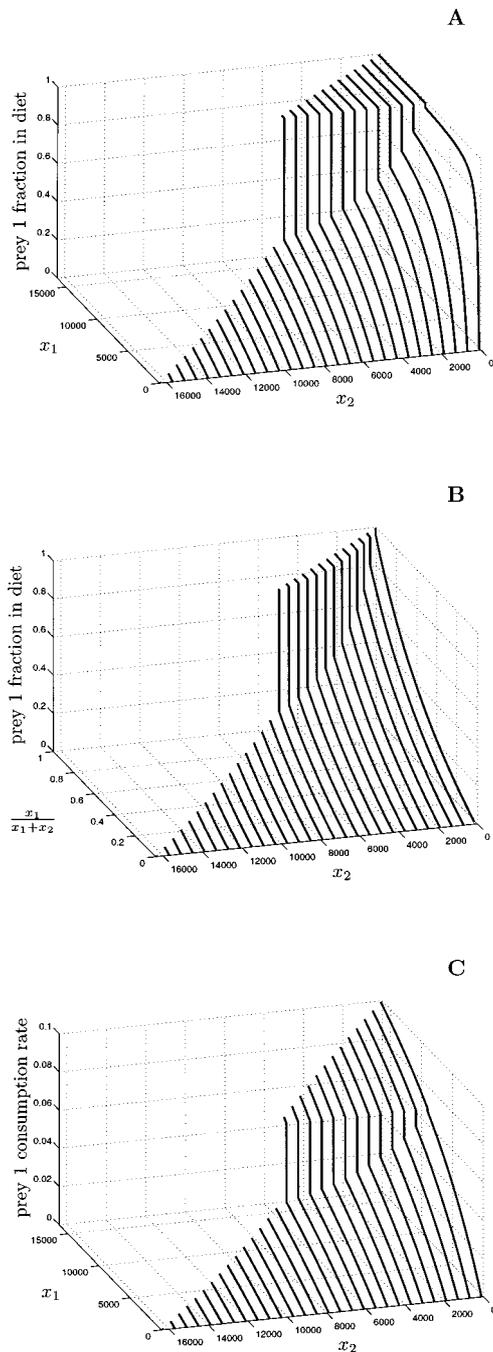
$$p_2(x_1) = \begin{cases} 1 & \text{if } x_1 < L_1, \\ 0 & \text{if } x_1 > L_1 \end{cases}, \quad (6)$$

upon encounter with prey 2, where

$$L_1 = S \frac{E_2}{P_a^1(E_1 T_h^2 - E_2 T_h^1)}; \quad (7)$$

see Stephens and Krebs (1986) or Křivan (1996) for a detailed derivation. The case  $x_1 = L_1$  is not considered here as the prey 1 abundance  $x_1$  can take only integer values within the IBM framework, limited by 0 from below and by the lattice size  $S$  from above; consequently, we can always make the threshold value  $L_1$  different from all the admissible values of  $x_1$  by a negligible change in model parameters. (Within the framework of ordinary differential equations, however, population densities may acquire any non-negative real value and such a case has to be treated properly (Křivan, 1996).)

The effects of the above optimal foraging strategy on the predator diet composition and functional response are shown in Fig. 1. Figure 1A plots the prey 1 fraction in the diet [Eq. (1)] for optimally foraging predators (that is, with  $p_1 = 1$  and  $p_2$  specified by (6)) against the prey 1 population abundance  $x_1$ , Fig. 1B plots the same quantity against the fraction of prey 1 in the environment, and Fig. 1C plots the predator functional response to prey 1 [Eq. (3)] for optimally foraging predators against the prey 1 population abundance  $x_1$ . All these dependences are inspected for several fixed values of  $x_2$ . Three observations are worth noting. First, both the prey 1 fraction



**FIG. 1.** The fraction of prey 1 individuals from all prey captured by the optimally foraging predators in a single time step (or by a single predator in a series of its food decisions) against the prey population abundances (Fig. 1A), the same quantity plotted against the fraction of prey 1 in the environment and prey 2 numbers (Fig. 1B), and the predator functional response of optimally foraging predators to prey 1 (the mean number of successfully attacked prey 1 individuals per predator per time step) against the number of prey in the environment (Fig. 1C). The parameter values:  $S = 16384(128 \times 128)$ ,  $P_a^1 = 0.2$ ,  $E_1 = 0.06$ ,  $T_h^1 = 5$ ,  $P_a^2 = 0.42$ ,  $E_2 = 0.05$ ,  $T_h^2 = 12$ .

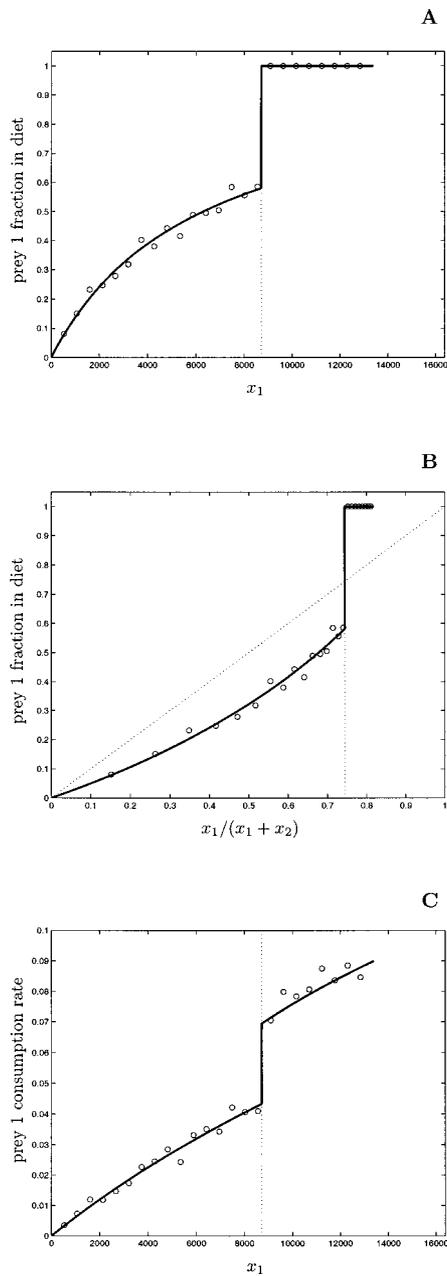
in the predator diet and the prey 1 consumption rate increase with prey 1 abundance but decrease with prey 2 abundance. Moreover, the abrupt changes of these quantities appear around the prey 1 threshold abundance  $L_1$  where the predator diet is modified. Finally, magnitudes of these abrupt changes increase with increasing prey 2 population abundance  $x_2$ .

Figure 2 compares the predator diet composition and functional response curves with an IBM simulation for a constant prey 2 density. The vertical dotted lines mark locations of the threshold value  $L_1$ . The circles, i.e., the simulation results, were obtained by counting and processing analogously the actual numbers of successfully attacked prey  $i = 1, 2$  individuals, for various values of prey 1 abundance. More rigorously, 100 time steps were simulated for each prey 1 abundance (prey 2 numbers were kept constant across these simulations) and the numbers of successfully attacked prey in the last time step, when the number of searching predators had relatively stabilized, were processed. One may notice a close fit of the stochastic simulation results by the approximate deterministic formulae (1) and (3). For a comparison, the dotted oblique line in Fig. 2B indicates behaviour of an opportunistic predator, consuming prey items at the ratio of their environmental numbers. We see that the predator consumes disproportionately more prey 2 items below the prey 1 abundance  $x_1 = L_1$ , due to higher probability  $P_a^2 > P_a^1$  used in the figure to successfully attack prey 2 upon encounter. The prey 1 fraction in the diet would coincide with the oblique line below  $L_1$  for  $P_a^1 = P_a^2$ .

For omniscient predators having exact knowledge of prey 1 abundance over the entire lattice at each time instant, partial preferences appear neither on the individual level nor on the population level. The decision probabilities  $p_i$  of individual predators follow the zero-one rule; that is, a prey type is either always attacked or always ignored upon encounter, and all predators change their diet synchronously. The latter observation is reflected in the above figures in the abrupt changes around the prey 1 threshold abundance  $L_1$ . This synchrony and the assumption of predator omniscience (particularly in large habitats) do not seem entirely realistic. In the rest of this section we consider the situation where predators have only a limited knowledge of their environment.

### Limited Perception by Predators

McNamara and Houston (1987) and Hirvonen *et al.* (1999) explained partial preferences by letting predators



**FIG. 2.** A projection of the dependencies plotted in Fig. 1 when the prey 2 population abundance is fixed at the value  $x_2 = 3000$ . The circles represent the IBM simulation results when prey are randomly distributed on the lattice at each time step, the solid line is the theoretical prediction. The vertical dotted lines mark locations of the prey 1 threshold value  $L_1$ . The parameter values are the same as in Fig. 1,  $y = 6000$ . All the predators were initially in the searching state. For each fixed prey 1 density  $x_1$ , simulation was running for 100 time steps, and the actual numbers of successfully attacked prey  $i$  individuals in the last time step were processed appropriately to get dependencies drawn in Fig. 1. The dotted oblique line in Fig. 2B indicates behaviour of an opportunistic predator, consuming prey types at the ratio of their environmental numbers.

estimate prey densities on the basis of actual encounters with prey. This is one possible approach to incorporating a limited knowledge of the environment by predators. We envisage another approach here. We suppose that predators know the exact numbers of individuals of each prey type, but only within a restricted neighbourhood of their respective spatial locations (for example, a square of  $5 \times 5$  lattice sites with the predator in its center), rather than within the environment as a whole. We motivate this idea by a limited detection range of volatile substances released by prey, or limited predator visual or auditory ranges (Rice, 1983; Kindvall *et al.*, 1998).

Let the perception neighbourhood have the same number  $N$  of sites for every predator individual; we refer to it as an  $N$ -neighbourhood further on. Let individuals of both prey be randomly distributed on the lattice at each time step. This assumption implies, among other things, that the actual form of the  $N$ -neighbourhood is not important and may vary with different predators, because the probability that a site is occupied by a prey  $i$  item is the same for each site. The question of interest is how a predator should decide upon encounter with prey if it perceives  $\tilde{x}_i$  prey  $i$  items in its  $N$ -neighbourhood. Obviously, these numbers vary as the predator and/or prey move. However, since the predator does not know the total prey abundance  $x_i$ , it cannot assess variability in these numbers and optimize its behaviour with respect to this variability. We adopt the approach that is common when dynamic consequences of foraging strategies are inspected (Gleeson and Wilson, 1986; Fryxell and Lundberg, 1994; Křivan, 1996): instantaneous/static predator behaviour is first derived for a range of conditions and then put into the changing environment. Let us suppose for a moment that the prey  $i$  number  $\tilde{x}_i$  does not vary in the  $N$ -neighbourhood of the predator. If we consider this neighbourhood as the effective environment of the predator, then the above derived optimal foraging rule predicts that the predator should always attack prey 1 upon encounter ( $p_1 = 1$ ), whereas its decision to attack prey 2 upon encounter depends on the relation between the local abundance  $\tilde{x}_1$  of prey 1 within the  $N$ -neighbourhood and the local threshold abundance

$$L'_1 = N \frac{E_2}{P_a^1(E_1 T_h^2 - E_2 T_h^1)}, \quad (8)$$

that is, the threshold abundance (7) with the size  $S$  of the whole environment replaced by the size  $N$  of the effective environment. The predator should attack prey 2 provided that  $\tilde{x}_1 < L'_1$  and ignore it when  $\tilde{x}_1 > L'_1$ . Note that  $L'_1/N = L_1/S$ : the threshold *densities* do not change with the transition from the global to a local scale.

Now, we put this strategy into a changing environment. As mentioned above, the local prey 1 abundance  $\tilde{x}_1$  need not be the same for every predator individual nor for the same individual under different spatial prey distributions (which may arise due to prey and/or predator movement). We show that this spatial variability in  $\tilde{x}_1$  gives rise to partial preferences on both the individual and population levels. Let a single predator individual share a site with a prey 2 individual. Obviously, the decision probability  $p_2$  that the predator will attack that prey item equals the probability that the number of prey 1 individuals  $\tilde{x}_1$  in the  $N$ -neighbourhood of this predator is less than the threshold value  $L'_1$ . Given  $0 < x_i < S$  prey  $i = 1, 2$  items ( $x_1 + x_2 \leq S$ ), there are

$$D_{\text{total}} = \binom{S-1}{x_1} \binom{S-1-x_1}{x_2-1} \quad (9)$$

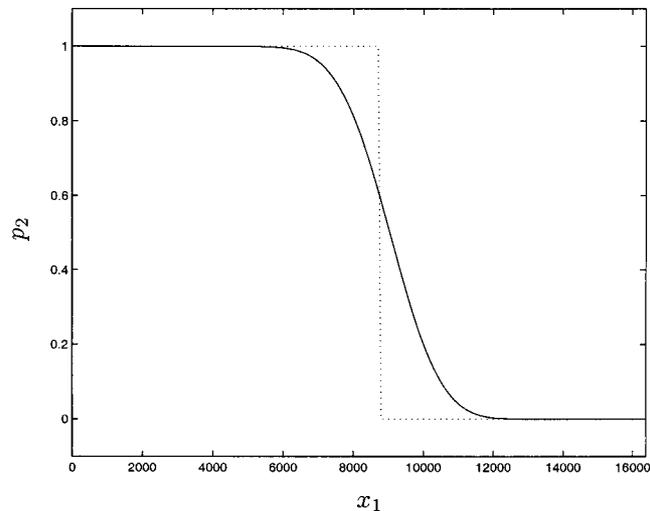
possibilities for the distribution of prey on the lattice, provided that the focus site is occupied by a prey 2 individual and the predator. The number of possibilities by which  $\tilde{x}_1$  prey 1 individuals can be located in the  $N$ -neighbourhood is

$$D_{\text{admissible}}(\tilde{x}_1) = \binom{S-N}{x_1-\tilde{x}_1} \binom{N-1}{\tilde{x}_1} \binom{S-1-x_1}{x_2-1}, \quad (10)$$

provided that this expression is defined, i.e., that  $\max(0, x_1 - S + N) \leq \tilde{x}_1 \leq \min(x_1, N - 1)$  and  $D_{\text{admissible}}(\tilde{x}_1) = 0$  otherwise. Hence, the probability that the number of more profitable prey individuals in the neighbourhood of size  $N$  is lower than the threshold value  $L'_1$  is

$$p_2(x_1) = \sum_{\tilde{x}_1=0}^{\lfloor L'_1 \rfloor} \frac{D_{\text{admissible}}(\tilde{x}_1)}{D_{\text{total}}}, \quad (11)$$

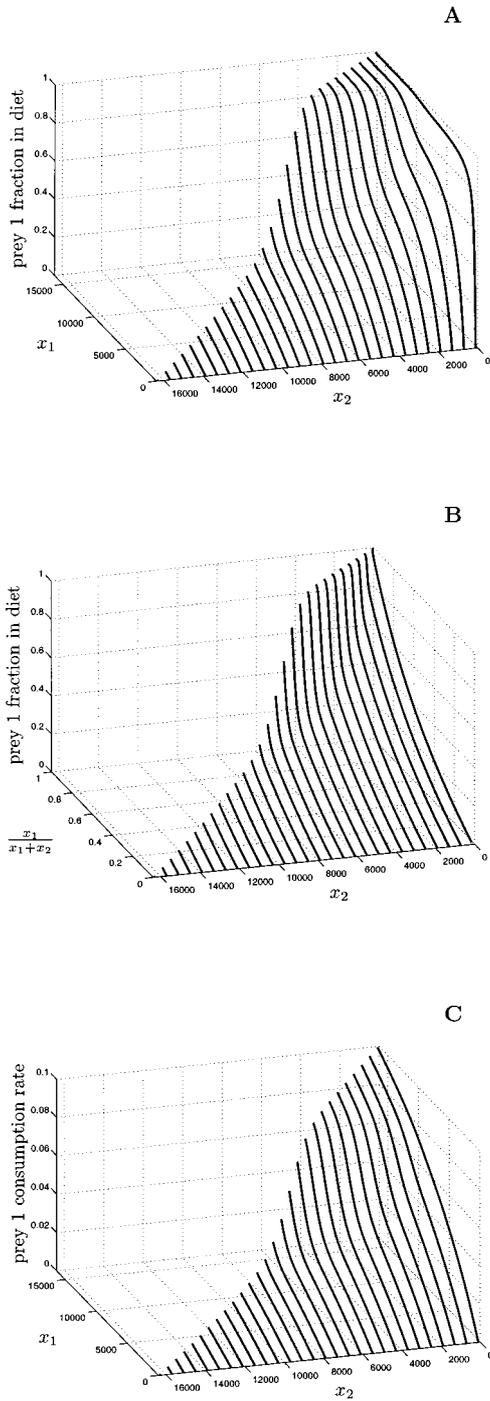
where  $\lfloor L'_1 \rfloor$  denotes the largest integer less than  $L'_1$ . Note that the probability (11) does not depend on the prey 2 abundance  $x_2$ , as the respective terms in the expressions (9) and (10) cancel out. Figure 3 shows the decision probability  $p_2$  as a function of prey 1 abundance  $x_1$ . The zero-one step function derived for the omniscient predators (dotted line) changes to a gradually decreasing sigmoid-like function (solid line). Therefore,  $0 < p_2(x_1) < 1$  for a range of prey 1 numbers. As  $N$  approaches  $S$ , the decision probability (11) approaches the zero-one step function. Indeed, for  $N = S$  it is  $L'_1 = L_1$ , and  $D_{\text{admissible}}(\tilde{x}_1) = 0$  for any  $\tilde{x}_1 \neq x_1$ . This implies  $p_2(x_1) = 1$  if  $x_1 < L_1$  and  $p_2(x_1) = 0$  if  $x_1 > L_1$ , that is, the formula (6).



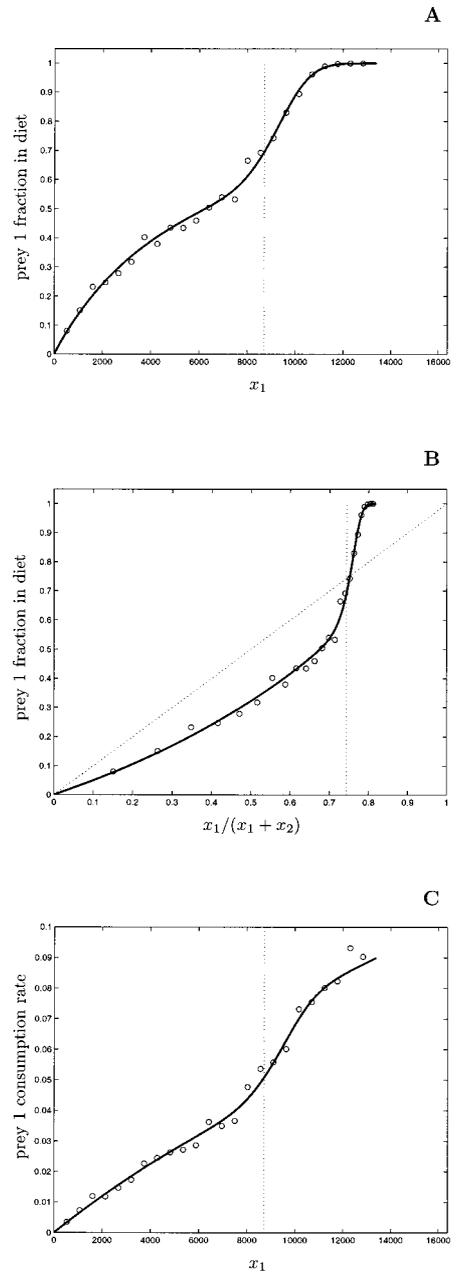
**FIG. 3.** The decision probability  $p_2$ , as a function of the prey 1 population abundance  $x_1$ , for globally omniscient predators (dotted line) and locally omniscient predators (solid line). The parameter values are the same as in Fig. 1,  $x_2 = 3000$ ,  $N = 49(7 \times 7)$ .

We claim that the decision probability  $p_2$  given by the expression (11) gives rise to partial preferences on both the individual and population levels, for a wide range of prey 1 population abundances/densities. To see the former, consider a single predator in the course of time and observe its food decisions. As  $x_1$  is kept constant, after  $m$  encounters with prey 2, the number of prey 2 items it has actually consumed is binomially distributed with parameters  $m$  and  $p_2(x_1)$ . Hence, the mean fraction of prey 2 items the predator has consumed is  $p_2(x_1)$ , which is neither 0 nor 1 for  $x_1$  such that  $0 < p_2(x_1) < 1$ . The actual fraction of prey 2 items the predator has consumed after  $m$  encounters with prey 2 approaches  $p_2(x_1)$  as  $m$  (that is, number of food decisions) tends to infinity. To elucidate the existence of partial preferences on the population level, consider a fixed time step and a number of predators on the lattice. Let  $m$  out of a number of searching predators encounter a prey 2 item in that time step. Then the actual number of predators that attack prey 2 is also binomially distributed with parameters  $m$  and  $p_2(x_1)$ . Hence, the mean fraction of predators that have both encountered and attacked prey 2 is  $p_2(x_1)$ , whereas the actual fraction of these predators approaches  $p_2(x_1)$  as  $m$  (that is, prey and predator numbers and, in turn, lattice size) tends to infinity.

Figures 4 and 5 are analogous to Figs. 1 and 2. They show the effects of perceptual limitations of predators on their diet composition [Eq. (1)] and functional response to prey 1 [Eq. (3)], for  $p_1 = 1$  and  $p_2$  specified by the



**FIG. 4.** The fraction of prey 1 individuals from all prey captured by the optimally foraging predators in a single time step (or by a single predator in a series of its food decisions) against the prey population abundances (Fig. 4A), the same quantity plotted against the fraction of prey 1 in the environment and prey 2 numbers (Fig. 4B), and the predator functional response of optimally foraging predators to prey 1 (the mean number of successfully attacked prey 1 individuals per predator per time step) against the number of prey in the environment (Fig. 4C). The parameter values are the same as in Fig. 1,  $N = 49$ .



**FIG. 5.** A projection of the dependencies plotted in Fig. 4 when the prey 2 population abundance is fixed at the value  $x_2 = 3000$ . The circles represent the IBM simulation results when prey are randomly distributed on the lattice at each time step, the solid line is the theoretical prediction. The vertical dotted lines mark locations of the prey 1 threshold value  $L_1$ . The parameter values are the same as in Fig. 1,  $N = 49$ ,  $y = 6000$ . All the predators were initially in the searching state. For each fixed prey 1 density  $x_1$ , simulation was running for 100 time steps, and the actual numbers of successfully attacked prey  $i$  individuals in the last time step were processed appropriately to get dependencies drawn in Fig. 4. The dotted oblique line in Fig. 5B indicates behaviour of an opportunistic predator, consuming prey types at the ratio of their environmental numbers.

formula (11). The fundamental distinction in these characteristics between globally and locally omniscient predators is the shift from the abrupt changes around the threshold abundance  $L_1$  (Figs. 1 and 2) to the gradual transitions over this threshold value for predators with perceptual limitations (Figs. 4 and 5). As a consequence, the predator functional response to prey 1 takes a sigmoidal form (Figs. 4C and 5C) which may have implications for dynamics of the whole predator–prey system.

## 4. DISCUSSION

### *Limited Perception*

In this article we have constructed and analyzed a spatially explicit individual-based model for one predator population feeding on two prey types. The majority of optimal diet models (Schoener, 1971; Pulliam, 1974; Werner and Hall, 1974; Charnov, 1976) assume random sequential encounters with prey and omniscient predators. This means that consumers have exact knowledge of their environment, and it results in simultaneous change of their diet at a certain threshold density of more profitable prey. Below this threshold all prey items should be attacked upon encounter with any searching predator, whereas above the threshold this strategy should be applied to more profitable prey only. The lack of variation between individual consumers thus leads to the zero–one preference for the less profitable prey type.

Whether animals are omniscient or not may depend on the spatial scale. On the scale which corresponds to the range of animal perception, the assumption on omniscience is reasonable. As the habitat in which animals live increases in size, they become less omniscient. Due to a variation in prey distribution across the environment, individual predators will face different prey densities in their respective perception ranges. Although all predators still change their diet at the same threshold abundance of more profitable prey given by formula (8), this change is no longer synchronized.

The variation in prey densities and local omniscience combine and lead to partial preferences analytically described by formula (11). This formula can be interpreted both from individual consumer and population viewpoints. If we observe a single predator during a series of its food decisions, each time it encounters less profitable prey the predator attacks or ignores that prey depending on the number of more profitable prey items it perceives. As the predator and/or prey move, the local prey density changes and the fraction of attacked

individuals of less profitable prey approaches the probability (11) with increasing number of decisions, provided that the total prey densities do not change. Alternatively, we may observe more predators at a single time step. For a range of more profitable prey densities, some of the predators experience higher prey 1 local abundance than the threshold value (8), whereas some experience lower abundance. In turn, the fraction of predators that attack less profitable prey of those encountering it approaches the probability (11) with increasing number of encounters (that is, prey and predators and, in turn, the lattice size).

Another mechanism accounting for an incomplete knowledge of predators on prey densities was presented by McNamara and Houston (1987) and Hirvonen *et al.* (1999). They assumed that predators perceive their environment through encounters with prey, and derived an analytical expression for partial preferences which is based on the assumption that more recent encounters have a higher weight. The partial preferences that appear are due to a variation in estimates of the encounter rate with more profitable prey, and can also be interpreted in terms of a single individual or a population of individuals. Mangel and Roitberg (1989) explored partial preferences in a host–parasite framework, through a variation in parasite memory and the time since last oviposition. Both these examples and our work replace the assumption of predator/parasite omniscience by a weaker one, and derive partial preferences within the classic optimal foraging framework. Yet they differ in the particular mechanisms they propose as omniscience substitutes.

### *Partial Preferences*

There seems to be an ambiguity in understanding the concept of partial preferences on the individual level. McNamara and Houston (1987) state that contrary to optimality models in which “the same behaviour is always followed in given circumstances, partial preferences mean that in given circumstances a prey type is sometimes taken and sometimes rejected.” This may be seen either by instantly observing food decisions of a group of predators (population level) or by observing a single predator in a series of its food decisions (individual level). We claim that the issue of whether partial preferences appear on the individual level or not is strongly influenced by what we consider to be the “circumstances.” Before we discuss this issue more thoroughly in the next paragraphs, we note that partial preferences may be observed on the population level but not on the individual level, and vice versa. The former may be the case, for example,

when predators know prey densities exactly but form two groups, each having different assessment of  $E_i$  and/or  $T_h^i$  (increase in experience or body size may, for example, reduce handling times and/or increase energetic efficiency of consuming prey). The latter may happen, for example, when all predators are identical and exactly know prey densities, but the threshold value at which predators change their diet varies with time.

Let us define a “predator decision state” as a set of variables that the predator uses as a basis for its decisions. It may generally involve such information as predator knowledge of prey profitabilities and encounter rates and predator physiological or motivational state (satiation level, prey type consumed last, time of day, etc.). Any value of the predator decision state can be understood as a circumstance in the above sense. Many suggested mechanisms leading to partial preferences are intrinsically deterministic; that is, the predator decision state space is split into two parts, one prescribing always ignoring an encountered prey type and the other always attacking it (the “individual” zero–one rule). Hence, under given circumstances, such predators decide consistently (always attack prey or always ignore it) and partial preferences do not appear on the individual level. In this conceptual context, classic predators decide according to the state  $[E_i, T_h^i, x_i]$ . On the other hand, the locally omniscient predators of this article use the state  $[E_i, T_h^i, \tilde{x}_i]$ , where  $\tilde{x}_i$  is the prey  $i$  local abundance, whereas McNamara and Houston’s predators use the state  $[E_i, T_h^i, \hat{x}_i]$ , where  $\hat{x}_i$  is the estimate of global prey  $i$  abundance. The predator decision state can be defined for any model with a deterministic decision policy (see McNamara and Houston (1987) for more examples of deterministic decision policies which even need not be optimal at all).

Let us also define an “experimenter state” as a set of variables with respect to which predictions are made. The experimenter state can be as detailed as the predator decision state (it makes no sense for the former to be more detailed than the latter), but usually it is less detailed. If both states are the same and predators decide in a deterministic way, we observe no partial preferences on the individual level. If the experimenter state is less detailed than the predator decision state (which, in reality, will always be the case), then a particular value of the latter may be uncertain given a value of the former. In other words, there is a set of circumstances giving the same experimenter state. In this case, we may ask for the probability that the predator decision state takes a value, given a value of the experimenter state. It is exactly this probability that specifies partial preferences on the individual level. In this article, the experimenter state is

that of the classic prey model of optimal foraging,  $[E_i, T_h^i, x_i]$ , while the formula (8) gives the probability specifying partial preferences.

We may also get partial preferences on the individual level in a completely different way. Namely, even though the predator decision state and the experimenter state coincide, mechanisms of prey choice can be intrinsically stochastic; e.g., predators may decide by “flipping a coin.” In reality, it is virtually impossible to distinguish these two cases due to the enormous complexity of the predator decision state, so that from a pragmatic viewpoint both the cases can be referred to as invoking partial preferences on the individual level. Yet it may be worthwhile being aware of the conceptual distinction.

The possible difference in the predator decision state and the experimenter state can also affect our view of optimality of predator behaviour. In the words of Mangel and Roitberg (1989), “if the external observer has an inaccurate model of optimal behaviour, then it may appear that the organism is highly suboptimal, when this is in fact not the case.” For example, any predator considered in our article behaves optimally within its local perception range, whereas it appears suboptimal when seen from the perspective of the whole lattice where the zero–one rule is the optimal one.

### Other Functions

In the theoretical work of Fryxell and Lundberg (1994) on dynamical consequences of optimal diet composition, sigmoidal forms of partial preferences,

$$p_2(x_1) = \frac{L_1^z}{L_1^z + x_1^z}, \quad z > 1, \quad (12)$$

are proposed and analyzed. Contrary to our approach, this choice lacks any mechanistic reasoning and is intended to phenomenologically mimic partial preferences only. We compared Fryxell and Lundberg’s function (12) with our formula (11) and found that for a properly chosen value of  $z$  the function (12) is very close to our function. Another formula phenomenologically describing partial preferences is inspected by Fryxell and Lundberg (1998).

The diet preference and the functional response curves, having a step at the threshold density  $L_1$  for the zero–one rule (see Figs. 1 and 2), become gradually increasing for the partial preference model (see Figs. 4 and 5). This is not always the case. For example, the assumption of Bélisle and Cresswell (1997) on limited memory capacity of predators also leads to partial preferences but does not completely remove the step form of the respective

dependencies (see Fig. 9 in Bélisle and Cresswell (1997)). We also note that the functional response plotted in Figs. 4C or 5C has an inflection at intermediate prey 1 numbers. It was obtained when a Holling type II functional response was combined with an adaptive predator behaviour, and produces a localized increase in the prey per capita mortality rate due to predation. Such a super-linear growth of functional responses has been shown to have a stabilizing effect on predator–prey dynamics (Murdoch and Oaten, 1975).

Consideration of the spatially explicit individual-based model proves to be a good tool for our purposes, as it allows us to treat each individual separately and naturally define and work with its perception neighbourhood. Within this IBM framework, our predator decision rule can be further extended to situations in which the neighbourhood size varies with different predators. The threshold values  $L_1$  and  $L'_1$  may become individual-dependent by separating the predator population into a number of groups, each having different parameters, e.g., the probability of successfully attacking more profitable prey,  $P_a^1$ . Both these extensions may be motivated by and made dependent on, e.g., predator age (gaining experience when aging) or variability in predator body size.

Our mechanism (like many others) invoking partial preferences for less profitable prey within the classic optimal foraging framework still does not explain two frequent observations, namely that (1) prey choice rules often seem to depend on the density of less profitable prey, too, and that (2) partial preferences are sometimes observed also for more profitable prey. The same mechanism as that presented in this article is now under investigation for a slightly different individual-based model and should involve both these features.

## APPENDIX: DIET COMPOSITION

Here we outline a derivation of the diet composition formula (1). We show that for a pair of decision probabilities  $p_1$  and  $p_2$  and a sufficiently large numbers of prey and predators (or number of food decisions of an individual predator), the fraction of prey  $i=1, 2$  individuals from all captured by a number of predators in a single time step (or by a single predator in a series of food decisions) can be well approximated by the formula

$$\frac{x_i}{S} p_i P_a^i \left/ \left( \frac{x_1}{S} p_1 P_a^1 + \frac{x_2}{S} p_2 P_a^2 \right) \right., \quad (13)$$

where  $S$  is the number of lattice sites,  $x_i$  is the prey  $i$  abundance, and  $P_a^i$  is the probability of successful attack on a prey  $i$  when the predator decides to attack that prey upon encounter.

Given that both prey types are randomly distributed on the lattice at each time step, with each site occupied by at most one prey item (regardless of its type), the probability that a searching predator shares a site with a prey  $i$  individual is  $w_i = x_i/S$ . In turn, the probability that the predator will successfully attack that prey is  $w_i p_i P_a^i$ , that is, the probability of encountering that prey times the probability of deciding to attack it times the probability of attacking it successfully. Consequently, the fraction of searching predators that consume prey  $i$  at a fixed time step approaches  $w_i p_i P_a^i$  as the number of encounters with prey  $i$  (that is, numbers of prey and predators and, in turn, the lattice size) tends to infinity (the law of large numbers), given no interference between predators. Similarly, the fraction of attacks at prey  $i$  upon encounter by a single predator approaches  $w_i p_i P_a^i$  as the number of food decisions tends to infinity, given constant prey densities. Hence, the fraction of prey  $i$  individuals of all prey items that are captured by a number of predators in a single time step or by a single predator within a series of its food decisions, is well approximated by the formula (13).

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