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Should "handled" prey be considered? Some consequences for functional response, predator–prey dynamics and optimal foraging theory

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Abstract

Predator–prey models consider those prey that are free. They assume that once a prey is captured by a predator it leaves the system. A question arises whether in predator–prey population models the variable describing prey population shall consider only those prey which are free, or both free and handled prey together. In the latter case prey leave the system after they have been handled. The classical Holling type II functional response was derived with respect to free prey. In this article we derive a functional response with respect to prey density which considers also handled prey. This functional response depends on predator density, i.e., it accounts naturally for interference. We study consequences of this functional response for stability of a simple predator–prey model and for optimal foraging theory. We show that, qualitatively, the population dynamics are similar regardless of whether we consider only free or free and handled prey. However, the latter case may change predictions in some other cases. We document this for optimal foraging theory where the functional response which considers both free and handled prey leads to partial preferences which are not observed when only free prey are considered.

Keywords: Functional response; Predator–prey models; Interference; Optimal foraging theory

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1. Introduction

The classical MacArthur–Rosenzweig predator–prey model with Holling type II functional response (and its later elaborations) assume that handled prey are removed from the system immediately after the encounter with a predator so that the effective size of the prey population is the number of free prey. Correspondingly, the Holling type II functional response is a function of free prey density only and predator–prey population dynamics describe the time evolution of free prey density. One may ask: What happens to the Holling type II functional response and to population models if free prey are replaced by all prey (i.e., free prey and prey that are currently handled by predators)?

The effect of considering total prey density on the functional response is that as the overall predator density increases, more prey will be handled and less prey will be available to a searching predator. This will decrease the encounter rate of a searching predator with free prey which, in turn, will have a negative impact on the functional response which becomes explicitly dependent on predator densities. A negative effect of predator density on its functional response is called predator interference. The Holling type II functional response was derived with respect to free prey and that is why it does not account for interference. However, Skalski and Gilliam (2001) showed that predator dependence in the functional response is a nearly ubiquitous property of the published data sets that they analysed. In 18 out of 19 studies, the classical Holling type II functional response was rejected in favor of one of three predator-dependent functional responses. The effect of interference on predator–prey population dynamics was considered in many theoretical studies (Beddington, 1975; De Angelis et al., 1975; Free et al., 1977; Freedman, 1979; Polis, 1988; Ruxton et al., 1992; van der Meer and

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Ens, 1997; Fretwell and Lucas, 1970), to mention a few. A general conclusion from these studies is that interference promotes predator–prey stability. Thus, considering both free and handled prey might result in a higher degree of stability in predator–prey population dynamics.

In this article we derive a functional response considering also those prey that are handled by predators. Naturally, this functional response coincides with the Holling type II functional response in environments with a single predator. Then we derive a predator–prey model which considers both free and handled prey, but only free prey reproduce. It is a well-known fact that the Holling type II functional response destabilizes the classical Lotka–Volterra population dynamics (Murdoch and Oaten, 1975). This is because the positive handling times decrease efficiency of predators to control an exponentially growing prey population. When handled prey are considered then we show that the interior population equilibrium can be stable, but only for ecologically unrealistic parameters. However, we also show that in some cases ecological predictions may differ depending on whether we consider only free, or all prey. As an example we choose in this article optimal foraging theory (Charnov, 1976; Stephens and Krebs, 1986) and we show that when both free and handled prey are considered, partial preferences for the alternative prey arise in multiple predator environments.

2. Predator consumption rate when handled prey are considered

Classical derivation of Holling type II functional response (Holling, 1959) considers a single predator in a time interval $(0, T)$. It is assumed that the prey density in this time interval does not change and the predator spends all the time either searching for or handling prey. In this case, it is irrelevant whether the functional response is derived with respect to free prey or with respect to all prey (i.e., free prey and the single prey which is being handled by the predator) because these two quantities are practically the same as there is only one predator. However, in multiple predator environments such a derivation cannot reflect the effect of predator abundance (i.e., interference) on the functional response. Here we derive a functional response for multiple predators with the overall density y. The density of searching predators is denoted by y_s and the density of predators already handling a prey item is denoted by y_h, respectively ($y = y_h + y_s$). If an average predator spends T_s time units searching for prey and T_h time units handling prey then

$$\frac{y_h}{y_s} = \frac{T_h}{T_s}.$$

Similar to predators, we can distinguish between prey that are free (x_f) and those that are handled by predators (x_h). Assuming that one predator is handling exactly one prey item then the abundance of handled prey equals the abundance of handling predators ($x_h = y_h$). Functional response can be derived either with respect to free prey abundance (x_f) or to overall prey abundance ($x = x_f + x_h$). If it is derived with respect to the abundance of free prey then we get the Holling type II functional response. This is because the encounter rate of a predator with prey does not depend on the number of prey handled because the abundance of free prey is assumed to be constant. However, if functional response is derived with respect to the overall prey density (free and handled prey), i.e., when the overall prey density is assumed to be constant then the number of available free prey for searching predators will decrease because some prey will be handled by predators. This later case leads to interference between searching predators and the corresponding functional response is given by

$$F(x,y) = \frac{\lambda x_f y_s}{y} = \frac{y_h}{yh} = \frac{2\lambda x}{(x+y)h\lambda + 1 + \sqrt{((x+y)h\lambda + 1)^2 - 4xyh^2\lambda^2}}, \quad (1)$$

see Appendix A. We remark that if handling time h equals zero then $x = x_f$ and

$$F(x,y) = \lambda x$$

which is the linear functional response used in the Lotka–Volterra model. For a low predator density the prey density (x) equals approximately to the density of free prey (x_f) and the functional response becomes again Holling type II functional response

$$F_h(x) = \frac{\lambda x}{1 + \lambda h x}. \quad (2)$$

The upper asymptote of $F(x,y)$ for every fixed predator density (y) is the same as for the Holling type II functional response, i.e., $1/h$. Moreover, the slope of the functional response at zero prey density

$$\frac{\lambda}{1 + yh\lambda}$$

decreases with increased predator densities (Fig. 1). This is due to the fact that as predator densities increase, the encounter rate of a searching predator with free prey decreases (because some prey are already handled) which leads to a lower per capita average predator intake rate. Fig. 1 shows the effect of increasing predator densities on the functional response $F(x,y)$. Parameters λ and h were estimated from Fig. 2 in Eveleigh and Chant (1982) for the case where only a single predator was present. Using these parameters we

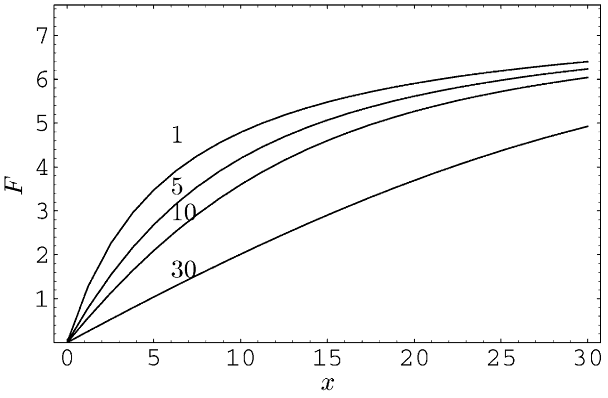

Fig. 1. Plot of the functional response F given by formula (1) for four predator densities: $y = 1, 5, 10, 30$. As predator density increases, the initial slope of F decreases. Parameter values $h = 0.13$, $\lambda = 1.27$ were estimated from data given in Eveleigh and Chant (1982), for details see text.

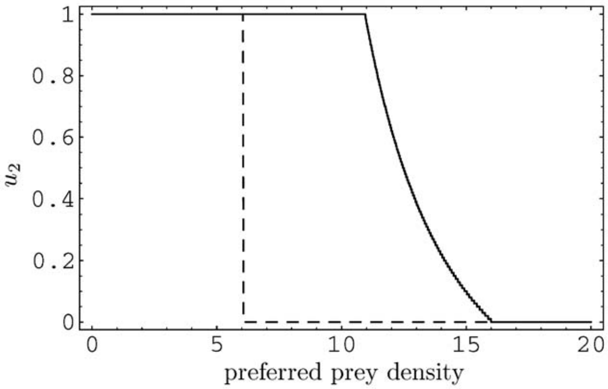

Fig. 2. This figure shows predator preferences for the preferred prey type as a function of the preferred prey type density. The dashed line shows zero–one preferences predicted by the classic optimal foraging model (here "prey" mean free prey only) while the solid line shows that partial preferences arise when prey include those that are handled (here "prey" mean both free and handled prey). Parameters for the preferred prey type are those given in Fig. 1. Parameters for the alternative prey type are the same with the exception that the energetic content of the alternative prey type is one half of the preferred prey type (i.e., $e_1/e_2 = \frac{1}{2}$). The density of the alternative prey type was set arbitrarily to $x_2 = 20$.

plotted then the corresponding functional responses for several predator densities.

3. Population dynamics

A predator–(free)prey population model with the Holling type II functional response

$$\frac{\mathrm{d}x_f}{\mathrm{d}t} = rx_f - F_h(x_f)y,$$
$$\frac{\mathrm{d}y}{\mathrm{d}t} = eF_h(x_f)y - my, \qquad (3)$$

describes interactions between free prey and predators. Here r is the per capita prey growth rate, e is the efficiency rate with which handled prey are converted to new predators, m is the per capita predator mortality rate, and $F_h(x_f)$ denotes the classic Holling type II functional response.

It is known that the above system has, for small handling times ($h < e/m$), one positive equilibrium

$$E_h = \left\{\frac{m}{\lambda(e - hm)}, \frac{er}{\lambda(e - hm)}\right\}$$

which is unstable for all parameter values. For small handling times, trajectories spiral away from the equilibrium with an increasing amplitude.

We are interested to know if a similar predator–prey model which describes the evolution of the overall prey and predator densities can lead to qualitatively different dynamics. Using functional response F, predator–prey population dynamics are described by

$$\frac{\mathrm{d}x}{\mathrm{d}t} = rx - (1 + mh + rh)F(x, y)y,$$
$$\frac{\mathrm{d}y}{\mathrm{d}t} = eF(x, y)y - my, \qquad (4)$$

see Appendix B. We remark, that model (4) assumes that only free prey reproduce (i.e., those that are handled do not reproduce) and newborn predators are deemed to be of the searching rather than handling type. Compared with model (3) the above system describes the total prey–predator dynamics (including those prey which are currently handled). Model (4) has the following non-zero equilibrium:

$$E = \left\{\frac{m(1 + hr + hm)}{\lambda(e - hm)(1 + hm)}, \frac{er}{\lambda(e - hm)(1 + hm)}\right\}.$$

Thus, when compared with model (3), the equilibrium for total prey density is higher and the predator density is lower. For small handling times ($h < e/m$) this equilibrium is positive. Contrary, to the interior equilibrium (E_h) of model (3), the above equilibrium can be stable but only for ecologically unrealistic efficiencies (e) which are higher than 1 (see Appendix B). Thus, we can conclude, that for ecologically plausible parameters, interference described by functional response F is not strong enough to stabilize predator–(total)prey population dynamics.

We remark that if handled prey can produce offspring just as free prey can then population dynamics are described by the predator–prey model (3) where the Holling type II functional response is replaced by the functional response $F(x, y)$, i.e.,

$$\frac{\mathrm{d}x}{\mathrm{d}t} = rx - F(x, y)y,$$
$$\frac{\mathrm{d}y}{\mathrm{d}t} = eF(x, y)y - my. \qquad (5)$$

4. Some consequences for optimal foraging theory

In multiple predator environments the distinction between free prey and total prey will have consequences for ecological predictions that relay on Holling disc equation. As an example, we present here some implications for optimal foraging theory. Optimal foraging theory predicts (Stephens and Krebs, 1986) that in environments with two prey types the alternative prey type will be either always included or always excluded from the predator's diet. This result was termed "zero–one" preference. In experiments a more gradual switching, called partial preferences, was observed (Stephens and Krebs, 1986). Various mechanisms can lead to partial preferences: incorrect classification of prey types by predators (Krebs et al., 1977; Rechten et al., 1983), uncertainty about the actual resource densities (McNamara and Houston, 1987), population dynamics (Křivan, 1996; Křivan and Sikder, 1999; Křivan and Eisner, 2003), a limited memory capacity of predators (Bélisle and Cresswell, 1997), limited spatial omniscience (Berec and Křivan, 2000) and interindividual differences in physiological state (Mangel and Clark, 1988; Houston and McNamara, 1999; Křivan and Vrkoč, 2000). Here we show that partial preferences for the less profitable prey type arise when handled prey are considered.

The prey model assumes that animals maximize a proxy of their fitness measured by the average energy intake rate. In the case of two prey types the energy intake rate is derived from the Holling disc equation which considers only free prey and has the following form:

$$E(x_{f1}, x_{f2}, u_1, u_2) = \frac{u_1\lambda_1 e_1 x_{f1} + u_2\lambda_2 e_2 x_{f2}}{1 + u_1\lambda_1 h_1 x_{f1} + u_2\lambda_2 h_2 x_{f2}}, \tag{6}$$

(Stephens and Krebs, 1986). Here x_{fi} is the density of free prey i and u_i is the probability that upon an encounter with prey type i predators will include this prey type in their diet. Other parameters have the same meaning as in the previous part, the subindex refers now to the first or second prey type. The main prediction of optimal foraging theory states that the more profitable prey type (i.e., the prey type with higher ratio e_i/h_i, which is implicitly assumed to be prey type 1 in this article) will always be attacked upon an encounter with a predator (i.e., $u_1 = 1$), and the less profitable prey type will be included in the predator diet only if the density of the more profitable free prey type is below a switching threshold given by

$$x_{f1}^* = \frac{e_2}{\lambda_1(e_1 h_2 - e_2 h_1)} \tag{7}$$

(Charnov, 1976; Stephens and Krebs, 1986). This implies, that the less profitable prey type is either always ignored, or always attacked by a searching predator, i.e., $u_2 = 0$ or 1 and no partial preferences for the less profitable prey type arise.

Now we consider the case where both free and handled prey are considered in an environment with multiple predators. The criterion to be maximized is now given by

$$R(x_1, x_2, u_1, u_2) = \frac{e_1\lambda_1 u_1(x_1 - y_{h1}) + e_2\lambda_2 u_2(x_2 - y_{h2})}{1 + \lambda_1 h_1 u_1(x_1 - y_{h1}) + \lambda_2 h_2 u_2(x_2 - y_{h2})}, \tag{8}$$

where densities of handling predators satisfy the following equations (see Appendix C):

$$\begin{aligned} y_{h1} &= \lambda_1 h_1 u_1(x_1 - y_{h1})(y - y_{h1} - y_{h2}), \\ y_{h2} &= \lambda_2 h_2 u_2(x_2 - y_{h2})(y - y_{h1} - y_{h2}). \end{aligned} \tag{9}$$

In general, we cannot compute explicitly the fraction of predators handling prey type 1 (y_{h1}) and prey type 2 (y_{h2}), respectively, from Eq. (9). We remark that these fractions will be functions of predator preferences u_1 and u_2, respectively. Maximization of R with respect to predators diet choice is more complicated than in the case of classical optimal foraging because in the present case densities of handling predators depend also on the predator diet choice. Nevertheless, it is proved in Appendix C that to maximize R the first, more profitable prey type must always be attacked when encountered, i.e., $u_1 = 1$. The optimal predator strategy with respect to the alternative prey type cannot be computed analytically. Numerical simulations show that contrary to the classic optimal foraging theory the inclusion of the less profitable prey type will be more gradual as density of the preferred prey type decreases (Fig. 2) and partial preferences for the alternative resources arise when handled prey are considered. We remark, that scales differ in Fig. 2 for the two curves. In the case of "zero-one" switch (dashed line) the meaning of "prey" is free prey while in the case of partial preference curve (solid line) "prey" means both free and handled prey. This causes that switching for the partial preference case occurs at higher "prey" densities.

5. Discussion

In predator–prey models prey are removed from the system once they have been captured. Thus, these models neglect the effect, if any, of handled prey on predator–prey population dynamics. In this article we have studied the effect of handled prey on predator–prey population dynamics, i.e., we have assumed that prey are removed from the system only after they have been handled. In this context "prey" mean those that are free and those that are handled. The question arises whether distinction between these two cases has any bearing on predictions of models of theoretical ecology. To shed some light on this controversy, we have first re-derived the Holling type II functional response with respect to the overall prey density. The classic Holling type II functional response (Holling, 1959) relates the consumption rate of a single predator to the density of free prey. Assuming that a single predator does not handle more than a single prey at a time, it does not make sense to distinguish between free and handled prey. However, when more predators are considered then functional response can be derived either with respect to free prey density, or with respect to the overall prey density (including those prey that are handled). The first case leads to the classical Holling type II functional response, while the second case leads to a functional response that depends explicitly on the predator density. This is because as some prey are handled, the encounter rate of a searching predator with free prey decreases which leads to interference between predators. In environments with a single predator, both scenarios lead to the same functional response. As the number of predators increases, the initial slope of the functional response declines. Such an effect was experimentally observed by Eveleigh and Chant (1982) in experiments with various numbers of predacious phytoseiid mites, *Phytoseiulus persimilis* (Athias-Henriot) and *Amblyseius degenerans* (Berlese). Although these experimental results qualitatively agree with our predictions (as predator number increases, the initial slope of the functional response decreases, Fig. 1), quantitatively our functional response predicts a slower decrease of the initial slope of the functional response than was observed by Eveleight and Chant.

Various forms of interference can be found in literature (for a recent review see Skalski and Gilliam, 2001). When compared with the Holling type II functional response, all these functional responses with interference assume an additional parameter, i.e., another degree of freedom. Contrary to this our functional response assumes only two parameters.

Then we have studied behavior of an analogue of the MacArthur–Rosenzweig predator–prey population dynamical model without any prey density dependence. It is well known that when only free prey are considered, this model has an unstable population equilibrium. We have proved in this article that when handled prey are considered and only free prey reproduce, then the population equilibrium can be stable but only for ecologically implausible parameter values (for stability the efficiency with which prey are converted to predators must be larger than 1). Thus, for realistic parameter values, population dynamics predict the same type unstable equilibrium behavior regardless of whether we consider only free prey, or both free and handled prey together. It is a well-known fact that density-dependent prey growth described by the logistic growth stabilizes the MacArthur–Rosenzweig predator–prey model for not too high values of the resource carrying capacity. For high carrying capacities the equilibrium is destabilized and a stable limit cycle emerges. Numerical simulations not reported here suggest the same pattern for our model. Thus, we conclude that the use of the classic predator–prey models with the Holling type II functional response seems to be a good approximation of reality. Including more detailed description of the foraging process that distinguishes between free and handled prey does not change the stability properties of the basic population dynamical model. However, it makes the functional response dependent on the predator density which is referred to as interference in ecological literature. It has been shown earlier that interference has stabilizing effect on predator–prey population dynamics (Beddington, 1975; DeAngelis et al., 1975; Free et al., 1977; Freedman, 1979; Polis, 1988; Ruxton et al., 1992; van der Meer and Ens, 1997; Fretwell and Lucas, 1970). In this article we have showed that interference caused by decrease in free prey density due to positive handling times in a multiple predator environment is not strong enough to stabilize the classical predator–prey population dynamics with exponentially growing prey population.

The interference which is naturally caused by positive handling times can, however, lead to some qualitatively new predictions. In this article we have showed that inclusion of handled prey leads to the emergence of partial preferences for the alternative, less profitable prey type. Partial preferences mean that the less profitable prey type is included in the predator's diet with a probability which is between zero and one. The classical optimal foraging theory that considers a single predator does not predict such partial preferences (Charnov, 1976), although partial preferences were widely reported in literature. In this article we have showed that in multiple predator environments partial preferences arise naturally as a consequence of interference among predators. If handling times are very small, than our form of the functional response in two-prey environment (8) will be very similar to the classical multiprey Holling type II functional response and partial preferences will be very weak. Thus, one can expect that the interference discussed in this article can lead to some stronger partial preferences only provided the handling times are long enough and there are more predators.

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Appendix A. Derivation of the functional response (1)

Let us consider a single predator in time interval $(0, T)$. By T_h we denote time devoted to handling a prey and by T_s the search time. Then we get

$$T_h = \lambda h x_f T_s,$$

where h denotes handling time of one prey item and λ is the search rate of predators. Because $T = T_h + T_s$ we get

$$T_s = \frac{T}{1 + \lambda h x_f}, \qquad T_h = \frac{\lambda h x_f T}{1 + \lambda h x_f}.$$

Thus,

$$y_h = \frac{T_h}{T_s} y_s = \lambda h x_f (y - y_h) = \lambda h (x - y_h)(y - y_h).$$

Solving the above quadratic equation for y_h gives

$$y_h = \frac{x + y + 1/(\lambda h) - \sqrt{(x + y + 1/(\lambda h))^2 - 4xy}}{2}$$

and

$$y_s = \frac{\sqrt{(x - y + 1/(h\lambda))^2 + 4y/(h\lambda)} - (x - y + 1/(h\lambda))}{2}.$$

This gives the functional response (1).

Appendix B. Derivation of model (4)

Predator–prey population dynamics are described by the following model:

$$\begin{aligned}
\frac{\mathrm{d}x_f}{\mathrm{d}t} &= r x_f - \lambda x_f y_s,\\
\frac{\mathrm{d}y_s}{\mathrm{d}t} &= -\lambda x_f y_s + \frac{y_h}{h} - m y_s + e\frac{y_h}{h},\\
\frac{\mathrm{d}y_h}{\mathrm{d}t} &= \lambda x_f y_s - \frac{y_h}{h} - m y_h,
\end{aligned} \tag{B.1}$$

where r is the per capita prey growth rate, λ is the predator cropping rate, h denotes handling time of one prey item, e is the efficiency rate in which handled prey are converted to new predators and m is per capita predator mortality rate. The number of handled prey (x_h) is equal to the number of handling predators (y_h). The above model assumes that only free prey reproduce and newborn predators become immediately searching predators. Functional response allows us to approximate the above system (B.1) by a two-dimensional system. Adding the last equation of (B.1) to the first and second one we obtain

$$\begin{aligned}
\frac{\mathrm{d}x}{\mathrm{d}t} &= rx - (1 + mh + rh) y_h / h,\\
\frac{\mathrm{d}y}{\mathrm{d}t} &= e y_h / h - m y,
\end{aligned}$$

where $x = x_f + y_h, y = y_s + y_h$ and substitution $y_h/h = F(x, y)y$ leads to model (4).

Characteristic polynomial of Eq. (4) with functional response F evaluated at the equilibrium E is

$$s^2 + \frac{hmr(1 - e + 2hm)}{hr(hm - e) - e(1 + hm)} s + \frac{mr(e - hm)(1 + hm)}{e(1 + hm) + hr(e - hm)}.$$

The last coefficient in the characteristic polynomial is positive. The coefficient by s is positive if $e > 1 + hm$ which implies local stability of E. Otherwise, E is unstable.

Appendix C. Optimal foraging theory

Let us consider a predator during a small time interval $(0, T)$. In this time interval the predator is either searching for a prey (for time T_s), or handling prey type 1 (for time T_h^1), or prey type 2 (for time T_h^2). In time T_s a searching predator will encounter $\lambda_i (x_i - y_{hi}) T_s$ free prey type i. Thus,

$$T_h^i = \lambda_i h_i u_i (x_i - y_{hi}) T_s$$

and

$$T_s = \frac{T}{1 + \lambda_1 h_1 u_1 (x_1 - y_{h1}) + \lambda_2 h_2 u_2 (x_2 - y_{h2})}.$$

Because

$$\frac{y_{hi}}{y_s} = \frac{T_{hi}}{T_s}, \quad i = 1, 2$$

we get the following system of equations for y_{h1} and y_{h2}

$$\begin{aligned}
y_{h1} &= \lambda_1 h_1 u_1 (x_1 - y_{h1})(y - y_{h1} - y_{h2}),\\
y_{h2} &= \lambda_2 h_2 u_2 (x_2 - y_{h2})(y - y_{h1} - y_{h2}).
\end{aligned}$$

Let $x_i > 0$, $i = 1, 2$, $y > 0$. We show that this system (see also (9)) has only one solution y_{hi}, $i = 1, 2$ such that

$$0 \leqslant y_{hi} < x_i, \quad i = 1, 2, \quad y_{h1} + y_{h2} < y.$$

Set $a_i = \lambda_i h_i u_i$ and assume $0 < a_1 < a_2$. Certainly

$$y_{h2} = \frac{a_2 x_2 y_{h1}}{a_1 x_1 + (a_2 - a_1) y_{h1}}.$$

Using this equality the first equation of (9) can be rewritten

$$\begin{aligned}
y_{h1}[a_1 x_1 + (a_2 - a_1) y_{h1}] = a_1 (x_1 - y_{h1}) [a_1 x_1 y\\
+ ((a_2 - a_1) y - a_1 x_1 - a_2 x_2) y_{h1}\\
- (a_2 - a_1)(y_{h1})^2].
\end{aligned} \tag{C.1}$$

The left side of the above equation is a quadratic polynomial (in y_{h1}) whereas the right side is a cubic polynomial. Taking into consideration their values at $y_{h1} = 0$ and x_1 we conclude that (C.1) has at least one solution in the interval $(0, x_1)$. Since left side of Eq. (C.1) converges to infinity and the right side converges to minus infinity as y_{h1} converges to minus infinity, Eq. (C.1) has a solution $y_{h1} < 0$. Since the cubic polynomial diverges to infinity faster then the quadratic one for y_{h1} converging to infinity, Eq. (C.1) has a solution with $y_{h1} > 0$. This implies that there exists exactly one solution in the interval $(0, x_1)$. If $0 < a_2 < a_1$ then we exchange y_{hi} and the proof follows exactly the same lines as above.

Now we prove that predator's optimal foraging strategy is to include the more profitable prey type in diet, i.e., $u_1 = 1$. For simplicity, we define

$$d_i = x_i - y_{hi}, \quad d = y - y_{h1} - y_{h2},$$
$$w_i = u_i\lambda_i h_i(x_i - y_{hi}), \quad i = 1, 2.$$

Thus,

$$R = \frac{(e_1/h_1)w_1 + (e_2/h_2)w_2}{1 + w_1 + w_2}. \tag{C.2}$$

Eq. (9) become

$$y_{h1} = \lambda_1 h_1 u_1 d_1 d, \quad y_{h2} = \lambda_2 h_2 u_2 d_2 d.$$

Deriving the above two equations with respect to u_1 yields

$$\begin{aligned}&\frac{\partial y_{h1}}{\partial u_1}(1 + \lambda_1 h_1 d u_1 + \lambda_1 h_1 d_1 u_1)\\&\quad + \frac{\partial y_{h2}}{\partial u_1}\lambda_1 h_1 d_1 u_1 = \lambda_1 h_1 d_1 d,\\&\frac{\partial y_{h1}}{\partial u_1}\lambda_2 h_2 d_2 u_2\\&\quad + \frac{\partial y_{h2}}{\partial u_1}(1 + \lambda_2 h_2 d u_2 + \lambda_2 h_2 d_2 u_2) = 0.\end{aligned} \tag{C.3}$$

From (C.3) we get

$$\frac{\partial y_{h1}}{\partial u_1} = \lambda_1 h_1 d_1 d(1 + \lambda_2 h_2 d u_2 + \lambda_2 h_2 d_2 u_2)/D,$$
$$\frac{\partial y_{h2}}{\partial u_1} = -\lambda_1 h_1 d_1 d \lambda_2 h_2 d_2 u_2/D,$$

where

$$\begin{aligned}D &= (1 + \lambda_1 h_1 d u_1 + \lambda_1 h_1 d_1 u_1)(1 + \lambda_2 h_2 d u_2 + \lambda_2 h_2 d_2 u_2)\\&\quad - \lambda_1 h_1 d_1 u_1 \lambda_2 h_2 d_2 u_2\\&= 1 + \lambda_1 h_1 d u_1 + \lambda_1 h_1 d_1 u_1 + \lambda_2 h_2 d u_2 + \lambda_2 h_2 d_2 u_2\\&\quad + \lambda_1 h_1 d u_1 \lambda_2 h_2 d u_2 + \lambda_1 h_1 d_1 u_1 \lambda_2 h_2 d u_2\\&\quad + \lambda_1 h_1 d u_1 \lambda_2 h_2 d_2 u_2 > 0.\end{aligned}$$

From (9) we get

$$\frac{\partial w_1}{\partial u_1} = \frac{\partial}{\partial u_1}\frac{y_{h1}}{y - y_{h1} - y_{h2}} = \frac{(\partial y_{h1}/\partial u_1)(y - y_{h2}) + y_{h1}(\partial y_{h2}/\partial u_1)}{(y - y_{h1} - y_{h2})^2},$$

$$\frac{\partial w_2}{\partial u_1} = \frac{\partial}{\partial u_1}\frac{y_{h2}}{y - y_{h1} - y_{h2}} = \frac{(\partial y_{h2}/\partial u_1)(y - y_{h1}) + y_{h2}(\partial y_{h1}/\partial u_1)}{(y - y_{h1} - y_{h2})^2}.$$

From (C.2) we get

$$\frac{\partial R}{\partial u_1} = \frac{(\partial w_1/\partial u_1)(e_1/h_1 + (e_1/h_1 - e_2/h_2)w_2) + (\partial w_2/\partial u_1)(e_2/h_2 - (e_1/h_1 - e_2/h_2)w_1)}{(1 + w_1 + w_2)^2}.$$

Because $y_{hi}, \partial y_i/\partial u_1, w_i, \partial w_i/\partial u_1$ are independent of e_i, $\partial R/\partial u_1$ is a linear function of e_2. We distinguish two cases.

First, let us assume that $e_2/h_2 = e_1/h_1$. Then

$$\begin{aligned}\frac{\partial R}{\partial u_1} &= \frac{e_1(\partial w_1/\partial u_1 + \partial w_2/\partial u_1)}{h_1(1 + w_1 + w_2)^2}\\&= \frac{e_1 y(\partial y_{h1}/\partial u_1 + \partial y_{h2}/\partial u_1)}{h_1(1 + w_1 + w_2)^2(y - y_{h1} - y_{h2})^2}\\&= \frac{e_1 y}{h_1(1 + w_1 + w_2)^2(y - y_{h1} - y_{h2})^2}\\&\quad \times \frac{\lambda_1 h_1 d_1 d(1 + \lambda_2 h_2 d u_2)}{D} > 0.\end{aligned}$$

Thus R is increasing function of u_1.

Second, let us assume that $e_2 = 0$. From (C.2) we have

$$R = \frac{e_1 w_1}{h_1(1 + w_1 + w_2)}.$$

Thus, R is an increasing function in w_1. Because

$$\begin{aligned}&\frac{D}{\lambda_1 h_1 d_1 d}(y - y_{h1} - y_{h2})^2\frac{\partial w_1}{\partial u_1}\\&\quad = \frac{D}{\lambda_1 h_1 d_1 d}\frac{\partial y_{h1}}{\partial u_1}(y - y_{h2}) + y_{h1}\frac{\partial y_{h2}}{\partial u_1}\\&\quad = (1 + \lambda_2 h_2 d u_2 + \lambda_2 h_2 d_2 u_2)(y - y_{h2}) - y_{h1}\lambda_2 h_2 d_2 u_2\\&\quad = (1 + \lambda_2 h_2 d u_2)(y - y_{h2})\\&\qquad + \lambda_2 h_2 d_2 u_2(y - y_{h1} - y_{h2}) > 0,\end{aligned}$$

w_1 is an increasing function of u_1 and, consequently, R is an increasing function of u_1 too.

It follows that $\partial R/\partial u_1$ is positive in the interval $0 \leqslant e_2/h_2 \leqslant e_1/h_1$ and, consequently, $u_1 = 1$.

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