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Optimal foraging and predator–prey dynamics III

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Abstract

In the previous two articles (Theor. Popul. Biol. 49 (1996) 265–290; 55 (1999) 111–126), the population dynamics resulting from a two-prey–one-predator system with adaptive predators was studied. In these articles, predators followed the predictions of optimal foraging theory. Analysis of that system was hindered by the incorporation of the logistic description of prey growth. In particular, because prey self-regulation dependence is a strong stabilizing mechanism, the effects of optimal foraging could not be easily separated from the effects of bottom-up control of prey growth on species coexistence. In this article, we analyze two models. The first model assumes the exponential growth of both prey types while the second model assumes the exponential growth of the preferred prey type and the logistic growth of the alternative prey type. This permits the effect of adaptive foraging on two-prey–predator food webs to be addressed. We show that optimal foraging reduces apparent competition between the two prey types, promotes species coexistence, and leads to multiple attractors.

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1. Introduction

It is well known that when two non-competing species share a common predator, predator-mediated apparent competition (Holt, 1977) often leads to competitive exclusion of one prey population. If predation is the only regulatory mechanism of prey exponential growth and predators are non-adaptive foragers, this will always hold for population dynamics modeled by Lotka–Volterra-type differential equations with either a linear or Holling type II functional response. If prey growth is density dependent then both prey species can survive with predators for an appropriate range of parameters (Holt, 1977). Thus, in classical models of population ecology, prey density dependence (bottom-up regulation) relaxes the strength of apparent competition making indefinite coexistence of both prey species possible.

In this article, we consider the effect of adaptive foraging (i.e., top-down regulation) on apparent prey competition. In Křivan (1996), a two-prey–one-predator

population model with optimal predator foraging behavior was studied in a fine-grained environment (Werner and Hall, 1974; Charnov, 1976; Stephens and Krebs, 1986). That model contained two regulatory mechanisms of prey growth: (i) prey self-regulation modeled by the logistic equation (bottom-up control), and (ii) optimal diet selection by predators (top-down control) modeled by a piece-wise Holling type II functional response which arises as a result of optimal predator diet choice. Analysis of the resulting system was hindered by the logistic prey growth and only partial stability analysis for the equal intrinsic per capita prey growth rates was given (Křivan, 1996). The analysis together with computer simulations suggested that optimal diet choice reduces the amplitude of population oscillations without stabilizing the system at an equilibrium. Similar results were obtained by Fryxell and Lundberg (1994, 1997) for systems in which switching was described by a more gradual sigmoidal function. However, Křivan (1996) also showed that optimal foraging can be destabilizing for certain parameter values. The stable equilibrium of a predator–prey system where predators behave as specialists was destabilized when predators became optimally foraging generalists

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because of the Paradox of Enrichment (Rosenzweig, 1971).

Using invasibility analysis, Křivan and Sikder (1999) proved that for logistically growing prey the range of model parameters for which the two prey populations indefinitely coexist with predators is larger for optimally foraging predators when compared with non-adaptive predators that choose their diet at random. However, their analysis was limited to those parameter ranges for which the Paradox of Enrichment does not hold (i.e., for relatively low levels of environmental carrying capacities for the two prey species). The invasibility analysis does not distinguish between various types of attractors, so it was not clear whether the increased persistence is due to increased stability of an interior equilibrium, emergence of a limit cycle or a more complex attractor.

A similar model without prey density dependence (no bottom-up regulation) was considered by van Baalen et al. (2001). They assumed exponential growth of the preferred prey type and showed that, for a fixed density of the alternative prey type, a locally stable predator–prey limit cycle emerges due to optimal predator foraging. This strongly suggests that optimal diet selection promotes species persistence without promoting species equilibrium stability. It is unclear however, whether the emergent limit cycle will be preserved when alternative prey type undergoes population dynamics.

In this article, we extend the van Baalen et al. (2001) study by considering population dynamics of both prey types. We want to disentangle the bottom-up effects from top-down control on population dynamics and therefore we start with the case where both prey types grow exponentially without predators. Compared with previous studies of predator–prey systems with optimal foraging (Gleeson and Wilson, 1986; Fryxell and Lundberg, 1994, 1997; Křivan, 1996; Genkai-Kato and Yamamura, 1999; Křivan and Sikder, 1999), the exclusion of bottom-up regulatory mechanism simplifies the analysis and allows for a deeper understanding of the role of adaptive food choice on apparent competition between two prey types. Then we also study the interplay between bottom-up and top-down control by assuming density-dependent growth of the alternative prey type. We compare two types of predator behavior: (i) non-adaptive feeding when predator preferences for either prey type are fixed and independent of prey density, and (ii) adaptive feeding that follows rules of optimal foraging theory. We ask: Can adaptive foraging relax the strength of apparent competition between the two prey types and lead to their indefinite coexistence? We show that this is indeed true. Adaptive foraging leads to the emergence of a limit cycle which is unstable if both prey types grow exponentially. However, if the alternative prey type is self-regulated, another locally stable limit cycle emerges together with the unstable limit cycle.

2. Population dynamics

Křivan (1996) and Křivan and Sikder (1999) considered a system consisting of two prey types with densities R_1 and R_2 , respectively, and optimally foraging predators with density C . In these two articles, population dynamics was described by the following model:

$$\begin{aligned} \frac{dR_1}{dt} &= R_1 \left(r_1(R_1) - \frac{\lambda_1 C}{1 + h_1 \lambda_1 R_1 + u_2 h_2 \lambda_2 R_2} \right), \\ \frac{dR_2}{dt} &= R_2 \left(r_2(R_2) - \frac{u_2 \lambda_2 C}{1 + h_1 \lambda_1 R_1 + u_2 h_2 \lambda_2 R_2} \right), \\ \frac{dC}{dt} &= C \left(\frac{e_1 \lambda_1 R_1 + u_2 e_2 \lambda_2 R_2}{1 + h_1 \lambda_1 R_1 + u_2 h_2 \lambda_2 R_2} - m \right). \end{aligned} \quad (1)$$

Here $r_i(R_i)$ is the per capita prey growth rate, λ_i is the cropping rate of a predator when feeding on the i th prey type, e_i is the conversion factor which relates predator reproduction to prey consumption, h_i is the expected handling time spent with the i th prey type, and m is the per capita consumer mortality rate. The first prey is more profitable than the second prey provided $e_1/h_1 > e_2/h_2$ which henceforth is assumed throughout this article. The above-mentioned two articles assumed that the prey growth rate is self-regulated (described by the logistic function). To study the regulatory effect of predation on exponentially growing prey population(s) alone, first we assume exponential prey growth when predators are absent ($r_i(R_i) = r_i$). This allows us to disentangle the top-down effect of optimally foraging predators from the bottom-up effect of resources on population dynamics. Optimal foraging theory implies that the preferred prey type (which we will assume is the first prey type) is included in predator diet and that the less preferred, alternative, prey type is either included or excluded, depending on the density of the preferred prey type. In order to model optimal foraging, we introduce a control parameter u_2 ($0 \leq u_2 \leq 1$) which denotes the probability that the alternative second prey type is included in predators diet.

2.1. Non-adaptive predators

Consider the situation where predators are non-adaptive foragers and their diet preference for the alternative prey type u_2 is fixed. Without loss of generality we assume that $u_2 = 1$. System (1) has no interior equilibrium and the prey type with higher ratio r_i/λ_i outcompetes the other prey type via apparent competition mediated through the common predator (Appendix A; Holt, 1977) For example, if the alternative prey type 2 is competitively weaker than prey type 1 (by which we mean that $r_2/\lambda_2 < r_1/\lambda_1$) then it will be excluded from the system. The population dynamics of the remaining prey type 1–predator system are then

described by

$$\begin{aligned} \frac{dR_1}{dt} &= R_1 \left(r_1 - \frac{\lambda_1 C}{1 + h_1 \lambda_1 R_1} \right), \\ \frac{dC}{dt} &= C \left(\frac{e_1 \lambda_1 R_1}{1 + h_1 \lambda_1 R_1} - m \right). \end{aligned} \quad (2)$$

If the internal equilibrium of model (2) exists then it is unstable and for small handling times, trajectories must spiral away from that equilibrium (Bazykin, 1998, p. 28). Qualitatively, trajectories of system (1) behave as shown in Fig. 1. Resource 2 density decreases to zero and the remaining-prey-predator system (2) fluctuates away from its internal equilibrium. If the internal equilibrium of model (2) does not exist then predators will die out and prey will grow to infinity (Bazykin, 1998). Therefore, model (1) with non-adaptive generalist predators is highly impermanent. First, the competitively weaker prey type 2 is competed out of the system due to apparent competition, second, the remaining-prey-predator system is impermanent because either predators or both prey and predators are excluded from the system (2), see Bazykin, 1998). We conclude that if predators are generalists which take prey in proportion to their abundance, inclusion of an alternative prey type in a predator-prey system cannot lead to species persistence whenever both prey species grow exponentially because of strong apparent competition between the two prey types.

2.2. Optimally foraging predators

We now consider the case in which predators are adaptive foragers and they follow predictions of optimal foraging theory (Charnov, 1976; Stephens and Krebs, 1986). Optimal foraging theory assumes that predators attempt to maximize their net rate of energy intake while foraging (for detailed description of assumptions and predictions see Chapter 2.2 in Stephens and Krebs, 1986). Then the alternative prey 2 is included in predators diet ($u_2 = 1$) if density of the more profitable prey type 1 drops below the critical threshold:

$$R_1^* = \frac{e_2}{\lambda_1(e_1 h_2 - e_2 h_1)}$$

(Charnov, 1976; Stephens and Krebs, 1986).

If prey 1 density is below the critical threshold R_1^* , population dynamics for optimally foraging predators are described by model (1) with $u_2 = 1$ and by the same model with $u_2 = 0$ above that threshold. We remark that for $R_1 = R_1^*$ the right-hand-side of model (1) is not well defined because optimal foraging strategy is not unique (any value of $0 \leq u \leq 1$ is optimal). Despite the non-uniqueness in model description, trajectories of model (1) are unique (Křivan, 1996). Prey switching makes prey 1 isocline piece-wise continuous (van Baalen et al., 2001) with a triangular gap at the switching prey 1

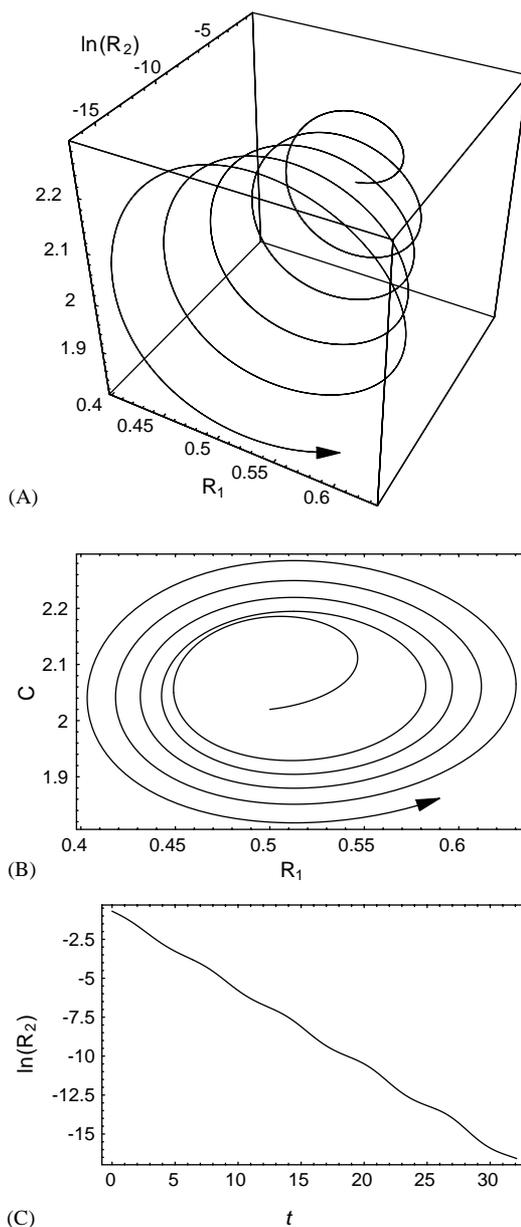


Fig. 1. Trajectories of system (1) when predator foraging behavior is non-adaptive. Competitively weaker prey type 2 is outcompeted from the system and the remaining prey 1–predator system follows diverging oscillations which result from the Holling type II functional response. (A) shows a trajectory in 3D-phase space, (B) shows the same trajectory in prey 1–predator phase space and (C) shows time dynamics of prey type 2. Parameters: $r_1 = 2, r_2 = 1.5, \lambda_1 = \lambda_2 = 1, e_1 = 1, e_2 = 0.1, h_1 = 0.05, h_2 = 0.1, m = 0.5$.

density (Fig. 2). This triangular region is described by (Křivan, 1996)

$$\frac{r_1 e_1 h_2}{\lambda_1(e_1 h_2 - e_2 h_1)} < C < \frac{r_1}{\lambda_1} \left(\frac{e_1 h_2}{e_1 h_2 - e_2 h_1} + h_2 \lambda_2 R_2 \right) \quad (3)$$

and trajectories of (1) which are driven by optimal foraging strategy cannot cross this vertical part of the prey 1 isocline (because, by the definition of isocline, $dR_1/dt = 0$ along the prey 1 isocline). The triangular

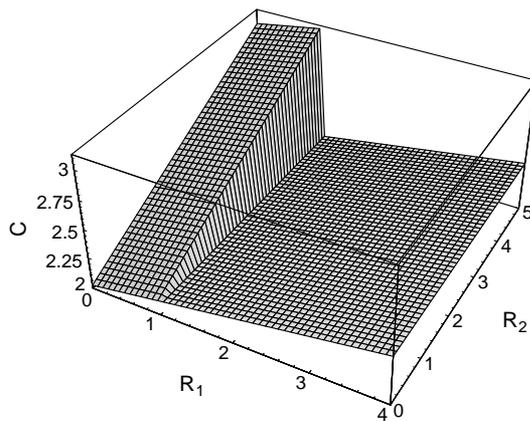


Fig. 2. Effect of optimal prey switching on prey 1 isocline. Prey switching causes a vertical gap at the switching prey 1 density. Trajectories of model (1) cannot go through the vertical part of the prey 1 isocline. Parameters: $r_1 = 2, r_2 = 0.1, \lambda_1 = \lambda_2 = 1, e_1 = 1, e_2 = 0.1, h_1 = 0.05, h_2 = 0.1, m = 1.1$.

region (3) is referred to as the partial preference domain (Křivan, 1996), because partial preferences for the alternative prey type arise in this area. Population dynamics on the partial preference domain are given in Appendix B.

When the alternative prey type is excluded from the predators diet ($u_2 = 0$) system (1) has one non-trivial unstable equilibrium

$$E^1 = \left(\frac{m}{\lambda_1(e_1 - h_1 m)}, 0, \frac{e_1 r_1}{\lambda_1(e_1 - h_1 m)} \right).$$

When the alternative prey is included in the predators diet ($u_2 = 1$) there will be, in addition to equilibrium E^1 , another equilibrium

$$E^2 = \left(0, \frac{m}{\lambda_2(e_2 - h_2 m)}, \frac{e_2 r_2}{\lambda_2(e_2 - h_2 m)} \right).$$

We shall show that the adaptive predator behavior can lead to indefinite coexistence of all three species.

First, we assume that the prey type 1 equilibrium density

$$\frac{m}{\lambda_1(e_1 - h_1 m)}$$

is larger than the switching threshold R_1^* which occurs when

$$m > \frac{e_2}{h_2}, \quad (4)$$

(see Figs. 3A and B). Under this condition, van Baalen et al. (2001) showed the existence of a locally stable limit cycle for constant density of the alternative prey type. Inequality (4) precludes the existence of a positive (unstable) equilibrium for the system consisting of predators and the alternative prey type only. There are two possibilities. Either (Fig. 3A) prey 1 is competitively dominant in which case the R_2 – C phase space repels nearby orbits and the part of the R_1 – C phase plane for

which $R_1 < R_1^*$ attracts nearby orbits. Or alternatively, (Fig. 3B) prey 2 is competitively dominant in which case the R_2 – C phase space attracts nearby orbits and the R_1 – C phase plane repels nearby orbits. In both situations, the part of the R_1 – C phase plane which satisfies $R_1 > R_1^*$ repels nearby orbits because prey 2 grows exponentially there. Fig. 3 also shows that in addition to the equilibrium point E^1 , an infinitely large heteroclinic cycle occurs in the R_1 – C phase plane. (In this figure, the phase space is projected on the unit sphere which is an efficient tool to study the behavior of trajectories in infinity, Bazykin, 1998). The infinitely large heteroclinic cycle consists of C and R_1 axes and the dotted arc which connects the ends of these axes. Trajectories which start in the R_1 – C phase plane converge to this heteroclinic orbit. In the R_2 – C phase plane no such infinitely large heteroclinic cycle exists because there is no interior equilibrium in this plane (because of inequality (4)). Trajectories converge to the end point on the R_2 axes which represent an infinitely large prey 2 population with predators extinct. The above analysis shows that the system can be permanent only provided prey 2 is competitively weaker than prey 1 (Fig. 3A). Otherwise, for low prey 1 initial densities prey 1 will be outcompeted by prey 2 (Fig. 3B). Thus, in what follows we focus mainly on the case where the alternative prey type is the weaker competitor ($r_2/\lambda_2 < r_1/\lambda_1$).

We shall demonstrate further that because a part of the R_1 isocline is vertical, indefinite coexistence of all three species really occurs. Consider initial species densities in the vicinity of the prey 1–predator equilibrium E^1 and that a low density of competitively weaker prey 2 is introduced (Fig. 3A). Because the prey 1–predator equilibrium E^1 repels orbits that start in its vicinity the corresponding trajectory will oscillate in the prey 1–predator phase plane with an increasing amplitude. Not being preyed upon, prey type 2 grows exponentially. However, after some time the trajectory of model (1) hits the switching plane $R_1 = R_1^*$. If it hits it in the partial preference domain where the prey 1 isocline is vertical it will move along this domain downwards (because predator density decreases in the partial preference domain, see population dynamics (6) in Appendix A and inequality (4)) until it reaches the lower boundary of the partial preference domain (see inequality (3)). On reaching this lower bound, the trajectory will move to the right part of the phase space where prey 2 is excluded from predators diet. Simulations show that there exists a point on the lower boundary of the partial preference domain (in other words, the point $(R_1^*, R_2^{crit}, r_1 e_1 h_2 / (\lambda_1 (e_1 h_2 - e_2 h_1)))$) such that the corresponding trajectory of model (1) forms a closed orbit in the phase space (the cycle in Fig. 4). However, this limit cycle is not stable. Alternative prey is outcompeted along trajectories of model (1) that start at the lower boundary of the partial

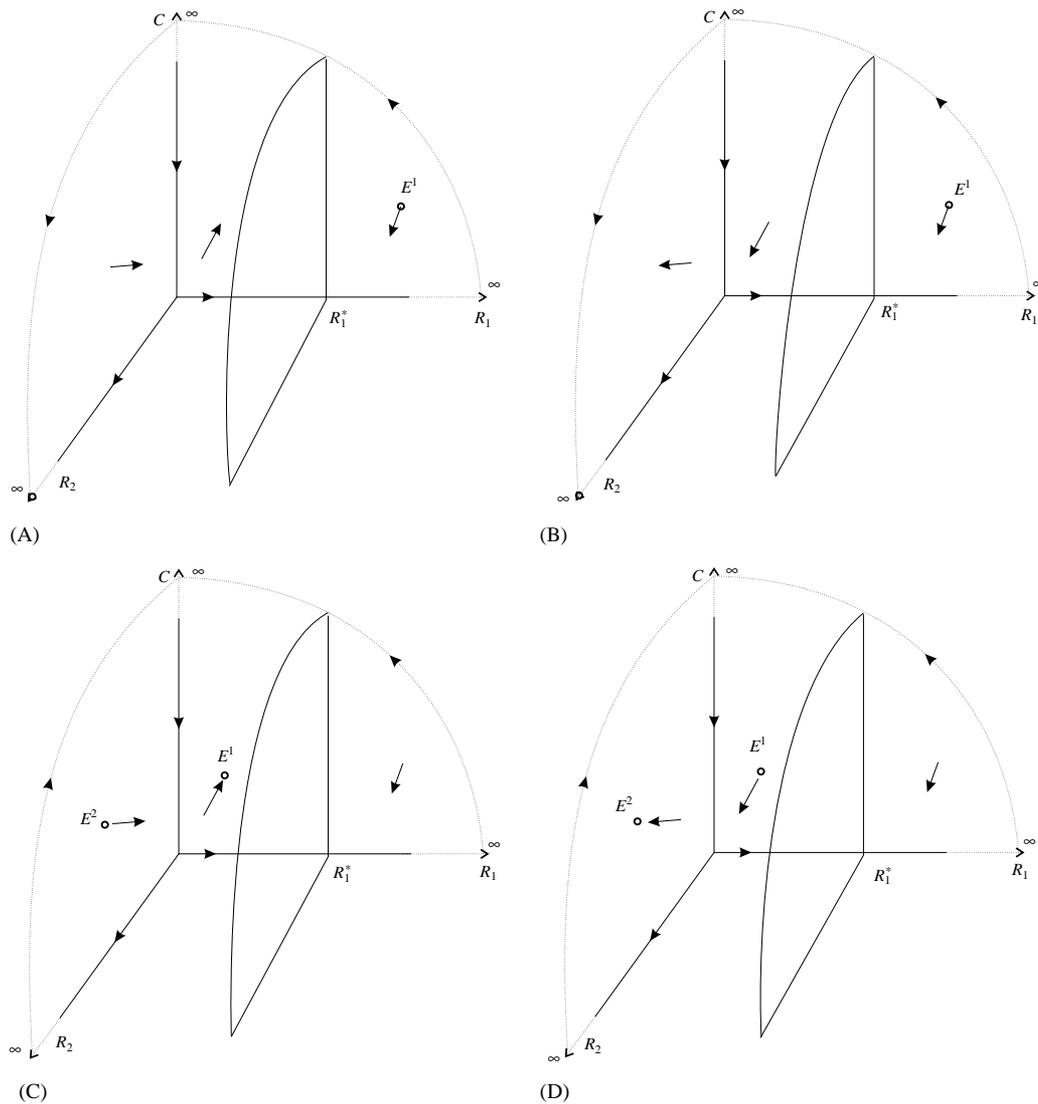


Fig. 3. This figure shows the projection of the phase space of model (1) onto a unit sphere. The projection allows us to study population dynamics at infinity. (A) and (B) assume that the equilibrium of prey 1–predator system is to the right from the switching plane while (C) and (D) assume the opposite case. (A) and (C) assume that prey 2 is competitively dominant over prey 1 while (B) and (D) assume the opposite case.

preference domain, whenever the initial density of the alternative prey type is lower than the critical density ($R_2(0) < R_2^{crit}$, Fig. 4). If the initial point is at the lower boundary of the partial preference domain and the initial density of the alternative prey type is above the critical density ($R_2(0) > R_2^{crit}$, Fig. 4) then the alternative prey survives in the system indefinitely and its density tends to infinity. Thus, optimal foraging leads to multiple attractors. We remark that numerical simulations show that as the alternative prey growth rate (r_2) decreases to zero, the unstable limit cycle moves in the R_2 direction to infinity.

If prey 2 is competitively dominant over prey 1 (Fig. 3B), then the unstable limit cycle cannot arise because prey 2 density increases everywhere in the partial preference domain (Appendix B).

Second, we assume that prey type 1 equilibrium density is below the switching threshold, which happens if the opposite inequality to that in (4) holds. This occurs when prey type 2 alone can support the predator population at a positive equilibrium. Qualitatively, there are again two possibilities shown in Figs. 3C and D. Fig. 3C shows the case where prey 1 is competitively dominant while Fig. 3D shows the case where prey 2 is competitively dominant. Once again it is clear that prey switching can make system permanent only provided prey 1 is stronger competitor. However, the situation is quite different than in the previous case where consumer density was decreasing in the partial preference domain, because now, consumer preference increases there (Appendix B). Extensive numerical simulations do not suggest existence of any limit cycle similar to the one we

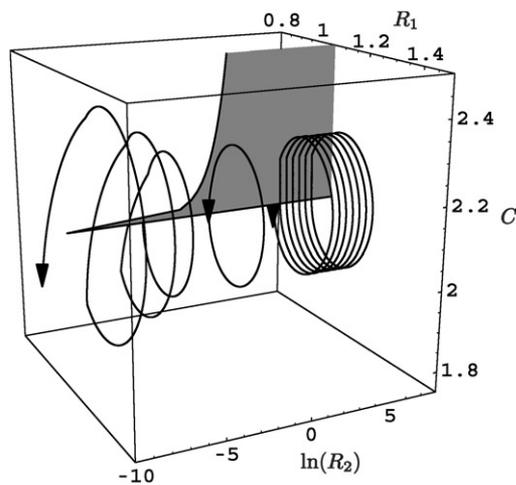


Fig. 4. Optimal foraging behavior of predators leads to the emergence of an unstable limit cycle for population dynamics described by (1). This limit cycle passes through the lower bound of the partial preference domain (lower solid line). The light shaded plane is the switching plane and the dark shaded area of this plane is the partial preference domain. If initial density of the alternative, competitively weaker prey type 2 is low, then the corresponding trajectory that starts at the lower boundary of the partial preference domain converges to the R_1 - C plane and the alternative prey type is outcompeted from the system. The remaining prey type 1-predator system follows diverging oscillations which result from the Holling type II functional response. If an initial density of the alternative prey type is high enough, all three species survive indefinitely along a trajectory which starts at the lower bound of the partial preference domain. This figure assumes that the alternative prey 2 alone cannot support predators at a positive equilibrium level (i.e., the equilibrium of prey 1-predator subsystem is to the right from the switching plane). Parameters are the same as those given in the legend of Fig. 2.

observed when prey 1 equilibrium density was above the switching threshold. However, species coexistence is still possible (Fig. 5) albeit the mechanism leading to it is different than in the previous case. Presently, coexistence is achieved along a trajectory of model (1) which is effectively trapped by the partial preference domain. Along such a trajectory, all three species coexist indefinitely without oscillations in prey and predator population densities and density of the alternative prey and predators grow to infinity.

Using the continuation AUTO package we studied the dependence of the unstable limit cycle on the predator mortality rate (Fig. 6). The open dots denote the maximum and minimum values along the unstable limit cycle. We observe that this limit cycle bifurcates for $m = e_2/h_2$ from the equilibrium E^1 [which for $m = e_2/h_2$ coincides with the point $(R_1^*, 0, \frac{r_1}{\lambda_1}(1 + h_1\lambda_1 R_1^*))$] in the plane $R_2 = 0$. As the predator mortality rate m increases, amplitude of the cycle increases too both in R_1 and R_2 . The bifurcation diagram for the consumer looks similar to that of the bifurcation diagram for prey 1.

The present analysis shows that adaptive foraging behavior of consumers can lead to sustained oscillations

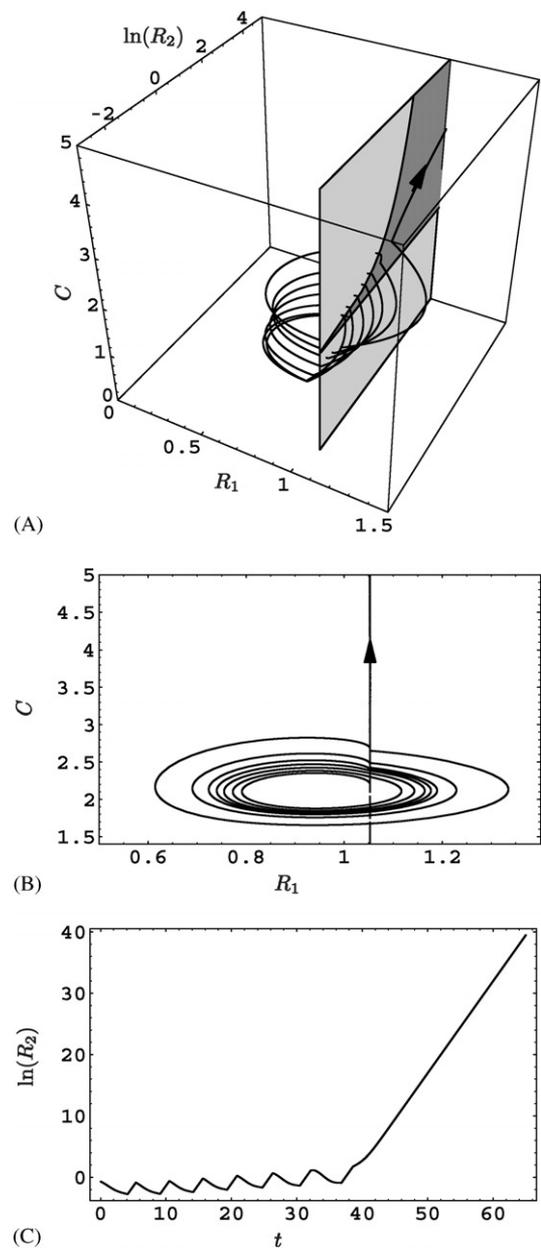


Fig. 5. This figure assumes that the alternative prey type 2 alone can support predators at a positive (unstable) equilibrium (i.e., the equilibrium of prey 1-predator subsystem is to the left from the switching plane). The figure also shows that in this case, species coexistence can be achieved because species densities converge to the partial preference domain where they can remain. (A) shows a trajectory in 3D-phase space, (B) shows the same trajectory in prey type 1-predator phase space and (C) shows time dynamics of prey type 2. Parameters: $r_1 = 2, r_2 = 1.5, \lambda_1 = \lambda_2 = 1, e_1 = 1, e_2 = 0.1, h_1 = 0.05, h_2 = 0.1, m = 0.9$.

in prey 1-predator system provided the alternative prey species persist in the system. This is the case where prey 1 is competitively dominant over the alternative prey and the alternative prey type profitability (e_2/h_2) is smaller than is the predator mortality rate (m). We also showed that adaptive prey switching cannot regulate exponential growth of both prey species because under

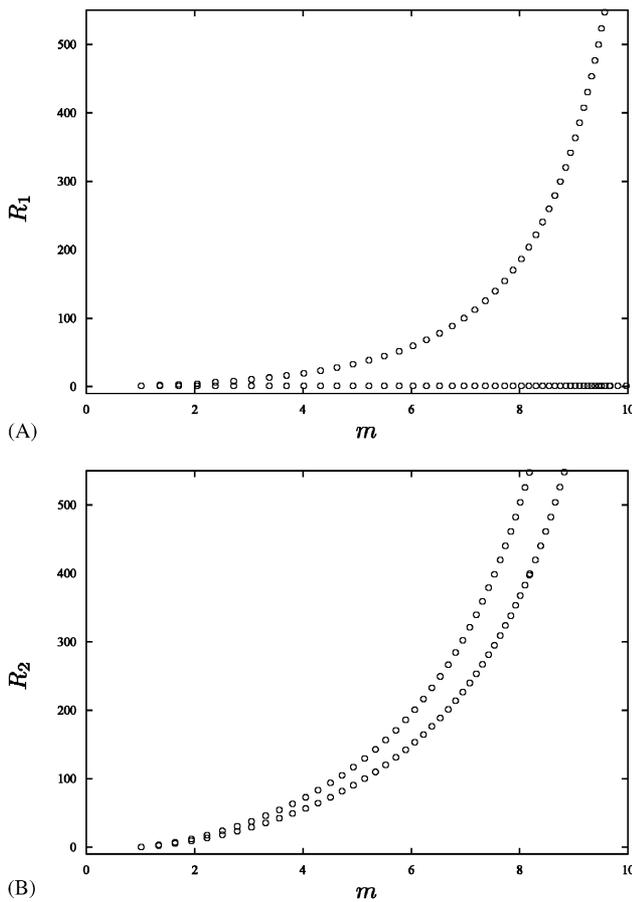


Fig. 6. The dependence of the unstable limit cycle that arises due to optimal prey switching in model (1) on predator mortality rate. The figure assumes that both prey types grow exponentially and it shows maximum and minimum values for the two prey species along the limit cycle (the open dots). Parameters are the same as those given in the legend of Fig. 2.

the above assumptions the alternative prey density grows to infinity.

3. Logistic prey growth

When prey growth was controlled by top-down control alone we showed in the previous section that predators are not able to keep both prey densities bounded. If both prey types are to coexist indefinitely, the alternative prey type will grow to infinity. Thus, there must be another kind of control that keeps the alternative prey type bounded. Here we assume that the alternative prey is also limited by bottom-up control while the primary prey type is limited by top-down control only. Numerical simulations show that the bottom-up regulation of the alternative prey species can lead to boundedness and coexistence of all three species because together with the unstable limit cycle that we observed in the previous section (the middle

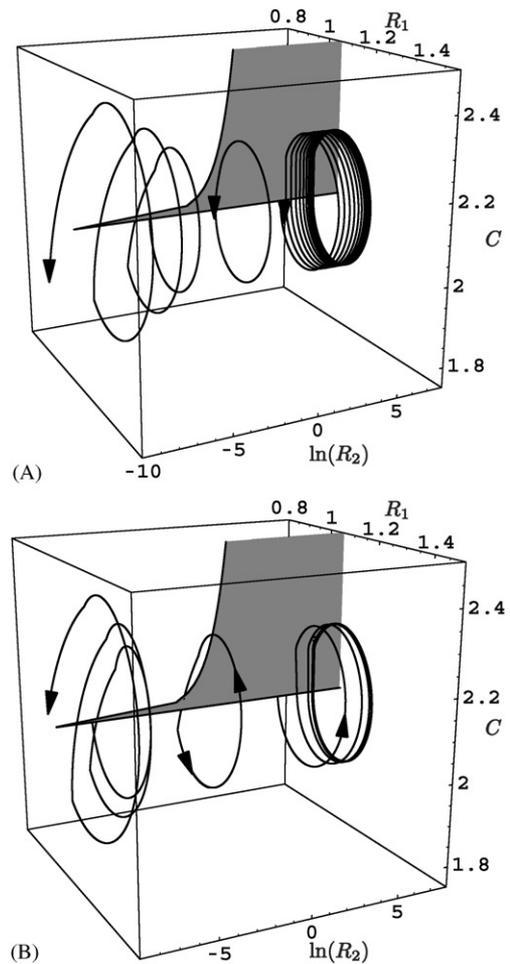
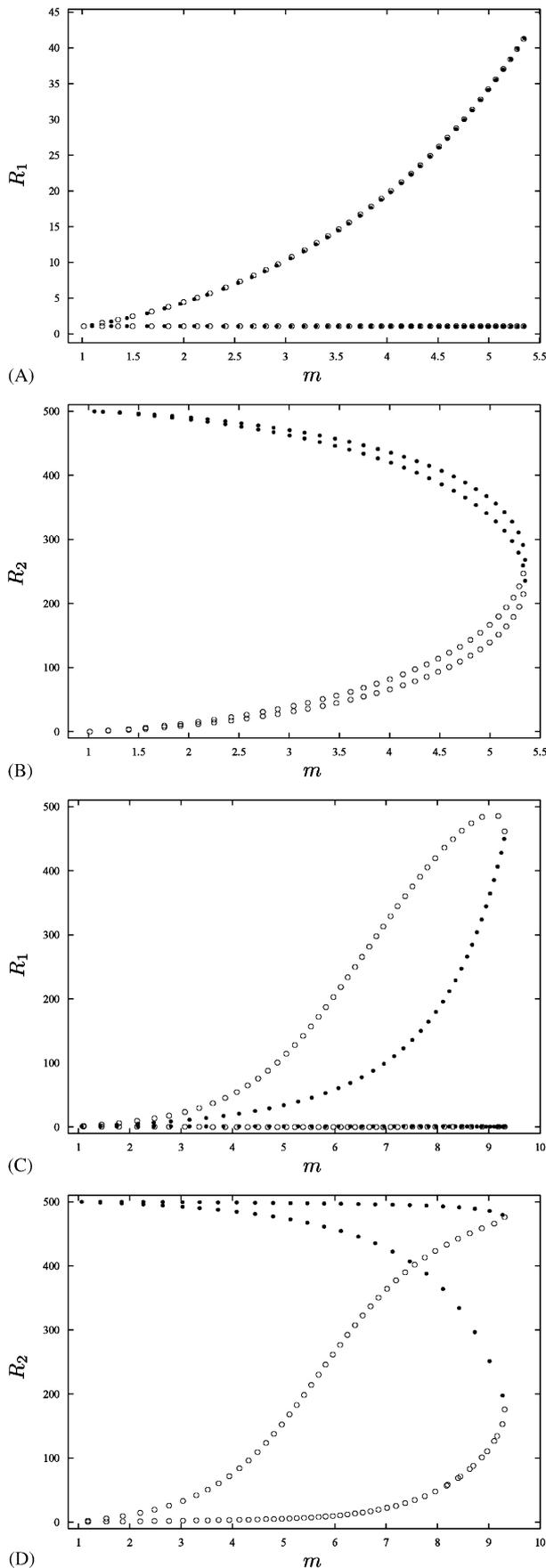


Fig. 7. The logistic growth of the alternative prey type with optimal prey switching leads to one unstable (the cycle in the middle of the figure) and one locally stable limit cycle (the right cycle). The unstable limit cycle either enters the partial preference domain if prey 1 is strongly competitively dominant over prey 2 (A) or circles round it if prey 1 is only weakly competitively dominant (B). Parameters are the same as those given in the legend of Fig. 2 with the exception $r_2 = 0.35$ in case (B). Alternative prey carrying capacity is $K_2 = 500$.

cycle in Fig. 7) a stable limit cycle appears (the right limit cycle in Fig. 7). Along this stable limit cycle, all three populations fluctuate indefinitely. We remark that the system without prey switching has no interior equilibrium under the assumption that the alternative prey type is the weaker competitor and we did not observe any interior limit cycles in our numerical simulations.

Using the continuation package AUTO we studied dependence of those two limit cycles that arise due to prey switching on the predator mortality rate parameter (m , Fig. 8). Figs. 7A and 8A and B show the situation where the alternative prey is much competitively weaker than prey 1 (i.e., $r_2/\lambda_2 \ll r_1/\lambda_1$; both the stable and unstable limit cycles coexist symmetrically with respect to R_2) while Figs. 7B and 8C and D show the situation where prey 2 is only slightly competitively weaker than



prey 1. Bifurcation diagrams for the consumer look similar as those for prey 1. The solid dots denote the maximum and minimum values along the stable limit cycle while the open dots denote the same for the unstable limit cycle. For $m = e_2/h_2$, we observe bifurcation of two limit cycles. The stable limit cycle bifurcates from the equilibrium

$$E^3 = \left(\frac{m}{\lambda_1(e_1 - h_1 m)}, K_2, \frac{e_1 r_1}{\lambda_1(e_1 - h_1 m)} \right)$$

while the unstable limit cycle bifurcates from the equilibrium E^1 . [For $m = e_2/h_2$ these two equilibria coincide with $(R_1^*, K_2, \frac{r_1}{\lambda_1}(1 + h_1 \lambda_1 R_1^*))$ and $(R_1^*, 0, \frac{r_1}{\lambda_1}(1 + h_1 \lambda_1 R_1^*))$, respectively.] As the predator mortality rate m increases, amplitude of both cycles increases too. The stable limit cycle is in the part of the species density phase space where the alternative prey is abundant while the unstable limit cycle is in the part of the phase space where the alternative prey abundance is low (Fig. 8B). The stable limit cycle always enters the partial preference domain and does not enter the domain behind the switching plane where the alternative prey would be fully included ($u_2 = 1$)—see Fig. 7. The unstable limit cycle enters the partial preference domain as on Fig. 7A irrespectively of the predator mortality rate m only if prey 1 is strongly competitively dominant over prey 2. In this case, both limit cycles are symmetric with respect to R_2 and have the same amplitude in all variables (see Figs. 8A and B). On the contrary, if prey 1 is only slightly competitively dominant over prey 2 then the unstable limit cycle does not enter the partial preference domain for any m and circles round it (Fig. 7B). Hence, the unstable limit cycle has larger amplitude in all variables and the symmetry is broken (see Figs. 8C and D). As m increases the two limit cycles tend together, for $m = m_{max}$ they coincide and for yet higher values of the predator mortality rates they do not exist.

4. Gradual switching

To assume that prey switching is instantaneous is unrealistic and we can ask how robust are our results when switching is more gradual. Following van Baalen et al. (2001), we model gradual switching by the

←
 Fig. 8. The dependence of the stable and unstable limit cycles that arise due to optimal prey switching in model with the logistic alternative prey growth on the predator mortality rate. The solid dots describe the stable limit cycle while the open dots describe the unstable cycle. Parameters for (A) and (B) are the same as those for Fig. 4 i.e., prey type 1 is strongly dominant over prey type 2 while in cases (C) and (D), prey type 1 is only weakly competitively dominant over prey type 2 ($r_2 = 1$). The alternative prey carrying capacity for all four cases is $K_2 = 500$.

following function:

$$u_2(R_1) = \frac{(R_1^*)^\mu}{R_1^\mu + (R_1^*)^\mu},$$

where parameter μ determines the width of the predator's switching interval. The larger μ is, the more closely u_2 approximates the optimum step-wise switch. Using the AUTO continuation package we can now study the dependence of the limit cycles (that we observed for step-wise switch) on the precision of switching μ . Fig. 9A shows the case where both prey types grow exponentially while Figs. 9B and C show the case where the alternative prey type grows logistically. Again, the solid dots denote the maximum and minimum values along the stable limit cycle while the open dots denote the same for the unstable limit cycle. We observe that the unstable limit cycle (in the case of the logistical growth) bifurcates for lower values of the switching parameter μ than the stable limit cycle does. These two bifurcation points are connected by the curve of inner equilibria (the solid line in Fig. 9—the heavy part denotes locally stable equilibria while the thin part denotes unstable equilibria). The amplitude of the stable limit cycles increases with μ to a constant level (in all Figs. 9A–C). The same holds for the unstable limit cycles providing prey 2 is competitively much weaker than prey 1 (Figs. 9A and B). If prey 2 is only slightly competitively inferior than prey 1 then the amplitude of the unstable limit cycles first rapidly increases and then decreases to a constant level (Fig. 9C).

5. Discussion

In this article, we have studied two-prey–one-predator population dynamics for two types of predator behaviors: (i) non-adaptive predators which choose their diet at random, and (ii) adaptive predators which follow the predictions of optimal foraging theory (Charnov, 1976; Stephens and Krebs, 1986). In the latter case, below a critical preferred prey (type 1) density, the alternative prey (type 2) is included in the predator diet while above that density prey (type 2) is excluded from diet. Such a model with adaptive predator behavior has been recently studied in several articles under various assumptions (for a review see Schmitz, 1997). The above model was numerically studied by Fryxell and Lundberg (1994, 1997), with density-dependent prey growth and switching between prey types occurring gradually. The same model with step-wise switching was studied by Křivan (1996) and Křivan and Sikder (1999). These studies showed that (i) switching can reduce fluctuations in species densities when compared with non-adaptive predators, and (ii) switching can destabilize a stable coexistence of prey and predators. Moreover, switching enhances species persistence because the set of model

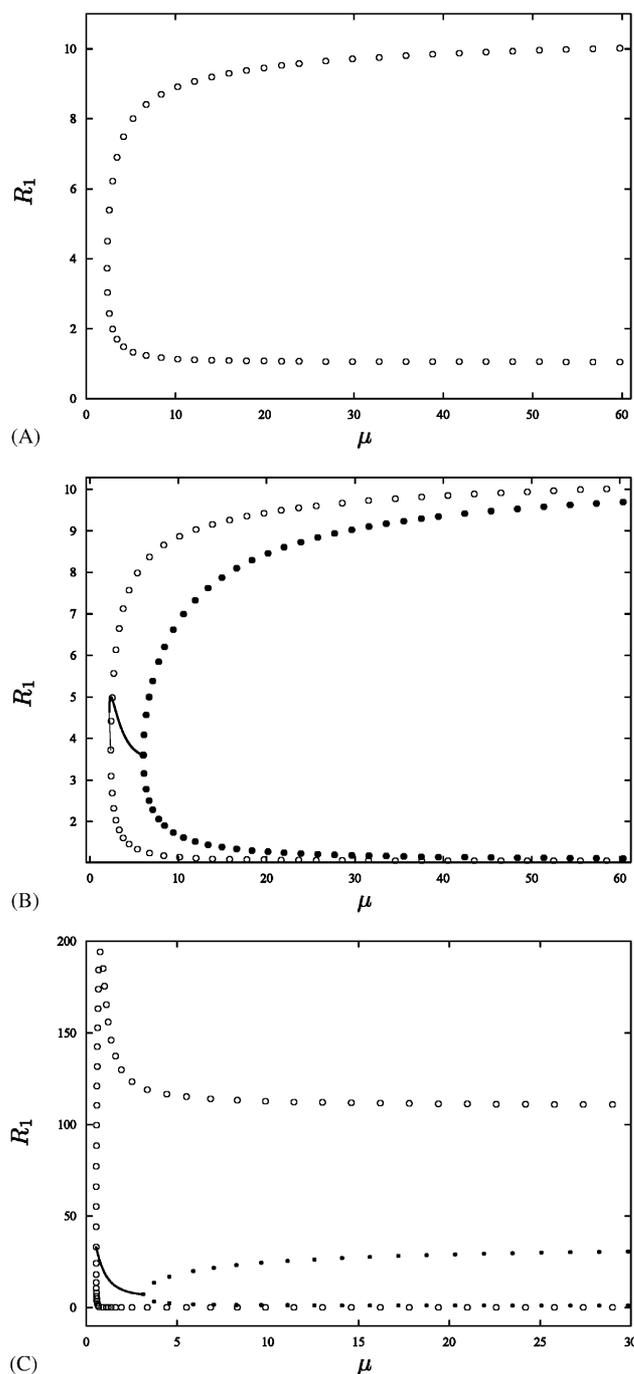


Fig. 9. The dependence of the stable and unstable limit cycles that arises due to optimal prey switching in model (1) on the predator's precision of switching. (A) shows the case where both prey types grow exponentially while (B) and (C) show the case where the alternative prey type grows logistically. The solid dots describe the stable limit cycle while the open dots describe the unstable cycle. In (A) and (B), predator's mortality rate $m = 3$ and the other parameters are the same as those used in Fig. 4. In (C), we have $r_2 = 1$ and $m = 5$. The alternative prey carrying capacity in (B) and (C) is $K_2 = 500$.

parameters for which all species coexist is larger for the system with switching when compared with non-adaptive predators (Křivan and Sikder, 1999). Two

factors influenced these results: (i) optimal predator foraging, and (ii) prey density-dependent growth. As it is known that prey density-dependent growth highly promotes species coexistence (either by stabilizing species densities at an equilibrium, or by the existence of a stable limit cycle due to the Paradox of Enrichment, Rosenzweig, 1971) it is not clear, how much the above-mentioned results depend on the description of prey-type dynamics. For this reason, van Baalen et al. (2001) studied a similar system without density-dependent prey-type growth but under a simplifying assumption that the alternative-prey-type density is constant, that is, not influenced by demographic and predation processes. They showed that adaptive foraging leads to the emergence of a limit cycle via which the predator–prey system becomes persistent. The present analysis which treats prey type 2 dynamically confirms their result. Even if the alternative prey type 2 grows exponentially it can still make the preferred-prey–predator system permanent (Fig. 4). This is because optimal foraging makes apparent competition (Holt, 1977) between the two prey types weaker when compared with a system where predators are non-adaptive. In the latter system, apparent competition is strong due to exponential prey growth which leads to the extinction of the competitively weaker prey species. In contrast, optimal foraging relaxes apparent competition because with high densities of the more profitable prey type, predators do not feed on the alternative prey type. If the alternative prey type is the weaker competitor and the profitability of the alternative prey type is lower than the predator mortality rate, this mechanism can lead to its survival in the system which cannot happen when predators are non-adaptive generalists. Because predators include the alternative prey type in their diet when the more profitable prey type is at low density, this relaxes the predation strength on the preferred prey type which leads to sustained oscillations in the preferred-prey–predator subsystem. However, this does not hold uniformly for all initial population densities. When, for example, initial densities of the alternative, competitively weaker prey type are low then coexistence is not achieved because apparent competition is still strong enough to exclude the alternative prey type from the system. This is because we have shown in this article that optimal foraging gives rise to an unstable limit cycle which leads to multiple attractors.

The results obtained in this article and in the previous articles (Křivan, 1996; Křivan and Sikder, 1999; van Baalen et al., 2001) strongly suggest that adaptive prey switching is a mechanism that promotes species coexistence without necessarily stabilizing species densities at an equilibrium. Thus, predation alone can effectively control exponential prey growth provided predators are adaptive and an alternative food resource exists. However, prey switching cannot regulate both the

preferred and the alternative prey type, i.e., when preferred prey-type growth is regulated, the alternative-prey-type density tends to infinity.

For this reason we also considered the case where alternative prey growth is bottom-up regulated. We have shown that in this case there exist two limit cycles as a consequence of optimal prey switching. One of them is unstable while the other is locally stable (Fig. 7). These two cycles exist provided the alternative prey type is the weaker competitor and its profitability is lower than the predator mortality rate.

This clearly has major implications for biological control. Consider the situation where predators are used (in long-term perspective) to control some pest. The classical Rosenzweig–MacArthur predator–prey model suggests that such a system is non-persistent. Either predators kill prey and not having enough food they die out (so that they will not be able to control newly immigrating prey), or, predators die out and prey grow exponentially. Even if predators are non-adaptive generalist, then adding an alternative exponentially growing prey does not lead to a qualitatively different situation because one of the two prey types is out-competed. Once again we arrive at Rosenzweig–MacArthur's impermanent remaining-prey–predator model. From the biological control point of view, it is desirable that predators survive in the system indefinitely so that they can control the pest when it appears. In this article, we have shown that this can be so provided predators follow optimal (or more gradual suboptimal) diet choice and the alternative prey is viable enough to survive in the system indefinitely. We demonstrated that there are two necessary conditions to achieve this. First, the alternative prey species is competitively weaker than the target prey species and, second, the profitability of the alternative prey species is lower than the predator mortality rate. However, because there are multiple attractors, whether or not the system with an alternative prey type will persist depends also on the initial species densities. In this article we have shown, that the initial density of the alternative prey type cannot be too low because in that case the alternative prey type is eliminated from the system.

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Appendix A

Transformation of (1) to cylindrical coordinates (ρ, ϕ, C) given by $R_1 = (\rho \cos \phi)^{\lambda_1}$ and $R_2 = (\rho \sin \phi)^{\lambda_2}$ gives the following equation for ϕ :

$$\frac{d\phi}{dt} = \frac{1}{2} \left(\frac{r_2}{\lambda_2} - \frac{r_1}{\lambda_1} \right) \rho \sin(2\phi). \quad (\text{A.1})$$

It follows that for $r_1/\lambda_1 > r_2/\lambda_2$, ϕ tends to zero which implies that the second species is outcompeted by the first species, while for $r_1/\lambda_1 < r_2/\lambda_2$, ϕ tends to $\pi/2$ which implies that the first species is outcompeted by the second species.

Appendix B

In the partial preference domain density of the more profitable prey type is constant and equal to R_1^* which implies that $\frac{dR_1}{dt} = 0$ in system (1). This allows us to compute preferences for the alternative prey type:

$$u_2 = \frac{1}{h_2 \lambda_2 R_2} \left(\frac{\lambda_1 C}{r_1} - \frac{e_1 h_2}{e_1 h_2 - e_2 h_1} \right),$$

for details see Křivan (1996). Substituting this expression for u_2 in model (1), the resulting population dynamics in the partial preference domain are described by

$$\begin{aligned} \frac{dR_1}{dt} &= 0, \\ \frac{dR_2}{dt} &= R_2 r_2 + \frac{e_1 r_1}{\lambda_1 (e_1 h_2 - e_2 h_1)} - \frac{C}{h_2}, \\ \frac{dC}{dt} &= C \left(\frac{e_2}{h_2} - m \right). \end{aligned} \quad (\text{B.1})$$

Model (B.1) implies that prey type 2 density decreases in the upper part of the partial preference domain

$$\begin{aligned} \frac{r_1}{\lambda_1} \left(\frac{e_1 h_2}{e_1 h_2 - e_2 h_1} + \frac{h_2 \lambda_1 r_2 R_2}{r_1} \right) \\ < C < \frac{r_1}{\lambda_1} \left(\frac{e_1 h_2}{e_1 h_2 - e_2 h_1} + h_2 \lambda_2 R_2 \right) \end{aligned} \quad (\text{B.2})$$

and increases in the lower part of the partial preference domain

$$\frac{r_1 e_1 h_2}{\lambda_1 (e_1 h_2 - e_2 h_1)} < C < \frac{r_1}{\lambda_1} \left(\frac{e_1 h_2}{e_1 h_2 - e_2 h_1} + \frac{h_2 \lambda_1 \lambda_2 R_2}{r_1} \right).$$

Note that when prey type 2 is competitively dominant over prey type 1 (i.e., $r_2/\lambda_2 > r_1/\lambda_1$) its density cannot

decrease in the partial preference domain because inequality (B.2) does not hold.

Appendix C

When the alternative prey growth is logistic there exist an interior equilibrium of model (1) which is

$$\begin{aligned} R_1^E &= \frac{mr_2 \lambda_1 - K_2 (e_2 - h_2 m) r_2 \lambda_1 \lambda_2 + K_2 (e_2 - h_2 m) r_1 \lambda_2^2}{(e_1 - h_1 m) r_2 \lambda_1^2}, \\ R_2^E &= \frac{K_2 \lambda_2}{r_2} \left(\frac{r_2}{\lambda_2} - \frac{r_1}{\lambda_1} \right), \\ C^E &= \frac{r_1 (e_2 h_1 K_2 \lambda_2 (r_1 \lambda_2 - r_2 \lambda_1) + e_1 (r_2 (\lambda_1 + h_2 K_2 \lambda_1 \lambda_2) - h_2 K_2 r_1 \lambda_2^2))}{(e_1 - h_1 m) r_2 \lambda_1^2}. \end{aligned}$$

We observe that when prey 1 is competitively dominant then this equilibrium is not positive.

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