Evolutionary stability of optimal foraging: Partial preferences in the diet and patch models

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A B S T R A C T

In this article the patch and diet choice models of the optimal foraging theory are reanalyzed with respect to evolutionary stability of the optimal foraging strategies. In their original setting these fundamental models consider a single consumer only and the resulting fitness functions are both frequency and density independent. Such fitness functions do not allow us to apply the classical game theoretical methods to study an evolutionary stability of optimal foraging strategies for competing animals. In this article frequency and density dependent fitness functions of optimal foraging are derived by separation of time scales in an underlying population dynamical model and corresponding evolutionarily stable strategies are calculated. Contrary to the classical foraging models the results of the present article predict that partial preferences occur in optimal foraging strategies as a consequence of the ecological feedback of consumer preferences on consumer fitness. In the case of the patch occupation model these partial preferences correspond to the ideal free distribution concept while in the case of the diet choice model they correspond to the partial inclusion of the less profitable prey type in predators diet.

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1. Introduction

Optimal foraging theory (OFT; e.g., MacArthur and Pianka, 1966; Charnov, 1976; Stephens and Krebs, 1986) assumes that organisms forage in such a way as to maximize their fitness measured as energy intake rate. These models assume a homogeneous (fine-grained) environment with several resource types that a consumer encounters sequentially, and predict the optimal consumer diet. This line of research led to the prey model (also called the "diet choice"; Charnov, 1976). This model assumes that consumer fitness is measured as the average energy intake rate. The classical example of such a situation is the experiment with great tits where a single animal feeds on two food types delivered on a conveyor belt (e.g., Krebs et al., 1977; Berec et al., 2003) which assures that prey are not depleted by predation. Thus, no interference or competition for food between consumers is considered. A similar reasoning can be applied to the case where a consumer forages in a heterogeneous environment consisting of discrete foraging patches. In this case the consumer should move to the patch with the highest payoff. These predictions are based on fitness functions that are both density and frequency independent. They consider a single consumer and resource densities that are not influenced by predation. Thus, they miss completely competition between consumers that can be either due to interference, or due to exploitation of resources. In fact, such models can be applied only to laboratory experiments with a single consumer that does not influence resource density (e.g., a single great tit feeding on two prey types delivered on the conveyor belt).

More realistic models must consider consumer competition (either interference competition, or exploitative competition). A density dependent approach in patchy environments led to the concept of the ideal free distribution (IFD; Fretwell and Lucas, 1969). These authors assumed that patch payoff decreases with increasing number of individuals in that patch (e.g., this captures interference among birds) and predicted that under the IFD no individual can increase its fitness by changing its strategy measured by residence times in different patches. Because under the IFD all patches provide animals with the same fitness the question arises whether such a situation is stable or not. Indeed, assuming a single mutant with an infinitely large resident population that is distributed according to the IFD, fitness of that mutant is independent and the same as is the fitness of resident animals. One approach to study stability in such situations is to use the concept of evolutionarily stable strategies (Maynard Smith and Price, 1973; Hofbauer and Sigmund, 1998). In fact it has been shown that the IFD is an evolutionarily stable strategy of the habitat selection game (Křivan et al., 2008). However, this concept of stability assumes that the fitness function is frequency dependent, i.e., it depends both on the mutant as well as on the

resident strategy. Frequency dependence allows us to predict whether a mutant strategy will increase in the resident population or not. Here the idea is that the resident strategy sets the environment (e.g., the resident consumer strategy sets the resource densities) and if a mutant strategy with a higher fitness exists then this strategy spreads, replaces residents, sets a new environment and so on until an evolutionarily stable strategy (ESS) is reached.

Another approach that considers explicitly resource–consumer population dynamics together with optimal foraging was also used in theoretical ecology (reviewed in Abrams, 2010). These models show how resident individuals that follow optimal foraging strategy influence resource levels which, in turn, influence consumer numbers and strategy. Although dynamical models capture the ecological feedback, they do not provide us with information about the evolutionary stability of optimal foraging strategies. To study this question it is necessary to study conditions under which the optimal foraging strategy is resistant to mutant invasions. Studying evolutionary stability in dynamic models of optimal foraging is more complicated than in static models of behavioral ecology (such as the Hawk–Dove model, or the Prisoners dilemma; Maynard Smith and Price, 1973; Hofbauer and Sigmund, 1998) because it requires to analyze population dynamics for both resources, resident and mutant consumers (e.g., Křivan and Cressman, 2009; Cressman and Křivan, 2010).

To sum up, the problem is that some models of optimal foraging are described by fitness functions that are both frequency and density independent, and they do not allow us to predict optimal foraging strategies when interference or resource depletion occur. On the other hand, in the full dynamic setting that describes explicitly the effect of resident strategies on resource densities, the resulting models are multidimensional and difficult to analyze with respect to evolutionary stability of optimal strategies. My aim is to show how frequency dependent fitness functions can be obtained from frequency independent fitness functions, using a time scale argument. I start with a frequency independent fitness function defined as per capita population growth rate. Then I consider resource–consumer population dynamics and I assume that resource dynamics run on a faster time scale when compared with consumer population dynamics. This is the case of many resource–consumer systems where resource generation time is shorter than consumer generation time (e.g., many plants have short generation times relative to mammalian herbivores). This time scale separation allows me to assume that at each consumer density resources are at the corresponding population equilibrium. Substituting this resource equilibrium to the consumer fitness function leads to a frequency dependent fitness function that can be analyzed from evolutionary perspective. I apply this approach to diet and patch choice paradigms of optimal foraging theory. In both cases this approach predicts emergence of partial preferences for alternative prey/patch types. In the case of the patch model partial preferences describe the consumer ideal free distribution (Fretwell and Lucas, 1969). Although partial preferences are not predicted by the classical frequency independent models of optimal foraging, they were observed in many foraging studies (for a review, see Stephens and Krebs, 1986). Explanations for partial preferences ranging from incorrect classification of resource and sampling by consumers (Krebs et al., 1977; Rechten et al., 1983), resource crypsis (Erichsen et al., 1980), incorrect estimation of encounter rates with resource by consumers (McNamara and Houston, 1987; Hirvonen et al., 1999), limited memory capacity of consumers (Mangel and Roitberg, 1989; Bélisle and Cresswell, 1997), and limited knowledge of the environment (Berec and Křivan, 2000). In this article I will show another mechanism that explains emergence of partial preferences by the ecological feedback of consumer preferences on their fitness.

2. The patch occupation model

I will consider an environment consisting of two foraging patches containing resources with abundance x_i in patch i ($i = 1, 2$). If e_i denotes the efficiency with which resources are converted to new consumers, λ_i is the consumer search rate for resources in patch i, and m_i is the consumer mortality rate in patch i then consumer fitness expressed as the instantaneous per capita population growth rate (cf. consumer per capita population growth rate in model (3) below) is

$$W = (e_1\lambda_1 x_1 - m_1)\nu_1 + (e_2\lambda_2 x_2 - m_2)\nu_2, \tag{1}$$

where ν_i ($\nu_1 + \nu_2 = 1$) is the proportion of the time a consumer stays in patch i. Thus, ν_i measures the consumer preference for patch i. Assuming that consumer preferences are adaptive, the optimal consumer strategy is to stay in patch 1 when patch payoff is higher there than in patch 2 and vice versa. Thus, the strategy that maximizes consumer fitness W is

$$\nu_1 = \begin{cases} 1 & \text{if } e_1\lambda_1 x_1 - m_1 > e_2\lambda_2 x_2 - m_2, \\ 0 & \text{if } e_1\lambda_1 x_1 - m_1 < e_2\lambda_2 x_2 - m_2. \end{cases} \tag{2}$$

This simple prediction states that consumers should move to the patch that provides them with the highest fitness. It is clear that mutants using a different strategy obtain a lower fitness and therefore, the above strategy is evolutionarily stable. However, due to interference or resource depletion it is also obvious that as more and more consumers move to a patch, this patch payoff must decrease, which is not captured by maximization of fitness function W. To model effects of consumers on resources, I will consider the following population dynamics (e.g., Fryxell and Lundberg, 1994, 1997; Křivan, 1997; Křivan and Schmitz, 2003)

$$\left. \begin{aligned} \frac{dx_1}{dt} &= a_1 x_1 \left(1 - \frac{x_1}{L_1}\right) - \nu_1\lambda_1 x_1 y, \\ \frac{dx_2}{dt} &= a_2 x_2 \left(1 - \frac{x_2}{L_2}\right) - \nu_2\lambda_2 x_2 y, \\ \frac{dy}{dt} &= (e_1\lambda_1 x_1 - m_1)\nu_1 y + (e_2\lambda_2 x_2 - m_2)\nu_2 y, \end{aligned} \right\} \tag{3}$$

where y is consumer density, L_i is the resource i carrying capacity, and a_i is the resource per capita population growth rate. I stress here that consumer fitness (1) is indeed the per capita consumer population growth rate in model (3).

Using model (3) I derive a new frequency dependent fitness function. I consider a mutant with a strategy $\tilde{\nu} = (\tilde{\nu}_1, \tilde{\nu}_2)$ in a population of residents with a strategy $\nu = (\nu_1, \nu_2)$ and I re-write frequency independent fitness function (1) as a function of both mutant and resident strategies

$$W(\tilde{\nu}, \nu) = (e_1\lambda_1 x_1 - m_1)\tilde{\nu}_1 + (e_2\lambda_2 x_2 - m_2)\tilde{\nu}_2.$$

The dependence of this function on the resident strategy ($\nu = (\nu_1, \nu_2)$) is indirect through resource abundance that is set by the resident strategy in model (3). To make this dependence explicit I will assume that resource population dynamics run on a fast time scale when compared with consumer population dynamics, so that for each consumer density resources relatively quickly reach their corresponding equilibrium densities. When residents use strategy $\nu = (\nu_1, \nu_2)$, the resource equilibrium at consumer density y, calculated from (3), is $x_i = L_i(1 - \lambda_i\nu_i y/a_i)$, ($i = 1, 2$). Substituting this density in W leads to a frequency dependent fitness function

$$W(\tilde{\nu}, \nu) = r_1\tilde{\nu}_1\left(1 - \frac{\nu_1 y}{K_1}\right) + r_2\tilde{\nu}_2\left(1 - \frac{\nu_2 y}{K_2}\right), \tag{4}$$

where

$$r_i = e_i\lambda_i L_i - m_i \quad \text{and} \quad K_i = \frac{a_i(e_i\lambda_i L_i - m_i)}{e_i L_i \lambda_i^2} \tag{5}$$

are the per capita consumer population growth rate and the environmental carrying capacity in patch i. It is an interesting observation that the new frequency dependent fitness function is described by logistic consumer population growth in each patch. In other words, if we assume that consumer population growth in each patch is logistic, we would arrive immediately to fitness function (4). Evolutionarily stable strategy for fitness function W was derived by Cressman et al. (2004) and I briefly recall main results here. Assuming that $r_1 > r_2$, there are two possibilities. Either consumer density is low ($y < (r_1 - r_2)K_1/r_1$) in which case only the better patch 1 will be occupied, or when consumer population is above the critical threshold then both patches will be occupied by consumers, patch payoffs will be the same and the corresponding ESS is

$$v_1^* = \frac{K_1 r_2}{K_1 r_2 + K_2 r_1} + \frac{K_1 K_2 (r_1 - r_2)}{(K_1 r_2 + K_2 r_1)y}. \tag{6}$$

Under this strategy no individual can increase its fitness by changing its strategy and this strategy cannot be invaded by individuals using a different strategy. This shows that when patch payoffs are the same the ESS depends on the consumer population density. This ESS corresponds to the IFD of Fretwell and Lucas (1969). When consumers redistribute instantaneously according to the IFD at each consumer density, consumer population growth is described by a piecewise logistic equation:

$$\frac{dy}{dt} = \begin{cases} r_1 y \left(1 - \dfrac{y}{K_1}\right) & \text{if } y \leq \dfrac{(r_1 - r_2)K_1}{r_1}, \\ \dfrac{r_1 r_2 (K_1 + K_2)}{K_2 r_1 + K_1 r_2} y \left(1 - \dfrac{y}{K_1 + K_2}\right) & \text{if } y > \dfrac{(r_1 - r_2)K_1}{r_1}, \end{cases} \tag{7}$$

(Křivan and Sirot, 2002). The equilibrium of this model is $K_1 + K_2$ and at this equilibrium consumer preferences satisfy

$$\frac{v_1^*}{v_2^*} = \frac{K_1}{K_2}. \tag{8}$$

These preferences correspond to the so-called balanced dispersal under which no mutants can invade (McPeek and Holt, 1992; Padrón and Trevisan, 2006; DeAngelis et al., 2007).

Now I compare solutions of the resource–consumer model (3) (Fig. 1, solid lines) with optimal consumer strategy given by (2), with solutions of the single-species logistic model (7) (Fig. 1, dashed lines). Křivan and Schmitz (2003) showed that for $L_i > m_i/(e_i\lambda_i)$, consumer population dynamics described by (3) converge on the equilibrium density $K_1 + K_2$ at which the corresponding IFD is given by formula (8) exactly as for model (7). This means that model (7) with optimal strategy (6) converges on the same equilibrium as the original resource–consumer model (3) (Fig. 1). In addition, if resource population dynamics are much faster than consumer population dynamics (Fig. 1, left panel), population trajectories of the reduced model (7) are close to trajectories of the original model (3). If both resource and consumer population dynamics operate on comparable time scales (Fig. 1, right panel) the differences between trajectories get larger.

3. The diet choice model

Now I will consider the diet choice model. Assuming two prey types, consumer fitness in a fine-grained environment is

$$\frac{e_1\lambda_1 u_1 x_1 + e_2\lambda_2 u_2 x_2}{1 + h_1\lambda_1 u_1 x_1 + h_2\lambda_2 u_2 x_2}, \tag{9}$$

(Charnov, 1976). Here x_i is the density of resource i in the environment, λ_i is the consumer search rate for prey type i, u_i is the consumer preference for prey type i ($0 \leq u_i \leq 1$), h_i is the handling time, and e_i is the net energy gain obtained from prey type i. I stress here that on the contrary to the patch model, the diet choice model does not assume that the sum of strategies equals to one. Optimal foraging theory assumes that resource densities are fixed, and maximization of (9), with respect to consumer preferences for either resource, leads to the zero-one rule (Charnov, 1976). This rule predicts that consumers will always forage on the most profitable resource type, i.e., the resource type with the highest ratio e_i/h_i. In what follows I will assume that the resource type 1 is more profitable than the alternative resource type 2 (i.e., $e_1/h_1 > e_2/h_2$). Therefore, resource 1 will be always included in the consumer diet ($u_1 = 1$) while the second resource type will be included only if density of the first resource decreases below the threshold density

$$x_1^* = \frac{e_2}{\lambda_1(e_1 h_2 - e_2 h_1)}, \tag{10}$$

(e.g., Charnov, 1976; Stephens and Krebs, 1986). Consumer strategy is not uniquely predicted by the diet choice model when the more profitable prey density equals x_1^*, because under this condition any strategy will lead to the same fitness.

Now I will derive a frequency dependent fitness function and find the corresponding ESS. For this I consider ecological feedback between consumers and resources that is described by the following Rosenzweig–MacArthur predator–prey dynamics (Křivan and Schmitz, 2003)

$$\left. \begin{array}{l} \dfrac{dx_1}{dt} = a_1 x_1 \left(1 - \dfrac{x_1}{L_1}\right) - \dfrac{\lambda_1 x_1 y}{1 + h_1\lambda_1 x_1 + h_2\lambda_2 u_2 x_2}, \\[4mm] \dfrac{dy}{dt} = \left(\dfrac{e_1\lambda_1 x_1 + e_2\lambda_2 u_2 x_2}{1 + h_1\lambda_1 x_1 + h_2\lambda_2 u_2 x_2} - m\right) y. \end{array} \right\} \tag{11}$$

This model considers population dynamics of the preferred resource (x_1) and consumers (y). It assumes that the alternative resource type density x_2 stays constant. This can be the case where there is an influx of alternative food resources to the system from outside sources (allochthonous resource; Huxel and McCann, 1998). Parameter u_2 describes consumer preferences for the alternative resource.

Fitness of a mutant consumer with strategy $\tilde{u}_2$ in a population of residents with strategy u_2 is

$$W(\tilde{u}_2, u_2) = \frac{e_1\lambda_1 x_1 + e_2\lambda_2 \tilde{u}_2 x_2}{1 + h_1\lambda_1 x_1 + h_2\lambda_2 \tilde{u}_2 x_2}, \tag{12}$$

and I derive a frequency dependent fitness function as in the case of the patch model. For each fixed consumer strategy the resource 1 isocline (given by $dx_1/dt = 0$) is an upside down parabola (Fig. 2). Assuming that resource dynamics run on a fast time scale when compared with consumer demography, trajectories move in the direction of the arrows in Fig. 2 and they quickly reach the stable part of the resource isocline (solid line)

$$x_{1+} = \frac{-1 + h_1 L_1 \lambda_1 - h_2 u_2 x_2 \lambda_2 + H(u_2)\sqrt{1 - c(u_2)y}}{2 h_1 \lambda_1}, \tag{13}$$

where

$$H(u_2) = 1 + h_1 L_1 \lambda_1 + h_2 x_2 u_2 \lambda_2, \quad c(u_2) = \frac{4 h_1 L_1 \lambda_1^2}{a_1 H^2(u_2)}.$$

I remark that the resource isocline is defined only for consumer densities that satisfy $y < 1/c(u_2)$ which I will assume below. Substituting the equilibrium resource density x_{1+} in (12) leads to
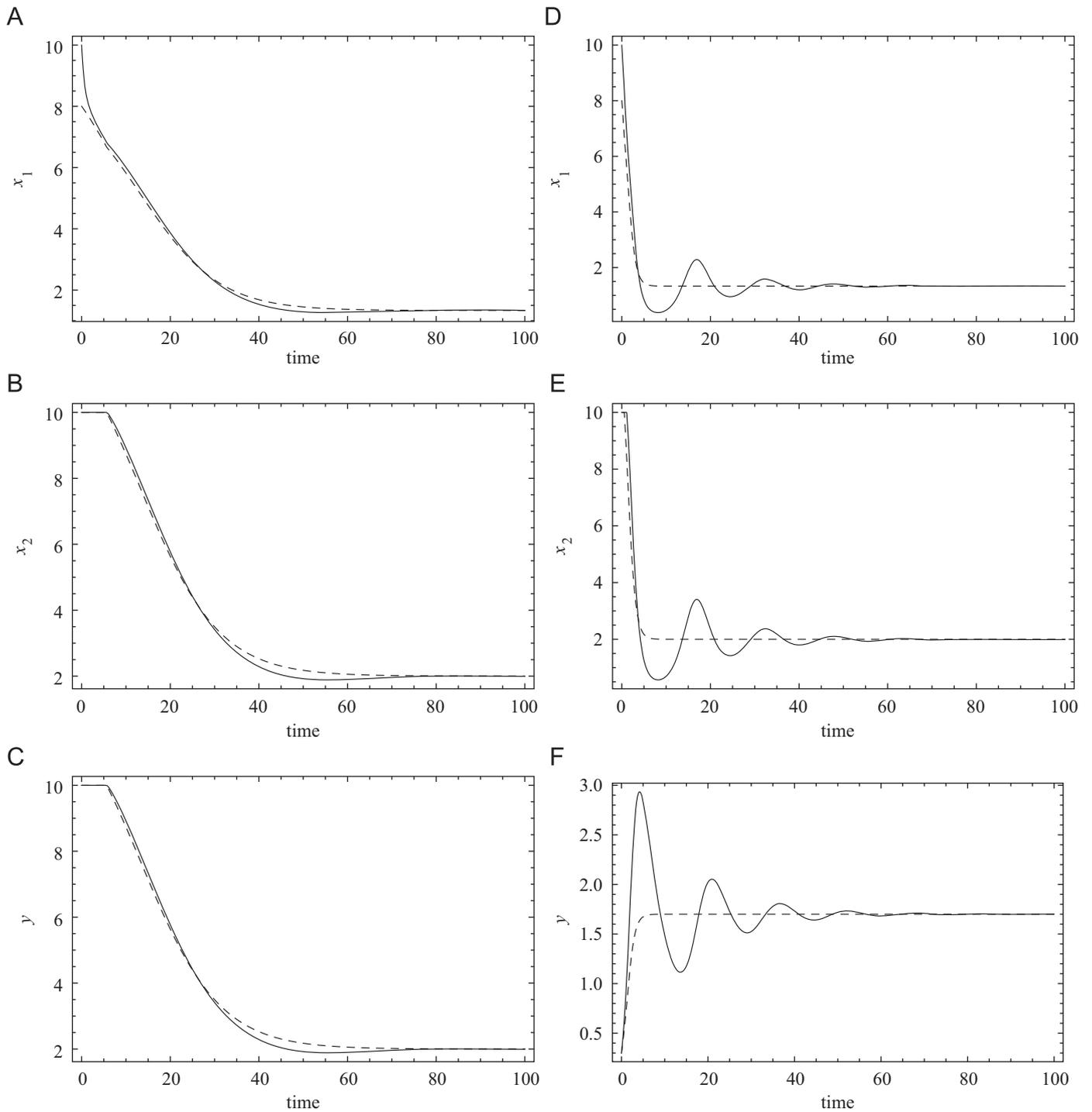
Fig. 1. Solutions of the patch model (3) (solid line) where consumers follow the optimal foraging strategy given by (2), and solutions of the single-species model (7) (dashed line). Resource densities for model (7) are given by $x_i = L_i(1-y(t)\lambda_i v_i/a_i)$ with the optimal strategy v_i given by (6). The left panel (A,B,C) assumes that consumer demographic parameters ($e_1 = 0.015$, $e_2 = 0.01$, $m_1 = m_2 = 0.02$) are much smaller when compared to resource parameters. This discrepancy causes resource population dynamics to run on a fast time scale when compared with consumer population dynamics. The right panel (D,E,F) assumes more similar time scales for both resource and consumer dynamics ($e_1 = 0.15$, $e_2 = 0.1$, $m_1 = m_2 = 0.2$). Other parameters used in simulations: $L_1 = L_2 = 10$, $a_1 = 1.5$, $a_2 = 0.5$, $\lambda_1 = \lambda_2 = 1$.

the frequency dependent fitness function

$$W(\tilde{u}_2, u_2) = \frac{2h_1(e_1 L_1 \lambda_1 + e_2 x_2 \tilde{u}_2 \lambda_2) - e_1 H(u_2)(1-\sqrt{1-c(u_2)y})}{2h_1 H(\tilde{u}_2) - h_1 H(u_2)(1-\sqrt{1-c(u_2)y})}. \quad (14)$$

The selection gradient $\partial W(\tilde{u}_2, u_2)/\partial \tilde{u}_2$ predicts the direction of selective pressure (Vincent and Brown, 2005; Dercole and Rinaldi, 2008). When the gradient is positive, preference for the alternative prey type will increase, while if it is negative, preference will

decrease. The gradient is zero at the singular strategy (Appendix A)

$$u_2^* = \frac{L_1 \lambda_1^2 (e_1 h_2 - e_2 h_1)}{a_1 h_2 \lambda_2 x_2 (L_1 \lambda_1 (e_1 h_2 - e_2 h_1) - e_2)} y - \frac{e_1}{\lambda_2 x_2 (e_1 h_2 - e_2 h_1)}, \quad (15)$$

provided this value is between zero and one, i.e., consumer density satisfies $y_1^* \le y \le y_2^*$ where

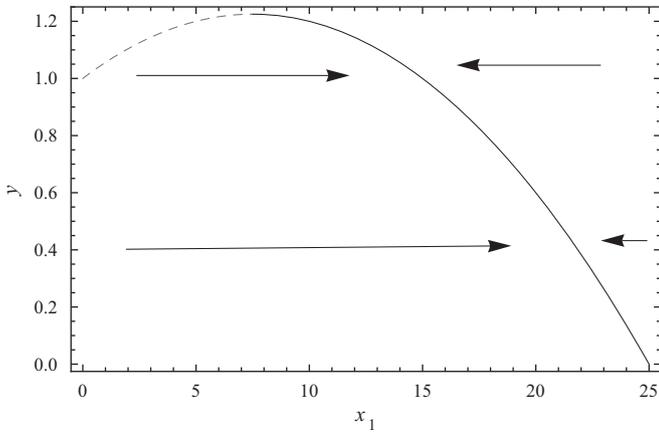$$y_1^* = \frac{a_1 e_1 h_2 (L_1 \lambda_1 (e_1 h_2 - e_2 h_1) - e_2)}{(e_2 h_1 - e_1 h_2)^2 L_1 \lambda_1^2},$$

Fig. 2. Resource isocline of model (11). Only the solid part of the isocline is stable provided resource 1 population dynamics are fast when compared to consumer population dynamics. Arrows indicate direction of trajectories.

and

$$y_2^* = \frac{a_1 h_2 (L_1 \lambda_1 (e_1 h_2 - e_2 h_1) - e_2)(e_1 + (e_1 h_2 - e_2 h_1) x_2 \lambda_2)}{(e_2 h_1 - e_1 h_2)^2 L_1 \lambda_1^2},$$

from Appendix A. For consumer densities for which $y < y_1^*$, I set $u_2^* = 0$ and for $y > y_2^*$, I set $u_2^* = 1$. Fig. 3A shows dependence of the singular strategy on consumer density. It is proved in Appendix A that the singular strategy is not only evolutionarily stable but also convergence stable (Eshel, 1983; Eshel et al., 1997). This means that (1) the singular strategy is resistant to invasion of a small number of mutants that use a different strategy, and (2) it is also resistant to changes in the resident strategy (i.e., when the resident strategy is slightly perturbed, it will return to the convergence stable singular point). Strategies that are evolutionarily and convergence stable are thought as the end point of evolution (Vincent and Brown, 2005; Dercole and Rinaldi, 2008).

Now I will analyze the singular consumer strategy as a function of consumer density. If resource 1 carrying capacity is low, so that

$$L_1 < x_1^*, \tag{16}$$

(where x_1^* is given by (10)) consumers will include the alternative prey type in their diet ($u_2^* = 1$) at all consumer densities, because the critical thresholds y_1^* and y_2^* are negative. Because x_1^* is the critical threshold predicted by the optimal foraging theory, below which the alternative prey type is included in the consumers' diet, the present model predicts that at low environmental carrying capacities for the preferred prey type consumers will behave as generalists. This is because at such low carrying capacities the density of the more profitable prey type can never be higher than is the switching threshold x_1^*.

When the carrying capacity of the preferred resource is higher than is the switching density (i.e., the inequality in (16) is reversed), u_2^* is a piecewise linear function of the consumer density y (Fig. 3A). In this case at low consumer densities consumers will behave as specialists feeding on the more profitable resource type only. As the number of consumers increases resource 1 density will decrease and consumers will start to feed on the alternative resource as well, and their preferences for this resource will increase with consumer numbers. When at high numbers consumers will feed on the alternative food items upon each encounter. This shows that when the consumer fitness reflects frequency and density dependence given by the ecological feedback, partial preferences do arise in the diet choice model.

Now I will consider consumer population dynamics. Consumer dynamics along the stable branch of the prey isocline are obtained by substituting expression for x_{1+} in the consumer equation

in (11). This leads to the following consumer population growth equation:

$$\frac{dy}{dt} = ry\left(1 - \frac{K(u_2)}{1 + \sqrt{1 - c(u_2)y}}\right), \tag{17}$$

where $r = (e_1/h_1) - m$ and $K(u_2) = 2(e_1 + (e_1 h_2 - e_2 h_1) x_2 \lambda_2 u_2)/(H(u_2)(e_1 - h_1 m))$ (Appendix B). Substituting for u_2 in model (17) the singular strategy (u_2^*), describes consumer dynamics with optimal diet selection. For consumer densities for which the consumer singular strategy u_2^* is between 0 and 1, consumer population dynamics simplify to

$$\frac{dy}{dt} = y\frac{e_2 - h_2 m}{h_2}.$$

Depending on the sign of $e_2 - h_2 m$, consumer density either increases or decreases when partial preferences occur. Because the above equation has no non-trivial population equilibrium it follows that no population equilibrium where consumers would show partial preferences for the alternative prey type exists. Consumer equilibria for consumer densities that are higher than y_2^* (i.e., when $u_2^* = 1$) or smaller than y_1^* (i.e., when $u_2^* = 0$) are given by the interior equilibrium of (17) $y^* = K(u_2)(2 - K(u_2))/c(u_2)$ where I substitute 0 or 1 for u_2 (these are given explicitly in Appendix B). Fig. 3B shows one such trajectory of model (17) driven by the consumer singular strategy (solid lines). The corresponding resource 1 density is calculated from (13). Fig. 3C shows the corresponding consumer singular strategy. These results predict that at low consumer densities where resource 1 density is near to its carrying capacity, consumers specialize on the more profitable resource type. As consumers increase in numbers, the preferred resource density decreases to the critical switching density (x_1^*) predicted by the classical model of optimal foraging. From then on, consumer preferences for the alternative prey type start to increase, keeping the preferred resource density at the switching threshold for some time (i.e., times approx. between 5 and 14 in Fig. 3B). Because $e_2 - mh_2 > 0$ in Fig. 3B, consumer density increases (it would decrease otherwise). Once the consumer preference reaches 1 (i.e., consumers attack the alternative resource upon each encounter), consumers and resources tend to a stable equilibrium. This general pattern of population dynamics is also clearly shown in Fig. 3D where the trajectory from panel B is projected on the consumer isocline (the solid dot denotes the population equilibrium). Thus, in the region of consumer densities where preferences for the less profitable resource type are between 0 and 1, consumers exhibit partial preferences. This is a new result because the classical diet choice model does not predict such a gradual shift in consumer preferences at the switching prey density (Stephens and Krebs, 1986). Trajectories of model (11) with the optimal consumer foraging strategy are shown in Fig. 3B as dashed lines. It is clear that they converge to the same equilibrium as trajectories of the single-species model. Using a completely different approach Křivan (1996) (see formula (32) there) calculated consumer strategy at the switching threshold $x_1 = x_1^*$ (i.e., when the classical diet choice model does not define consumer preference for the alternative prey type uniquely). It is an interesting observation that the formula for partial preferences obtained there coincides with the singular strategy u_2^*.

4. Discussion

In this article I have shown how to derive a frequency dependent fitness function from a frequency independent fitness function by using a time scale argument. The time scale argument assumes that resource population dynamics run on a faster time scale when compared with consumer population dynamics.
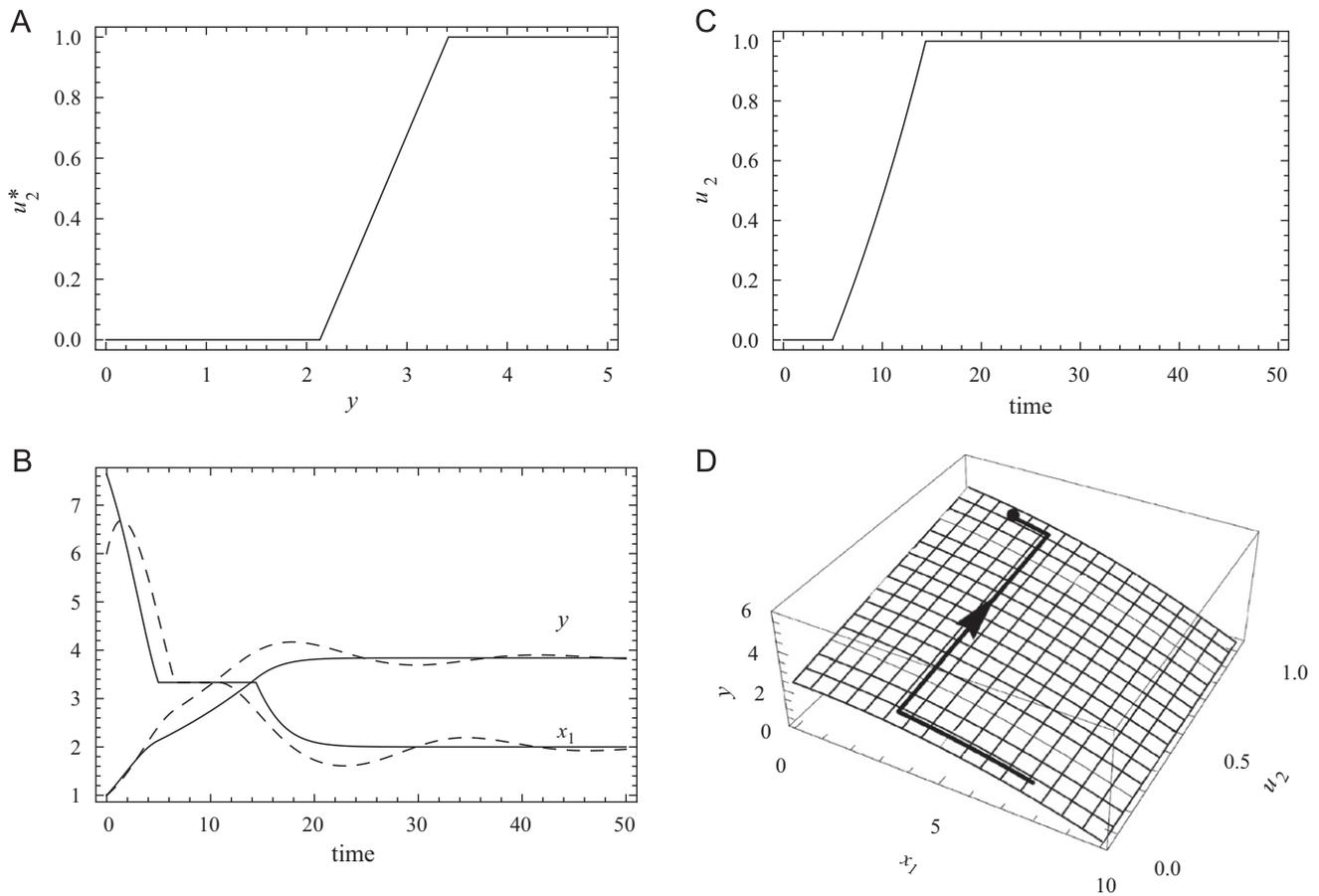
Fig. 3. Panel A shows consumer preference (15) for the alternative prey type in the diet choice model as a function of consumer density. Panel B compares a trajectory of the resource–consumer model (11) (dashed lines) where consumers follow predictions of the classical prey model (i.e., zero-one rule) with a trajectory of the reduced model (17) (solid lines). The corresponding trajectory for resources is given by (13). Panel C shows the corresponding consumer optimal strategy. Panel D shows the solid trajectory from panel B in the resource 1–consumer preference–consumer density phase space. Parameters: $a_1 = 1.2$, $h_1 = h_2 = 0.2$, $e_1 = 0.2$, $e_2 = 0.05$, $\lambda_1 = \lambda_2 = 0.5$, $x_2 = 8$, $m = 0.2$, $L_1 = 10$.

Having a frequency dependent fitness function allowed me to study optimal foraging strategies for multiple consumers and depletable resources. In particular I showed that partial preferences for alternative resources arise in the diet and patch models of optimal foraging.

The diet and patch choice models are two paradigms of the optimal foraging theory (MacArthur and Pianka, 1966; Emlen, 1966). They assume that per capita energy intake rate is a proxy for consumer fitness that is maximized by adaptive consumer foraging behavior. The diet choice model assumes that two or more resources are evenly distributed in the environment and consumption of these resources does not influence their numbers. This assumption is clearly violated in most natural systems. To comply with these assumptions, e.g., conveyor belts that bring food directly to consumers were used in experiments (Krebs et al., 1977; Berec et al., 2003). So what is missing in the diet choice model is the link between consumer numbers and consumer strategy. This link defines an ecological feedback mechanism: consumer foraging strategy influences resource densities which, in turn, set the consumer strategy and density. To model this ecological feedback mechanism some authors considered population dynamics together with the optimal foraging models (e.g., Fryxell and Lundberg, 1994, 1997; Křivan, 1996, 1997; Křivan and Schmitz, 2003; Ma et al., 2003). In these models it often happens that population dynamics tend to densities at which models of optimal foraging do not predict the optimal strategy uniquely. For example, in the patch model consumers will distribute between

the two patches, so that patch payoffs will equalize (Křivan, 1997). Under this situation there is no selection against mutants that can use any strategy, because individual fitness is independent of the strategy. Similarly, dynamical models of diet choice drive periodically density of the more profitable prey type to the threshold where optimal consumer diet is not uniquely predicted (Křivan, 1996). In fact, this non-uniqueness causes fundamental problems for the existence of solutions to these population models (Colombo and Křivan, 1993; Křivan, 1996).

A simpler approach to study the evolutionary stability is based on the concept of evolutionarily stable strategies (e.g., Maynard Smith and Price, 1973; Hofbauer and Sigmund, 1998; Cressman, 2003; Vincent and Brown, 2005). However, to apply methods of static game theory, the fitness function must be frequency dependent, i.e., it must allow us to measure the effect of mutants on the resident strategy. In this article I derived two frequency dependent fitness functions for patch and diet choice models. These fitness functions are based on the assumption that resource population dynamics run on a faster population time scale when compared with consumer population dynamics. Using these fitness functions I derived the corresponding evolutionarily stable strategies for the patch and the diet choice model. In both cases the corresponding ESS predicts partial preferences for resources to occur. In the case of the patch model separation of the resource and consumer time scales leads to consumer population growth that is described by the logistic equation for which the evolutionarily stable strategies were studied (e.g., Křivan and

Sirot, 2002; Morris, 2003; Cressman and Křivan, 2006). These works show that the evolutionarily stable strategy corresponds with the IFD (Fretwell and Lucas, 1969). Similarly, when time scaling is applied to the diet choice model the resulting consumer population growth equation seems to be new. Moreover, partial preferences arise for a range of consumer densities in both models. This is a new prediction because partial preferences were not predicted by the optimal foraging theory (Charnov, 1976). In fact, my present analysis clearly shows that at low consumer densities consumers should specialize on the more profitable prey/patch type only. However, as consumer density increases, consumers also start to utilize the alternative, less profitable prey/patch type with an increasing strength. This prediction should be easily tested using an appropriate data on consumer preferences.

These predictions may have several consequences in population ecology. For example, if consumer preferences depend on consumer numbers, functional responses used in multiple species models should reflect this situation. Thus, they should depend not only on resource densities, but also on consumer densities (for a recent review of flexible foraging on the functional response, see Abrams, 2010). Such a dependency could lead to a more mechanistic explanation of the effect of consumer density on the functional response.

Acknowledgments

Appendix A. Evolutionary stability of the diet choice model

Fitness function (14) can be written as

$$W(\tilde{u}_2, u_2) = \frac{A\tilde{u}_2 + B}{C\tilde{u}_2 + D},$$

where

$A = 2e_2 h_1 x_2 \lambda_2$, $B = 2h_1 e_1 L_1 \lambda_1 - e_1 H(u_2)(1 - \sqrt{1 - c(u_2)y})$,

$C = 2h_1 h_2 x_2 \lambda_2$, $D = 2h_1(1 + h_1 L_1 \lambda_1) - h_1 H(u_2)(1 - \sqrt{1 - c(u_2)y})$,

$$c(u_2) = \frac{4h_1 L_1 \lambda_1^2}{a_1(1 + h_1 L_1 \lambda_1 + h_2 x_2 u_2 \lambda_2)^2}, \quad H(u_2) = 1 + h_1 L_1 \lambda_1 + h_2 x_2 u_2 \lambda_2.$$

First, I calculate the singular strategy and study its evolutionary stability. The gradient of the fitness function with respect to the mutant strategy

$$\frac{\partial W}{\partial \tilde{u}_2}(\tilde{u}_2, u_2) = \frac{AD - BC}{(D + C\tilde{u}_2)^2}.$$

At the singular strategy this gradient when evaluated at $\tilde{u}_2 = u_2$ must be zero, i.e., $AD - BC = 0$. When I substitute expressions for A, B, C, D and after some simplification I obtain the following equation:

$$\sqrt{1 - \frac{4h_1 L_1 y \lambda_1^2}{a_1(1 + h_1 L_1 \lambda_1 + h_2 u_2 x_2 \lambda_2)^2}} = 1 - \frac{2h_1((e_1 h_2 - e_2 h_1)L_1 \lambda_1 - e_2)}{(e_1 h_2 - e_2 h_1)(1 + h_1 L_1 \lambda_1 + h_2 u_2 x_2 \lambda_2)}. \tag{18}$$

This equation posses a solution only provided the right-hand side is between 0 and 1, i.e., when

$$\frac{e_2}{\lambda_1(e_1 h_2 - e_2 h_1)} < L_1 < \frac{e_2 h_1 + e_1 h_2 + h_2(e_1 h_2 - e_2 h_1)u_2 x_2 \lambda_2}{h_1(e_1 h_2 - e_2 h_1)\lambda_1}.$$

Solving Eq. (18) yields the singular strategy (15). Of course, u_2^* must be between 0 and 1 which holds for consumer densities that satisfy $y_1^* \le y \le y_2^*$ where

$$y_1^* = \frac{a_1 e_1 h_2(L_1 \lambda_1(e_1 h_2 - e_2 h_1) - e_2)}{(e_2 h_1 - e_1 h_2)^2 L_1 \lambda_1^2},$$

and

$$y_2^* = \frac{a_1 h_2(L_1 \lambda_1(e_1 h_2 - e_2 h_1) - e_2)(e_1 + (e_1 h_2 - e_2 h_1)x_2 \lambda_2)}{(e_2 h_1 - e_1 h_2)^2 L_1 \lambda_1^2}.$$

If consumer density is too low ($y < y_1^*$), consumers will feed on the more profitable prey type only while at high densities ($y > y_2^*$) they will feed on the alternative prey type upon each encounter. In particular, the carrying capacity for the more profitable prey type must be high enough, i.e.,

$$L_1 > \frac{e_2}{\lambda_1(e_1 h_2 - e_2 h_1)}$$

for consumer partial preferences to arise. If the opposite inequality holds, fitness maximizes at $u_2 = 1$. I derived the singular strategy under the assumption that the right-hand side of Eq. (18) is positive, because otherwise no singular solution exists. Substituting the singular strategy to the right-hand side of (18) leads to expression

$$\frac{(e_2 h_1 - e_1 h_2)^2 L_1 y \lambda_1^2 - a_1 h_1(e_2 + e_2 h_1 L_1 \lambda_1 - e_1 h_2 L_1 \lambda_1)^2}{(e_2 h_1 - e_1 h_2)^2 L_1 y \lambda_1^2 + a_1 h_1(e_2 + e_2 h_1 L_1 \lambda_1 - e_1 h_2 L_1 \lambda_1)^2},$$

that is positive provided

$$y > \frac{a_1 h_1(e_2 + e_2 h_1 L_1 \lambda_1 - e_1 h_2 L_1 \lambda_1)^2}{(e_2 h_1 - e_1 h_2)^2 L_1 \lambda_1^2}. \tag{19}$$

This condition must hold together with other constraints for the singular strategy to be between 0 and 1.

Because $AD - BC = 0$ at the singular strategy, $W(\tilde{u}_2, u_2^*)$ is independent of the mutant strategy $\tilde{u}_2$ and, after some calculations, $W(\tilde{u}_2, u_2^*) = e_2 / h_2$ for all mutant strategies u_2.

To study the evolutionary stability of the singular strategy I need to check the local stability condition (Hofbauer and Sigmund, 1998) that asserts that mutants cannot spread in the resident population. The local stability condition requires that

$$W(u_2^*, u_2) > W(u_2, u_2) \tag{20}$$

for every $u_2 \ne u_2^*$ in a neighborhood of the singular strategy u_2^*. Let $g(u_2) = W(u_2^*, u_2) - W(u_2, u_2)$. Thus, $g(u_2^*) = 0$ and with a help of some computer algebra package (e.g., Mathematica) it is easy to show that provided inequality (19) holds, $g'(u_2^*) = 0$ and

$$g''(u_2^*) = \frac{2a_1^3 h_2 x_2^2(e_2 + (e_2 h_1 - e_1 h_2)L_1 \lambda_1)^4 \lambda_2^2}{(e_1 h_2 - e_2 h_1)L_1^2 y^2 \lambda_1^4((e_2 h_1 - e_1 h_2)^2 L_1 y \lambda_1^2 - a_1 h_1(e_2 + (e_2 h_1 - e_1 h_2)L_1 \lambda_1)^2)} > 0.$$

Thus, $g(u_2) > 0$ in a neighborhood of the singular strategy ($u_2 \ne u_2^*$) and the local ESS condition (20) holds.

Second, I will prove that the singular strategy is also continuously stable. This follows from the fact (Eshel, 1983) that

$$\frac{\partial^2 W(u_2^*, u_2^*)}{\partial \tilde{u}_2^2} + \frac{\partial^2 W(u_2^*, u_2^*)}{\partial \tilde{u}_2 \partial u_2}$$

$$= \frac{a_1^3 h_2 x_2^2(e_2 + e_2 h_1 L_1 \lambda_1 - e_1 h_2 L_1 \lambda_1)^4 \lambda_2^2}{(e_1 h_2 - e_2 h_1)L_1^2 y^2 \lambda_1^4(-(e_2 h_1 - e_1 h_2)^2 L_1 y \lambda_1^2 + a_1 h_1(e_2 + e_2 h_1 L_1 \lambda_1 - e_1 h_2 L_1 \lambda_1)^2)} < 0$$

for consumer densities that satisfy (19).

Appendix B. Derivation of model (17)

Substituting x_{1+} given by (13) in the right-hand side of the consumer population growth Eq. (11) leads to

$$\frac{dy}{dt} = \frac{y(A + (e_1 - h_1 m)\sqrt{-4h_1 L_1 y \lambda_1^2 + a_1 H^2})}{h_1\left(\sqrt{a_1}H + \sqrt{-4h_1 L_1 y \lambda_1^2 + a_1 H^2}\right)},$$

where

$$A = \sqrt{a_1}(-e_1 - h_1 m + e_1 h_1 L_1 \lambda_1 - h_1^2 L_1 m \lambda_1$$
$$+ (2e_2 h_1 - h_2(e_1 + h_1 m))u_2 x_2 \lambda_2),$$

$$H = 1 + h_1 L_1 \lambda_1 + h_2 x_2 u_2 \lambda_2.$$

Extending the above fraction by expression $h_1(\sqrt{a_1}H - \sqrt{-4h_1 L_1 y \lambda_1^2 + a_1 H^2})$ leads to

$$\frac{dy}{dt} = \frac{(e_1 - h_1 m)y}{h_1} + \frac{\sqrt{a_1}(u_2 x_2 \lambda_2 (e_2 h_1 - e_1 h_2) - e_1)\left(\sqrt{a_1}H - \sqrt{a_1 H^2 - 4h_1 L_1 y \lambda_1^2}\right)}{2h_1^2 L_1 \lambda_1^2}$$

$$= \frac{(e_1 - h_1 m)y}{h_1} - \frac{2\sqrt{a_1}y(e_1 + u_2 x_2 \lambda_2(e_1 h_2 - e_2 h_1))}{h_1\left(\sqrt{a_1}H + \sqrt{a_1 H^2 - 4h_1 L_1 y \lambda_1^2}\right)}$$

$$= \frac{(e_1 - h_1 m)y}{h_1}\left(1 - \frac{2h_1 \sqrt{a_1}(e_1 + u_2 x_2 \lambda_2(e_1 h_2 - e_2 h_1))}{(e_1 - h_1 m)h_1 \sqrt{a_1}H\left(1 + \sqrt{1 - 4h_1 L_1 y \lambda_1^2/(a_1 H^2)}\right)}\right)$$

$$= ry\left(1 - \frac{K}{1 + \sqrt{1 - cy}}\right), \qquad (21)$$

where $r = (e_1/h_1) - m$, $K = 2(e_1 + u_2 \lambda_2 x_2(e_1 h_2 - e_2 h_1))/((e_1 - h_1 m)H)$ and $c = 4h_1 L_1 \lambda_1^2/a_1 H^2$. There exists a non-zero equilibrium of the single-species consumer model (21)

$$y^* = \frac{K(2 - K)}{c}$$
$$= \frac{a_1(e_1 + (e_1 h_2 - e_2 h_1)u_2 x_2 \lambda_2)(L_1(e_1 - h_1 m)\lambda_1 - m + (e_2 - h_2 m)u_2 x_2 \lambda_2)}{L_1 \lambda_1^2 (e_1 - h_1 m)^2},$$

which is exactly the same as the interior consumer equilibrium of model (11). For y^* to be an equilibrium, it must be positive, i.e., $0 < K < 2$. This condition is equivalent to

$$h_1 < e_1/m, \quad L_1 > \frac{m - (e_2 - h_2 m)u_2 x_2 \lambda_2}{\lambda_1(e_1 - mh_1)}.$$

Equilibrium y^* is asymptotically stable when the sign of the derivative of the right-hand side of (21) evaluated at this equilibrium

$$J = \frac{d}{dy}\left(ry\left(1 - \frac{K}{1 + \sqrt{1 - cy}}\right)\right)\Bigg|_{y = y^*} = \frac{r(K - 2)}{2(K - 1)}$$

is negative, i.e., $1 < K < 2$. I remark that condition $1 < K$ is equivalent to

$$L_1 < \frac{e_1 + h_1 m + (-2e_2 h_1 + h_2(e_1 + h_1 m))u_2 x_2 \lambda_2}{h_1(e_1 - h_1 m)\lambda_1},$$

which is the condition for the interior equilibrium of the resource–consumer model (11), to be stable. For larger values of the environmental carrying capacities the interior equilibrium is unstable and a stable limit cycle arises in the Rosenzweig–MacArthur model (11) (Hofbauer and Sigmund, 1998).

The above analysis assumed fixed consumer preference for the alternative resource. Now I will study population dynamics (17) driven by the singular strategy. Substituting singular strategy (15)

in population dynamics (17) I get

$$\frac{dy}{dt} = y\frac{(e_2 - h_2 m)}{h_2}$$

for consumer densities satisfying $y_1^* < y(t) < y_2^*$ and (19). For $h_2 < e_2/m$ consumer densities increase, while for larger handling times they decrease. No non-trivial equilibrium exists. If $y \geq y_2^*$ then $u_2 = 1$ and population dynamics on the stable manifold are obtained by substituting $u_2 = 1$ to (17). These population dynamics have equilibrium

$$y_{eq}^1 = \frac{a_1(e_1 + (e_1 h_2 - e_2 h_1)x_2 \lambda_2)(e_1 L_1 \lambda_1 + e_2 x_2 \lambda_2 - m(1 + h_1 L_1 \lambda_1 + h_2 x_2 \lambda_2))}{L_1(e_1 - h_1 m)^2 \lambda_1^2}.$$

Similarly when $y < y_1^*$, $u_2 = 0$ and population dynamics on the stable manifold are obtained by substituting $u_2 = 0$ to (17). These population dynamics have equilibrium

$$y_{eq}^0 = \frac{a_1 e_1(e_1 L_1 \lambda_1 - m(1 + h_1 L_1 \lambda_1))}{L_1(e_1 - h_1 m)^2 \lambda_1^2}.$$

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