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

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Abstract

In this article the patch and diet choice models of the optimal foraging theory are re-analyzed 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 function do not allow us to apply the classical game theoretical methods to study 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.

Keywords: evolutionarily stable strategy, game theory, ideal free distribution, population growth, predator-prey models

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

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15 of such a situation is the experiment with great tits where a single animal feeds on
16 two food types delivered on a conveyor belt (e. g., Krebs et al., 1977; Berec et al.,
17 2003) which assures that prey are not depleted by predation. Thus, no interference
18 or competition for food between consumers is considered. A similar reasoning can be
19 applied to the case where a consumer forages in a heterogeneous environment consisting
20 of discrete foraging patches. In this case the consumer should move to the patch with
21 the highest payoff. These predictions are based on fitness functions that are both
22 density and frequency independent. They consider a single consumer and resource
23 densities that are not influenced by predation. Thus, they miss completely competition
24 between consumers that can be either due to interference, or due to exploitation of
25 resources. In fact, such models can be applied only to laboratory experiments with a
26 single consumer that does not influence resource density (e. g., a single great tit feeding
27 on two prey types delivered on the conveyor belt).

28 More realistic models must consider consumer competition (either interference com-
29 petition, or exploitative competition). A density dependent approach in patchy envi-
30 ronments led to the concept of the Ideal Free Distribution (IFD; Fretwell and Lucas,
31 1969). These authors assumed that patch payoff decreases with increasing number of
32 individuals in that patch (e. g., this captures interference among birds) and predicted
33 that under the IFD no individual can increase its fitness by changing its strategy
34 measured by residence times in different patches. Because under the IFD all patches
35 provide animals with the same fitness the question arises whether such a situation is
36 stable or not. Indeed, assuming a single mutant with an infinitely large resident pop-
37 ulation that is distributed according to the IFD, fitness of that mutant is independent
38 and the same as is the fitness of resident animals. One approach to study stability in
39 such situations is to use the concept of evolutionarily stable strategies (Maynard Smith
40 and Price, 1973; Hofbauer and Sigmund, 1998). In fact it has been shown that the IFD
41 is an evolutionarily stable strategy of the habitat selection game (Křivan et al., 2008).
42 However, this concept of stability assumes that the fitness function is frequency depen-
43 dent, i. e., it depends both on the mutant as well as on the resident strategy. Frequency
44 dependence allows us to predict whether a mutant strategy will increase in the resident
45 population or not. Here the idea is that the resident strategy sets the environment
46 (e. g., the resident consumer strategy sets the resource densities) and if a mutant strat-
47 egy with a higher fitness exists then this strategy spreads, replaces residents, sets a
48 new environment and so on until an evolutionarily stable strategy (ESS) is reached.

49 Another approach that considers explicitly resource–consumer population dynam-
50 ics together with optimal foraging was also used in theoretical ecology (reviewed in
51 Abrams, 2010). These models show how resident individuals that follow optimal for-
52 aging strategy influence resource levels which, in turn, influence consumer numbers
53 and strategy. Although dynamical models capture the ecological feedback, they do
54 not provide us with information about the evolutionary stability of optimal foraging
55 strategies. To study this question it is necessary to study conditions under which
56 the optimal foraging strategy is resistant to mutant invasions. Studying evolution-
57 ary stability in dynamic models of optimal foraging is more complicated than in static

58 models of behavioral ecology (such as the Hawk-Dove model, or the Prisoners dilemma;
59 Maynard Smith and Price, 1973; Hofbauer and Sigmund, 1998) because it requires to
60 analyze population dynamics for both resources, resident and mutant consumers (e. g.,
61 Křivan and Cressman, 2009; Cressman and Křivan, 2010).

62 To sum up, the problem is that some models of optimal foraging are described by fit-
63 ness functions that are both frequency and density independent, and they do not allow
64 us to predict optimal foraging strategies when interference or resource depletion occur.
65 On the other hand, in the full dynamic setting that describes explicitly the effect of
66 resident strategies on resource densities, the resulting models are multidimensional and
67 difficult to analyze with respect to evolutionary stability of optimal strategies. My aim
68 is to show how frequency dependent fitness functions can be obtained from frequency
69 independent fitness functions, using a time scale argument. I start with a frequency
70 independent fitness function defined as the per capita population growth rate. Then I
71 consider resource–consumer population dynamics and I assume that resource dynamics
72 run on a faster time scale when compared with consumer population dynamics. This is
73 the case of many resource–consumer systems where resource generation time is shorter
74 than consumer generation time (e. g., many plants have short generation times rela-
75 tive to mammalian herbivores). This time scale separation allows me to assume that
76 at each consumer density resources are at the corresponding population equilibrium.
77 Substituting this resource equilibrium to the consumer fitness function leads to a fre-
78 quency dependent fitness function that can be analyzed from evolutionary perspective.
79 I apply this approach to diet and patch choice paradigms of optimal foraging theory.
80 In both cases this approach predicts emergence of partial preferences for alternative
81 prey/patch types. In the case of the patch model partial preferences describe the con-
82 sumer Ideal Free Distribution (Fretwell and Lucas, 1969). Although partial preferences
83 are not predicted by the classical frequency independent models of optimal foraging,
84 they were observed in many foraging studies (for a review see Stephens and Krebs,
85 1986). Explanations for partial preferences range from incorrect classification of re-
86 source and sampling by consumers (Krebs et al., 1977; Rechten et al., 1983), resource
87 crypsis (Erichsen et al., 1980), incorrect estimation of encounter rates with resource
88 by consumers (McNamara and Houston, 1987; Hirvonen et al., 1999), limited mem-
89 ory capacity of consumers (Mangel and Roitberg, 1989; Bélisle and Cresswell, 1997),
90 and limited knowledge of the environment (Berec and Křivan, 2000). In this article
91 I will show another mechanism that explains emergence of partial preferences by the
92 ecological feedback of consumer preferences on their fitness.

93 **2. The patch occupation model**

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

99 capita population growth rate in model (3) below) is

$$100 \quad W = (e_1\lambda_1x_1 - m_1)v_1 + (e_2\lambda_2x_2 - m_2)v_2 \quad (1)$$

101 where v_i ($v_1 + v_2 = 1$) is the proportion of the time a consumer stays in patch i . Thus,
 102 v_i measures the consumer preference for patch i . Assuming that consumer preferences
 103 are adaptive, the optimal consumer strategy is to stay in patch 1 when patch payoff
 104 is higher there than in patch 2 and vice versa. Thus, the strategy that maximizes
 105 consumer fitness W is

$$106 \quad v_1 = \begin{cases} 1 & \text{if } e_1\lambda_1x_1 - m_1 > e_2\lambda_2x_2 - m_2 \\ 0 & \text{if } e_1\lambda_1x_1 - m_1 < e_2\lambda_2x_2 - m_2. \end{cases} \quad (2)$$

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

$$115 \quad \begin{aligned} \frac{dx_1}{dt} &= a_1x_1 \left(1 - \frac{x_1}{L_1}\right) - v_1\lambda_1x_1y \\ 116 \quad \frac{dx_2}{dt} &= a_2x_2 \left(1 - \frac{x_2}{L_2}\right) - v_2\lambda_2x_2y \\ 117 \quad \frac{dy}{dt} &= (e_1\lambda_1x_1 - m_1)v_1y + (e_2\lambda_2x_2 - m_2)v_2y \end{aligned} \quad (3)$$

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

121 Using model (3) I derive a new frequency dependent fitness function. I consider
 122 a mutant with a strategy $\tilde{v} = (\tilde{v}_1, \tilde{v}_2)$ in a population of residents with a strategy
 123 $v = (v_1, v_2)$ and I re-write frequency independent fitness function (1) as a function of
 124 both mutant and resident strategies

$$125 \quad W(\tilde{v}, v) = (e_1\lambda_1x_1 - m_1)\tilde{v}_1 + (e_2\lambda_2x_2 - m_2)\tilde{v}_2.$$

126 The dependence of this function on the resident strategy ($v = (v_1, v_2)$) is indirect
 127 through resource abundance that is set by the resident strategy in model (3). To make
 128 this dependence explicit I will assume that resource population dynamics run on a
 129 fast time scale when compared with consumer population dynamics so that for each
 130 consumer density resources relatively quickly reach their corresponding equilibrium

131 densities. When residents use strategy $v = (v_1, v_2)$, the resource equilibrium at con-
 132 sumer density y , calculated from (3), is $x_i = L_i(1 - \lambda_i v_i y / a_i)$, ($i = 1, 2$). Substituting
 133 this density in W leads to a frequency dependent fitness function

$$134 \quad W(\tilde{v}, v) = r_1 \tilde{v}_1 \left(1 - \frac{v_1 y}{K_1}\right) + r_2 \tilde{v}_2 \left(1 - \frac{v_2 y}{K_2}\right), \quad (4)$$

135 where

$$136 \quad r_i = e_i \lambda_i L_i - m_i \quad \text{and} \quad K_i = \frac{a_i (e_i \lambda_i L_i - m_i)}{e_i L_i \lambda_i^2} \quad (5)$$

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

$$147 \quad v_1^* = \frac{K_1 r_2}{K_1 r_2 + K_2 r_1} + \frac{K_1 K_2 (r_1 - r_2)}{(K_1 r_2 + K_2 r_1) y}. \quad (6)$$

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

$$154 \quad \frac{dy}{dt} = \begin{cases} r_1 y \left(1 - \frac{y}{K_1}\right) & \text{if } y \leq \frac{(r_1 - r_2)K_1}{r_1} \\ \frac{r_1 r_2 (K_1 + K_2)}{K_2 r_1 + K_1 r_2} y \left(1 - \frac{y}{K_1 + K_2}\right) & \text{if } y > \frac{(r_1 - r_2)K_1}{r_1}, \end{cases} \quad (7)$$

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

$$157 \quad \frac{v_1^*}{v_2^*} = \frac{K_1}{K_2}. \quad (8)$$

158 These preferences correspond to the so called balanced dispersal under which no mu-
 159 tants can invade (McPeck and Holt, 1992; Padrón and Trevisan, 2006; DeAngelis et al.,
 160 2007).

161 Now I compare solutions of the resource-consumer model (3) (Figure 1, solid lines)
 162 with optimal consumer strategy given by (2), with solutions of the single-species lo-
 163 gistic model (7) (Figure 1, dashed lines). Křivan and Schmitz (2003) showed that
 164 for $L_i > m_i/(e_i\lambda_i)$, consumer population dynamics described by (3) converge on the
 165 equilibrium density $K_1 + K_2$ at which the corresponding IFD is given by formula (8)
 166 exactly as for model (7). This means that model (7) with optimal strategy (6) con-
 167 verges on the same equilibrium as the original resource-consumer model (3) (Figure
 168 1). In addition, if resource population dynamics are much faster than consumer pop-
 169 ulation dynamics (Figure 1, left panel), population trajectories of the reduced model
 170 (7) are close to trajectories of the original model (3). If both resource and consumer
 171 population dynamics operate on comparable time scales (Figure 1, right panel) the
 172 differences between trajectories get larger.

173 3. The diet choice model

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

$$176 \frac{e_1\lambda_1u_1x_1 + e_2\lambda_2u_2x_2}{1 + h_1\lambda_1u_1x_1 + h_2\lambda_2u_2x_2}, \quad (9)$$

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

$$190 x_1^* = \frac{e_2}{\lambda_1(e_1h_2 - e_2h_1)}, \quad (10)$$

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

194 Now I will derive a frequency dependent fitness function and find the corresponding
 195 ESS. For this I consider ecological feedback between consumers and resources that is
 196 described by the following Rosenzweig-MacArthur predator-prey dynamics (Křivan

197 and Schmitz, 2003)

$$\begin{aligned}
 \frac{dx_1}{dt} &= a_1 x_1 \left(1 - \frac{x_1}{L_1}\right) - \frac{\lambda_1 x_1 y}{1 + h_1 \lambda_1 x_1 + h_2 \lambda_2 u_2 x_2} \\
 \frac{dy}{dt} &= \left(\frac{e_1 \lambda_1 x_1 + e_2 \lambda_2 u_2 x_2}{1 + h_1 \lambda_1 x_1 + h_2 \lambda_2 u_2 x_2} - m \right) y.
 \end{aligned}
 \tag{11}$$

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

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

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

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

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

214 where

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

216 I remark that the resource isocline is defined only for consumer densities that satisfy
 217 $y < 1/c(u_2)$ which I will assume below. Substituting the equilibrium resource density
 218 x_{1+} in (12) leads to the frequency dependent fitness function

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

220 The selection gradient $\frac{\partial W}{\partial \tilde{u}_2}(\tilde{u}_2, u_2)$ predicts the direction of selective pressure (Vincent
 221 and Brown, 2005; Dercole and Rinaldi, 2008). When the gradient is positive, preference
 222 for the alternative prey type will increase, while if it is negative, preference will decrease.
 223 The gradient is zero at the singular strategy (Appendix A)

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

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

$$227 \quad y_1^* = \frac{a_1 e_1 h_2 (L_1 \lambda_1 (e_1 h_2 - e_2 h_1) - e_2)}{(e_2 h_1 - e_1 h_2)^2 L_1 \lambda_1^2}$$

228 and

$$229 \quad y_2^* = \frac{a_1 h_2 (L_1 \lambda_1 (e_1 h_2 - e_2 h_1) - e_2) (e_1 + (e_1 h_2 - e_2 h_1) x_2 \lambda_2)}{(e_2 h_1 - e_1 h_2)^2 L_1 \lambda_1^2}$$

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

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

$$241 \quad L_1 < x_1^* \tag{16}$$

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

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

260 Now I will consider consumer population dynamics. Consumer dynamics along the
 261 stable branch of the prey isocline are obtained by substituting expression for x_{1+} in the
 262 consumer equation in (11). This leads to the following consumer population growth

263 equation

$$264 \quad \frac{dy}{dt} = ry \left(1 - \frac{K(u_2)}{1 + \sqrt{1 - c(u_2)y}} \right) \quad (17)$$

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

$$269 \quad \frac{dy}{dt} = y \frac{e_2 - h_2 m}{h_2}.$$

270 Depending on the sign of $e_2 - h_2 m$, consumer density either increases or decreases
 271 when partial preferences occur. Because the above equation has no non-trivial pop-
 272 ulation equilibrium it follows that no population equilibrium where consumers would
 273 show partial preferences for the alternative prey type exists. Consumer equilibria for
 274 consumer densities that are higher than y_2^* (i. e., when $u_2^* = 1$) or smaller than y_1^*
 275 (i. e., when $u_2^* = 0$) are given by the interior equilibrium of (17) $y^* = \frac{K(u_2)(2-K(u_2))}{c(u_2)}$
 276 where I substitute 0 or 1 for u_2 (these are given explicitly in Appendix B). Figure
 277 3B shows one such trajectory of model (17) driven by the consumer singular strategy
 278 (solid lines). The corresponding resource 1 density is calculated from (13). Figure 3C
 279 shows the corresponding consumer singular strategy. These results predict that at low
 280 consumer densities where resource 1 density is near to its carrying capacity, consumers
 281 specialize on the more profitable resource type. As consumers increase in numbers, the
 282 preferred resource density decreases to the critical switching density (x_1^*) predicted by
 283 the classical model of optimal foraging. From then on, consumer preferences for the
 284 alternative prey type start to increase, keeping the preferred resource density at the
 285 switching threshold for some time (i. e., times approx. between 5 and 14 in Figure 3B).
 286 Because $e_2 - m h_2 > 0$ in Figure 3B, consumer density increases (it would decrease oth-
 287 erwise). Once the consumer preference reaches 1 (i. e., consumers attack the alternative
 288 resource upon each encounter), consumers and resources tend to a stable equilibrium.
 289 This general pattern of population dynamics is also clearly shown in Figure 3D where
 290 the trajectory from panel B is projected on the consumer isocline (the solid dot de-
 291 notes the population equilibrium). Thus, in the region of consumer densities where
 292 preferences for the less profitable resource type are between 0 and 1, consumers exhibit
 293 partial preferences. This is a new result because the classical diet choice model does
 294 not predict such a gradual shift in consumer preferences at the switching prey density
 295 (Stephens and Krebs, 1986). Trajectories of model (11) with the optimal consumer
 296 foraging strategy are shown in Figure 3B as dashed lines. It is clear that they converge
 297 to the same equilibrium as trajectories of the single species model. Using a completely
 298 different approach Křivan (1996) (see formula (32) there) calculated consumer strategy
 299 at the switching threshold $x_1 = x_1^*$ (i. e., when the classical diet choice model does not
 300 define consumer preference for the alternative prey type uniquely). It is an interesting

301 observation that the formula for partial preferences obtained there coincides with the
302 singular strategy u_2^* .

303 4. Discussion

304 In this article I have shown how to derive a frequency dependent fitness function
305 from a frequency independent fitness function by using a time-scale argument. The time
306 scale argument assumes that resource population dynamics run on a faster time scale
307 when compared with consumer population dynamics. Having a frequency dependent
308 fitness function allowed me to study optimal foraging strategies for multiple consumers
309 and depletable resources. In particular I showed that partial preferences for alternative
310 resources arise in the diet and patch models of optimal foraging.

311 The diet and patch choice models are two paradigms of the optimal foraging theory
312 (MacArthur and Pianka, 1966; Emlen, 1966). They assume that per capita energy
313 intake rate is a proxy for consumer fitness that is maximized by adaptive consumer
314 foraging behavior. The diet choice model assumes that two or more resources are evenly
315 distributed in the environment and consumption of these resources does not influence
316 their numbers. This assumption is clearly violated in most natural systems. To comply
317 with these assumptions, e. g., conveyor belts that bring food directly to consumers were
318 used in experiments (Krebs et al., 1977; Berec et al., 2003). So what is missing in the
319 diet choice model is the link between consumer numbers and consumer strategy. This
320 link defines an ecological feedback mechanism: consumer foraging strategy influences
321 resource densities which, in turn, set the consumer strategy and density. To model this
322 ecological feedback mechanism some authors considered population dynamics together
323 with the optimal foraging models (e. g., Fryxell and Lundberg, 1994; Křivan, 1996;
324 Fryxell and Lundberg, 1997; Křivan, 1997; Křivan and Schmitz, 2003; Ma et al., 2003).
325 In these models it often happens that population dynamics tend to densities at which
326 models of optimal foraging do not predict the optimal strategy uniquely. For example,
327 in the patch model consumers will distribute between the two patches so that patch
328 payoffs will equalize (Křivan, 1997). Under this situation there is no selection against
329 mutants that can use any strategy, because individual fitness is independent of the
330 strategy. Similarly, dynamical models of diet choice drive periodically density of the
331 more profitable prey type to the threshold where optimal consumer diet is not uniquely
332 predicted (Křivan, 1996). In fact, this non-uniqueness causes fundamental problems
333 for the existence of solutions to these population models (Colombo and Křivan, 1993;
334 Křivan, 1996).

335 A simpler approach to study evolutionary stability is based on the concept of evo-
336 lutionarily stable strategies (e. g., Maynard Smith and Price, 1973; Hofbauer and Sig-
337 mund, 1998; Cressman, 2003; Vincent and Brown, 2005). However, to apply methods
338 of static game theory, the fitness function must be frequency dependent, i. e., it must
339 allow us to measure the effect of mutants on the resident strategy. In this article I
340 derived two frequency dependent fitness functions for patch and diet choice models.
341 These fitness functions are based on the assumption that resource population dynamics

342 run on a faster population time scale when compared with consumer population dy-
343 namics. Using these fitness functions I derived the corresponding evolutionarily stable
344 strategies for the patch and the diet choice model. In both cases the corresponding
345 ESS predicts partial preferences for resources to occur. In the case of the patch model
346 separation of the resource and consumer time scales leads to consumer population
347 growth that is described by the logistic equation for which the evolutionarily stable
348 strategies were studied (e. g., Křivan and Sirot, 2002; Morris, 2003; Cressman and
349 Křivan, 2006). These works show that the evolutionarily stable strategy corresponds
350 with the IFD (Fretwell and Lucas, 1969). Similarly, when time scaling is applied to the
351 diet choice model the resulting consumer population growth equation seems to be new.
352 Moreover, partial preferences arise for a range of consumer densities in both models.
353 This is a new prediction because partial preferences were not predicted by the optimal
354 foraging theory (Charnov, 1976). In fact, my present analysis clearly shows that at
355 low consumer densities consumers should specialize on the more profitable prey/patch
356 type only. However, as consumer density increases, consumers also start to utilize the
357 alternative, less profitable prey/patch type with increasing strength. This prediction
358 should be easily tested using appropriate data on consumer preferences.

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

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457 **Appendix A: Evolutionary stability of the diet choice model**

458 Fitness function (14) can be written as

$$459 \quad W(\tilde{u}_2, u_2) = \frac{A\tilde{u}_2 + B}{C\tilde{u}_2 + D}$$

460 where

$$461 \quad A = 2e_2h_1x_2\lambda_2, \quad B = 2h_1e_1L_1\lambda_1 - e_1H(u_2)(1 - \sqrt{1 - c(u_2)y}),$$

$$462 \quad C = 2h_1h_2x_2\lambda_2, \quad D = 2h_1(1 + h_1L_1\lambda_1) - h_1H(u_2)(1 - \sqrt{1 - c(u_2)y}),$$

$$463 \quad c(u_2) = \frac{4h_1L_1\lambda_1^2}{a_1(1 + h_1L_1\lambda_1 + h_2x_2u_2\lambda_2)^2}, \quad H(u_2) = 1 + h_1L_1\lambda_1 + h_2x_2u_2\lambda_2.$$

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

$$466 \quad \frac{\partial W}{\partial \tilde{u}_2}(\tilde{u}_2, u_2) = \frac{AD - BC}{(D + C\tilde{u}_2)^2}.$$

467 At the singular strategy this gradient when evaluated at $\tilde{u}_2 = u_2$ must be zero, i. e.,
468 $AD - BC = 0$. When I substitute expressions for A, B, C, D and after some simplifi-
469 cation I obtain the following equation

$$470 \quad \sqrt{1 - \frac{4h_1L_1y\lambda_1^2}{a_1(1 + h_1L_1\lambda_1 + h_2u_2x_2\lambda_2)^2}} = 1 - \frac{2h_1((e_1h_2 - e_2h_1)L_1\lambda_1 - e_2)}{(e_1h_2 - e_2h_1)(1 + h_1L_1\lambda_1 + h_2u_2x_2\lambda_2)}. \quad (18)$$

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

$$473 \quad \frac{e_2}{\lambda_1(e_1h_2 - e_2h_1)} < L_1 < \frac{e_2h_1 + e_1h_2 + h_2(e_1h_2 - e_2h_1)u_2x_2\lambda_2}{h_1(e_1h_2 - e_2h_1)\lambda_1}.$$

474 Solving equation (18) yields the singular strategy (15). Of course, u_2^* must be between
475 0 and 1 which holds for consumer densities that satisfy $y_1^* \leq y \leq y_2^*$ where

$$476 \quad y_1^* = \frac{a_1e_1h_2(L_1\lambda_1(e_1h_2 - e_2h_1) - e_2)}{(e_2h_1 - e_1h_2)^2L_1\lambda_1^2}$$

477 and

$$478 \quad y_2^* = \frac{a_1h_2(L_1\lambda_1(e_1h_2 - e_2h_1) - e_2)(e_1 + (e_1h_2 - e_2h_1)x_2\lambda_2)}{(e_2h_1 - e_1h_2)^2L_1\lambda_1^2}.$$

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

$$483 \quad L_1 > \frac{e_2}{\lambda_1(e_1h_2 - e_2h_1)}$$

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

$$490 \frac{(e_2 h_1 - e_1 h_2)^2 L_1 y \lambda_1^2 - a_1 h_1 (e_2 + e_2 h_1 L_1 \lambda_1 - e_1 h_2 L_1 \lambda_1)^2}{(e_2 h_1 - e_1 h_2)^2 L_1 y \lambda_1^2 + a_1 h_1 (e_2 + e_2 h_1 L_1 \lambda_1 - e_1 h_2 L_1 \lambda_1)^2}$$

491 that is positive provided

$$492 y > \frac{a_1 h_1 (e_2 + e_2 h_1 L_1 \lambda_1 - e_1 h_2 L_1 \lambda_1)^2}{(e_2 h_1 - e_1 h_2)^2 L_1 \lambda_1^2}. \quad (19)$$

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

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

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

$$501 W(u_2^*, u_2) > W(u_2, u_2) \quad (20)$$

502 for every $u_2 \neq u_2^*$ in a neighborhood of the singular strategy u_2^* . Let $g(u_2) = W(u_2^*, u_2) -$
 503 $W(u_2, u_2)$. Thus, $g(u_2^*) = 0$ and with a help of some computer algebra package (e. g.,
 504 Mathematica) it is easy to show that provided inequality (19) holds, $g'(u_2^*) = 0$ and

$$505 g''(u_2^*) = \frac{2a_1^3 h_2 x_2^2 (e_2 + (e_2 h_1 - e_1 h_2) L_1 \lambda_1)^4 \lambda_2^2}{(e_1 h_2 - e_2 h_1) L_1^2 y^2 \lambda_1^4 ((e_2 h_1 - e_1 h_2)^2 L_1 y \lambda_1^2 - a_1 h_1 (e_2 + (e_2 h_1 - e_1 h_2) L_1 \lambda_1)^2)} > 0.$$

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

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

$$510 \frac{\partial^2 W(u_2^*, u_2^*)}{\partial \tilde{u}_2^2} + \frac{\partial^2 W(u_2^*, u_2^*)}{\partial \tilde{u}_2 \partial u_2} =$$

$$511 \frac{a_1^3 h_2 x_2^2 (e_2 + e_2 h_1 L_1 \lambda_1 - e_1 h_2 L_1 \lambda_1)^4 \lambda_2^2}{(e_1 h_2 - e_2 h_1) L_1^2 y^2 \lambda_1^4 (-(e_2 h_1 - e_1 h_2)^2 L_1 y \lambda_1^2 + a_1 h_1 (e_2 + e_2 h_1 L_1 \lambda_1 - e_1 h_2 L_1 \lambda_1)^2)} < 0$$

513 for consumer densities that satisfy (19).

514 **Appendix B: Derivation of model (17).**

515 Substituting x_{1+} given by (13) in the right hand side of the consumer population
516 growth equation (11) leads to

$$517 \quad \frac{dy}{dt} = \frac{y(A + (e_1 - h_1m)\sqrt{-4h_1L_1y\lambda_1^2 + a_1H^2}}{h_1(\sqrt{a_1}H + \sqrt{-4h_1L_1y\lambda_1^2 + a_1H^2})}$$

518 where

$$519 \quad A = \sqrt{a_1}(-e_1 - h_1m + e_1h_1L_1\lambda_1 - h_1^2L_1m\lambda_1 + (2e_2h_1 - h_2(e_1 + h_1m))u_2x_2\lambda_2),$$

$$520 \quad H = 1 + h_1L_1\lambda_1 + h_2x_2u_2\lambda_2.$$

522 Extending the above fraction by expression $h_1(\sqrt{a_1}H - \sqrt{-4h_1L_1y\lambda_1^2 + a_1H^2})$ leads to

$$523 \quad \frac{dy}{dt} = \frac{(e_1 - h_1m)y}{h_1} + \frac{\sqrt{a_1}(u_2x_2\lambda_2(e_2h_1 - e_1h_2) - e_1)(\sqrt{a_1}H - \sqrt{a_1H^2 - 4h_1L_1y\lambda_1^2})}{2h_1^2L_1\lambda_1^2}$$

$$524 \quad = \frac{(e_1 - h_1m)y}{h_1} - \frac{2\sqrt{a_1}y(e_1 + u_2x_2\lambda_2(e_1h_2 - e_2h_1))}{h_1(\sqrt{a_1}H + \sqrt{a_1H^2 - 4h_1L_1y\lambda_1^2})}$$

$$525 \quad = \frac{(e_1 - h_1m)y}{h_1} \left(1 - \frac{2h_1\sqrt{a_1}(e_1 + u_2x_2\lambda_2(e_1h_2 - e_2h_1))}{(e_1 - h_1m)h_1\sqrt{a_1}H(1 + \sqrt{1 - 4h_1L_1y\lambda_1^2/(a_1H^2)})} \right)$$

$$526 \quad = ry \left(1 - \frac{K}{1 + \sqrt{1 - cy}} \right) \quad (21)$$

530 where $r = \frac{e_1}{h_1} - m$, $K = 2\frac{e_1 + u_2x_2\lambda_2(e_1h_2 - e_2h_1)}{(e_1 - h_1m)H}$ and $c = \frac{4h_1L_1\lambda_1^2}{a_1H^2}$. There exists a non-zero
531 equilibrium of the single species consumer model (21)

$$532 \quad y^* = \frac{K(2 - K)}{c} = \frac{a_1(e_1 + (e_1h_2 - e_2h_1)u_2x_2\lambda_2)(L_1(e_1 - h_1m)\lambda_1 - m + (e_2 - h_2m)u_2x_2\lambda_2)}{L_1\lambda_1^2(e_1 - h_1m)^2}$$

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

$$536 \quad h_1 < e_1/m, \quad L_1 > \frac{m - (e_2 - h_2m)u_2x_2\lambda_2}{\lambda_1(e_1 - mh_1)}.$$

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

$$539 \quad J = \frac{d}{dy} \left(ry \left(1 - \frac{K}{1 + \sqrt{1 - cy}} \right) \right) \Big|_{y=y^*} = \frac{r(K - 2)}{2(K - 1)}$$

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

$$541 \quad L_1 < \frac{e_1 + h_1 m + (-2e_2 h_1 + h_2(e_1 + h_1 m))u_2 x_2 \lambda_2}{h_1(e_1 - h_1 m)\lambda_1}$$

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

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

$$549 \quad \frac{dy}{dt} = y \frac{(e_2 - h_2 m)}{h_2}$$

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

$$554 \quad y_{eq}^1 = \frac{a_1(e_1 + (e_1 h_2 - e_2 h_1)x_2 \lambda_2)(e_1 L_1 \lambda_1 + e_2 x_2 \lambda_2 - m(1 + h_1 L_1 \lambda_1 + h_2 x_2 \lambda_2))}{L_1(e_1 - h_1 m)^2 \lambda_1^2}.$$

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

$$557 \quad y_{eq}^0 = \frac{a_1 e_1 (e_1 L_1 \lambda_1 - m(1 + h_1 L_1 \lambda_1))}{L_1(e_1 - h_1 m)^2 \lambda_1^2}.$$

558 Figures caption.

559 Figure 1: Solutions of the patch model (3) (solid line) where consumers follow
 560 the optimal foraging strategy given by (2), and solutions of the single-species model
 561 (7)(dashed line). Resource densities for model (7) are given by $x_i = L_i(1 - y(t)\lambda_i v_i/a_i)$
 562 with the optimal strategy v_i given by (6). The left panel (A,B,C) assumes that con-
 563 sumer demographic parameters ($e_1 = 0.015$, $e_2 = 0.01$, $m_1 = m_2 = 0.02$) are much
 564 smaller when compared to resource parameters. This discrepancy causes resource pop-
 565 ulation dynamics to run on a fast time scale when compared with consumer population
 566 dynamics. The right panel (D,E,F) assumes more similar time scales for both resource
 567 and consumer dynamics ($e_1 = 0.15$, $e_2 = 0.1$, $m_1 = m_2 = 0.2$). Other parameters used
 568 in simulations: $L_1 = L_2 = 10$, $a_1 = 1.5$, $a_2 = 0.5$, $\lambda_1 = \lambda_2 = 1$.

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

572 Figure 3: Panel A shows consumer preference (15) for the alternative prey type in
 573 the diet choice model as a function of consumer density. Panel B compares a trajectory
 574 of the resource–consumer model (11) (dashed lines) where consumers follow predictions
 575 of the classical prey model (i. e., zero–one rule) with a trajectory of the reduced model
 576 (17) (solid lines). The corresponding trajectory for resources is given by (13). Panel C
 577 shows the corresponding consumer optimal strategy. Panel D shows the solid trajectory
 578 from panel B in the resource 1–consumer preference–consumer density phase space.
 579 Parameters: $a_1 = 1.2$, $h_1 = h_2 = 0.2$, $e_1 = 0.2$, $e_2 = 0.05$, $\lambda_1 = \lambda_2 = 0.5$, $x_2 = 8$,
 580 $m = 0.2$, $L_1 = 10$.

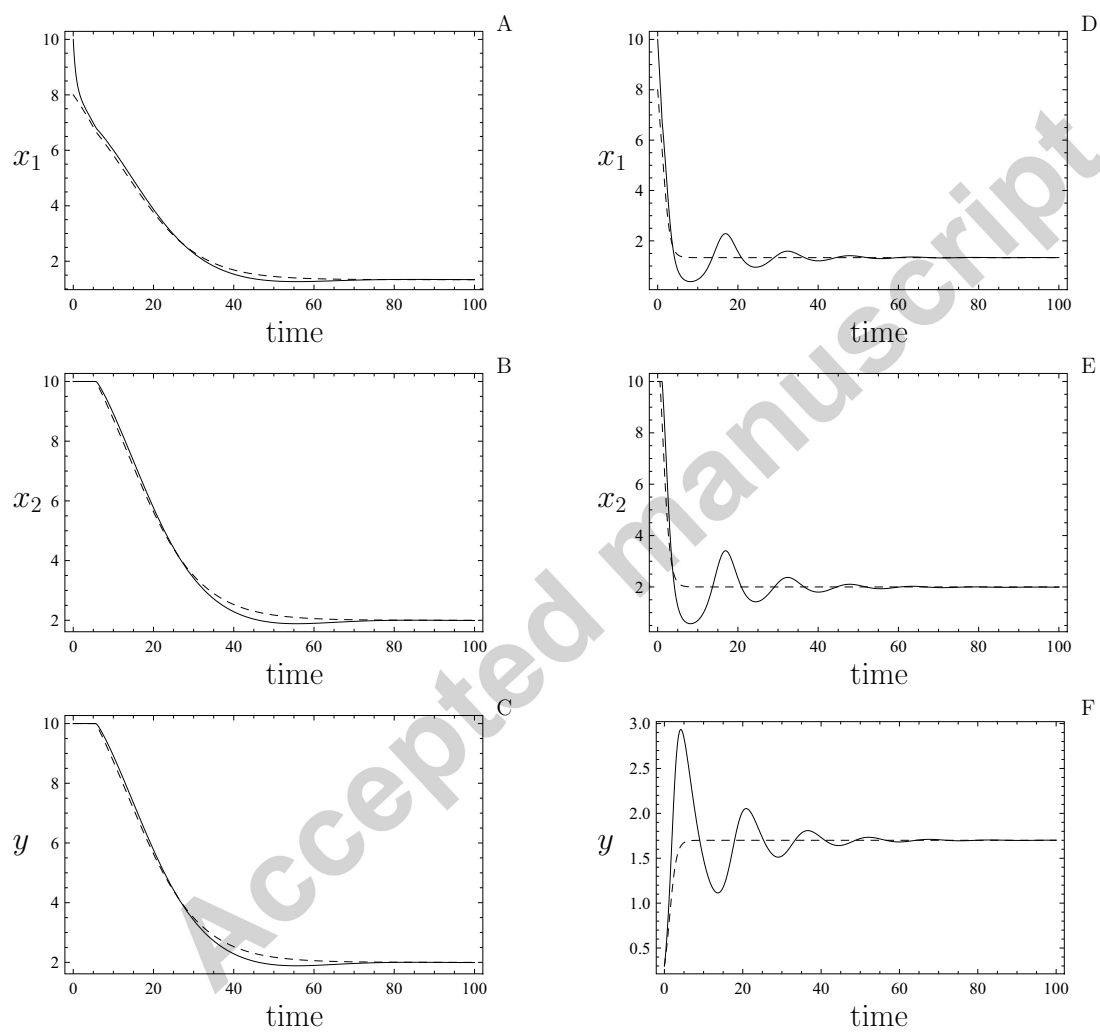


Figure 1:

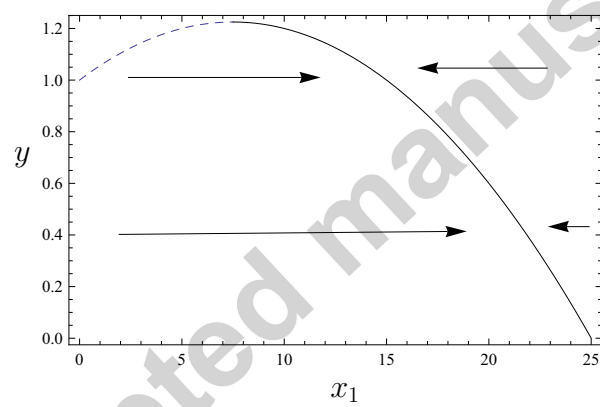


Figure 2:

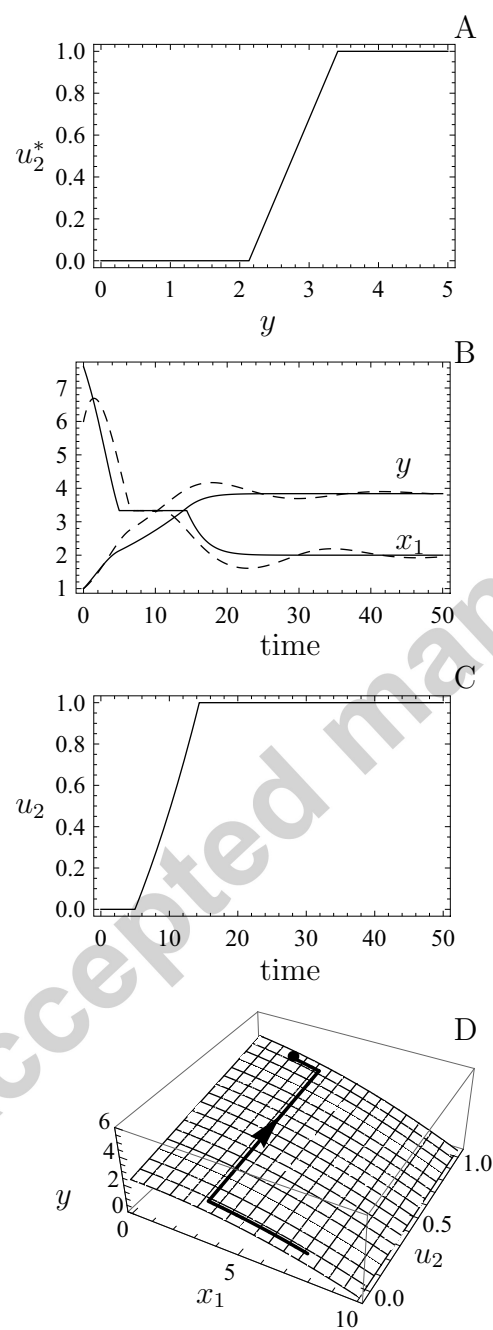


Figure 3: