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

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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 a single animal feeds on two food types delivered on a conveyor belt.

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.
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 evolutionaryarily 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 cryptis (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 (Berc 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, \( s_i \) 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 consumer growth rate (cf. consumer per capita population growth rate in model (3) below) is

\[
W = (e_1 s_1 x_1 - m_1) v_1 + (e_2 s_2 x_2 - m_2) v_2,
\]

where \( v_1 (v_1 + v_2 = 1) \) is the proportion of the time a consumer stays in patch \( i \). Thus, \( v_i \) 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

\[
v_1 = \begin{cases} 
1 & \text{if } e_1 s_1 x_1 - m_1 > e_2 s_2 x_2 - m_2, \\
0 & \text{if } e_1 s_1 x_1 - m_1 < e_2 s_2 x_2 - m_2.
\end{cases}
\]

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)

\[
\frac{dx_1}{dt} = a_1 x_1 \left( \frac{x_1}{L_1} - v_1 s_1 y \right), \\
\frac{dx_2}{dt} = a_2 x_2 \left( \frac{x_2}{L_2} - v_2 s_2 y \right), \\
\frac{dy}{dt} = (e_1 s_1 x_1 - m_1) v_1 y + (e_2 s_2 x_2 - m_2) v_2 y,
\]

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 \( \tilde{v} = (\tilde{v}_1, \tilde{v}_2) \) in a population of residents with a strategy \( v = (v_1, v_2) \) and I re-write frequency independent fitness function (1) as a function of both mutant and resident strategies

\[
W(\tilde{v}, v) = (e_1 s_1 x_1 - m_1) \tilde{v}_1 + (e_2 s_2 x_2 - m_2) \tilde{v}_2.
\]

The dependence of this function on the resident strategy \( v = (v_1, v_2) \) 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 \( v = (v_1, v_2) \), the resource equilibrium at consumer density \( y \), calculated from (3), is \( x_i = L_i (1 - v_i y / a_i), \) \( (i=1,2) \). Substituting this density in \( W \) leads to a frequency dependent fitness function

\[
W(\tilde{v}, v) = r_1 \tilde{v}_1 \left( 1 - \frac{v_1 y}{K_1} \right) + r_2 \tilde{v}_2 \left( 1 - \frac{v_2 y}{K_2} \right),
\]

where \( r_1 \) and \( r_2 \) are the resident fitness in patch 1 and patch 2, respectively.
where
\[ r_i = e_i L_i - m_i \quad \text{and} \quad K_i = \frac{a_i e_i L_i - m_i}{e_i L_i}, \]
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 \((y < (r_2 - r_1)K_2/(r_1))\) 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

\[ v^*_1 = \frac{K_1}{K_1 + K_2}, \]
\[ v^*_2 = \frac{K_2}{K_1 + K_2}. \]

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:

\[ dy \quad dt = \begin{cases} \frac{r_1 y (1 - y/K_1)}{K_1} & \text{if } y \leq \frac{(r_1 - r_2)K_1}{r_1}, \\ r_2 y (K_1 + K_2)/(K_1 r_1 + K_2 r_2) & \text{if } y > \frac{(r_1 - r_2)K_1}{r_1}. \end{cases} \]

\[ (\text{Křivan and Sirot, 2002}). \]

The equilibrium of this model is \(K_1 + K_2\) and at this equilibrium consumer preferences satisfy

\[ v^*_1 = \frac{K_1}{K_1 + K_2}, \]
\[ v^*_2 = \frac{K_2}{K_1 + K_2}. \]

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

\[ e_1 \lambda_1 u_1 x_1 + e_2 \lambda_2 u_2 x_2, \]

\[ \frac{1}{1 + h_1 \lambda_1 u_1 x_1 + h_2 \lambda_2 u_2 x_2}, \]

\[ (\text{Charnov, 1976}). \]

Here \(x_i\) is the density of resource \(i\) in the environment, \(\lambda_i\) is the consumer search rate for prey type \(i\), \(u_i\) is the consumer preference for prey type \(i\) \((0 \leq u_i \leq 1)\), \(h_1\) 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

\[ x^*_1 = \frac{e_2}{e_1 (e_1 h_1 - e_2 h_2)}, \]

\[ (e.g., \text{Charnov, 1976; Stephens and Krebs, 1986}). \]

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)

\[ \frac{dx_1}{dt} = a_1 x_1 \left(1 - \frac{x_1}{L_1} \right) - \lambda_1 x_1 y, \]

\[ \frac{dy}{dt} = \frac{e_1 \lambda_1 x_1 + e_2 \lambda_2 u_2 x_2}{1 + h_1 \lambda_1 x_1 + h_2 \lambda_2 u_2 x_2} y. \]

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 \(u_2^*\) in a population of residents with strategy \(u_2\) is

\[ W(u_2, u_2^*) = \frac{e_1 \lambda_1 x_1 + e_2 \lambda_2 u_2 x_2}{1 + h_1 \lambda_1 x_1 + h_2 \lambda_2 u_2 x_2}, \]

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)

\[ x_{1+} = -1 + h_1 L_1 \lambda_1 - h_2 u_2 x_2 + H(u_2) \sqrt{1 - c(u_2) W}, \]

where

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

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
the frequency dependent fitness function

\[ W(\tilde{u}_2, u_2) = \frac{2h_1(e_1L_1 + e_2u_2\tilde{u}_2) - e_1H(u_2)(1 - \sqrt{1 - c(u_2)y})}{2h_1H(u_2) - L_1H(u_2)(1 - \sqrt{1 - c(u_2)y})}. \] (14)

The selection gradient \( \frac{\partial W(\tilde{u}_2, u_2)}{\partial \tilde{u}_2} \) 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)

\[ u_2^* = \frac{L_1e_1h_2 - e_2h_1}{a_1h_2L_2\tilde{u}_2(e_1h_2 - e_2h_1)} - \frac{e_1}{L_2h_2 - e_2h_1}, \] (15)

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

\[ y_1^* = \frac{e_1(a_1h_2L_1 + a_2e_1h_2 - e_2h_1)}{(e_2h_1 - e_1h_2)^2L_1}, \]

\[ y_2^* = \frac{e_2(a_1h_2L_1 + a_2e_1h_2 - e_2h_1)}{(e_2h_1 - e_1h_2)^2L_1}. \]

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 \( x_i = L_i(1 - y(s_i, v_i, a_i)) \) with the optimal strategy \( s_i \) 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: \( L_1 = L_2 = 10, a_1 = 1.5, a_2 = 0.5, \tilde{v}_1 = \tilde{v}_2 = 1. \)
Křivan (1996) (see formula (32) there) calculated 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) $y^* = K(u_2)/(2-K(u_2)) \times (c/u_2)$ 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 $e_2 - m h_2 > 0$ 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 isoline (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 $x^*_1 = c/u_2$ (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.
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; Krivan, 1996, 1997; Krivan 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 (Krivan, 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 (Krivan, 1996). In fact, this non-uniqueness causes fundamental problems for the existence of solutions to these population models (Colombo and Krivan, 1993; Krivan, 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., Krivan and

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: $a_1=1.2$, $h_1=h_2=0.2$, $e_1=0.2$, $e_2=0.05$, $x_1=x_2=0.5$, $x_2=8$, $m=0.2$, $L_1=10$. 
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.

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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

\[ A = 2\epsilon_2 h_1 x_2 \tilde{\lambda}_2, \quad B = 2h_1 e_1 L_1 \tilde{\lambda}_1 - e_1 H(u_2)(1 - \sqrt{1 - C(u_2)\tilde{\lambda}_2}), \]

\[ C = 2h_1 h_2 x_2 \tilde{\lambda}_2, \quad D = 2h_1 (1 + h_1 L_1 \tilde{\lambda}_1 - h_1 H(u_2)(1 - \sqrt{1 - C(u_2)\tilde{\lambda}_2})). \]

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

\[ \frac{\partial W}{\partial \tilde{u}_2}(\tilde{u}_2, u_2) = \frac{AD - BC}{(D + Cu_2)\tilde{\lambda}_2^2}. \]

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:

\[ \frac{1 - 4h_1 L_1 \tilde{\lambda}_1^2}{a_1(1 + h_1 L_1 \tilde{\lambda}_1 + h_2 x_2 \tilde{\lambda}_2)\tilde{\lambda}_2^3} = 1 - \frac{2h_1(e_2 h_2 - e_2 h_1 x_2 \tilde{\lambda}_1 - e_2)}{(e_2 h_2 - e_2 h_1 x_1 + h_1 L_1 \tilde{\lambda}_1 + h_2 x_2 \tilde{\lambda}_2)\tilde{\lambda}_2^3}. \]

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

\[ \frac{e_2}{L_1(e_2 h_2 - e_2 h_1 \tilde{\lambda}_1)} < L_1 \leq \frac{e_2 h_1 + e_1 h_2 + h_2(e_2 h_2 - e_2 h_1 u_2 x_2 \tilde{\lambda}_2)}{h_1(e_2 h_2 - e_2 h_1 \tilde{\lambda}_1)}. \]

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 \( y^* \leq y(u_2) \) where

\[ y^*_1 = \frac{a_1 h_2 L_1 \tilde{\lambda}_1(e_1 h_2 - e_2 h_1 - e_2)}{(e_2 h_2 - e_1 h_2)\tilde{\lambda}_1^2}, \]

and

\[ y^*_2 = \frac{a_1 h_2 L_1 \tilde{\lambda}_1(e_1 h_2 - e_2 h_1 - e_2)(e_1 h_2 - e_2 h_1 x_2 \tilde{\lambda}_2)}{(e_2 h_1 - e_1 h_2)\tilde{\lambda}_1^2}. \]

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.,

\[ L_1 > \frac{e_2}{L_1(e_2 h_2 - e_2 h_1 \tilde{\lambda}_1)} \]

for consumer partial preferences to arise. If the opposite inequality holds, fitness maximizes at \( u_2 = 1 \). A 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

\[ \frac{e_2 h_1 - e_1 h_2}{L_1 \tilde{\lambda}_1^2} - a_1 h_2(e_2 + e_2 h_1 L_1 \tilde{\lambda}_1 - e_1 h_2 L_1 \tilde{\lambda}_1)^2 \]

\[ (e_2 h_1 - e_1 h_2)\tilde{\lambda}_1^2 + a_1 h_2(e_2 + e_2 h_1 L_1 \tilde{\lambda}_1 - e_1 h_2 L_1 \tilde{\lambda}_1)^2 \]

that is positive provided

\[ y > \frac{a_1 h_2(e_2 + e_2 h_1 L_1 \tilde{\lambda}_1 - e_1 h_2 L_1 \tilde{\lambda}_1)^2}{(e_2 h_1 - e_1 h_2)\tilde{\lambda}_1^2} \]

(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

\[ W(u_2^*, u_2) > W(\tilde{u}_2, u_2) \]

for every \( u_2 \neq u_2^* \) in a neighborhood of the singular strategy \( u_2^* \). Let \( g(u_2) = W(u_2^*, u_2) - W(\tilde{u}_2, u_2) \). 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

\[ g'(u_2) = \frac{2a_1 h_2 x_2(e_2 + e_2 h_1 L_1 \tilde{\lambda}_1 - e_1 h_2 L_1 \tilde{\lambda}_1)^2}{(e_2 h_1 - e_1 h_2)\tilde{\lambda}_1^2} > 0. \]

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

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

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

\[ = \frac{4 a_1 h_2 x_2(e_2 + e_2 h_1 L_1 \tilde{\lambda}_1 - e_1 h_2 L_1 \tilde{\lambda}_1)^2}{(e_2 h_1 - e_1 h_2)\tilde{\lambda}_1^2} < 0 \]

for consumer densities that satisfy (19).
Appendix B. Derivation of model (17)

Substituting $x_t$ given by (13) in the right-hand side of the consumer population growth Eq. (11) leads to

\[
\frac{dy}{dt} = \frac{y(A + (e_1 - h_1)m - 4h_1L_1y_2^2 + a_1H^2)}{h_1\left(\sqrt{a_1H} + \sqrt{-4h_1L_1y_2^2 + a_1H^2}\right)},
\]

where

\[
A = \sqrt{\alpha_1(-e_1 - h_1m + e_1h_1L_1\lambda_1 - h_1^2L_1m\lambda_1)} \\
+ (2e_1h_1 - h_2)e_1 + (h_1m)u_xu_x\lambda_2),
\]

\[
H = 1 + h_1L_1\lambda_1 + h_2x_2u_x\lambda_2.
\]

Extending the above fraction by expression $h_1(\sqrt{a_1H} - \sqrt{-4h_1L_1y_2^2 + a_1H^2})$ leads to

\[
\frac{dy}{dt} = \frac{(e_1 - h_1m)y}{h_1}
\left(1 - \frac{2\sqrt{a_1}(e_1 + u_xu_x\lambda_2(e_1 - e_2h_2))}{h_1\left(\sqrt{a_1H} + \sqrt{-4h_1L_1y_2^2 + a_1H^2}\right)}\right)
\]

\[
= \frac{(e_1 - h_1m)y}{h_1}
\left(1 - \frac{2\sqrt{a_1}(e_1 + u_xu_x\lambda_2(e_1 - e_2h_2))}{(e_1 - h_1m)\sqrt{a_1H} + \sqrt{-4h_1L_1y_2^2 + a_1H^2}}\right)
\]

\[
= ry\left(1 - \frac{K}{1 + \sqrt{1 - ry}}\right),
\]

where $r = (e_1/h_1 - m, K = 2(e_1 + u_xu_x\lambda_2(e_1 - e_2h_2))/((e_1 - h_1m)H)$ and $c = 4h_1L_1\lambda_2^2/a_1H^2$. There exists a non-zero equilibrium of the single-species consumer model (21)

\[
y^* = \frac{K(2-K)}{c}
\]

\[
a_1(e_1 + e_2h_2 - e_2h_2u_xu_x\lambda_2)(L_1(e_1 - h_1m)\lambda_2 - m + (e_2 - h_2m)u_xu_x\lambda_2)
\]

\[
L_1\lambda_2^2(e_1 - h_1m)^2
\]

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

\[
h_1 < e_1/m, L_1 > \frac{m(e_2 - h_2m)u_xu_x\lambda_2}{\lambda_2(e_1 - mh_1)}.
\]

Equilibrium $y^*$ is asymptotically stable when the sign of the derivative of the right-hand side of (21) evaluated at this equilibrium is negative, i.e., $1 < K < 2$. I remark that condition $1 < K$ is equivalent to

\[
L_1 < \frac{e_1 + h_1m + (-2e_1h_1 + h_2(e_1 + h_1m)u_xu_x\lambda_2)}{h_1(e_1 - h_1m)\lambda_2}.
\]

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 Rosenzveig–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

\[
\frac{dy}{dt} = y\left(\frac{e_2 - h_2m}{h_2}\right)
\]

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

\[
y_{eq}^1 = \frac{a_1(e_1 + (e_2 - h_2)u_xu_x\lambda_2)(e_1L_1\lambda_1 + e_2u_xu_x\lambda_2 - m(1 + h_1L_1\lambda_1 + h_2u_xu_x\lambda_2))}{L_1(e_1 - h_1m)^2\lambda_2^2}
\]

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

\[
y_{eq}^0 = \frac{a_1(e_1L_1\lambda_1 - m(1 + h_1L_1\lambda_1))}{L_1(e_1 - h_1m)^2\lambda_2^2}
\]

References


