Journal of Theoretical Biology 339 (2013) 112–121

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

Behavioral refuges and predator–prey coexistence

Vlastimil Křivan [a,b,*]

[a] Institute of Entomology, Biology Center, Academy of Sciences of the Czech Republic, Branišovská 31, 370 05 České Budějovice, Czech Republic
[b] Department of Mathematics and Biomathematics, Faculty of Science, University of South Bohemia, Branišovská 31, 370 05 České Budějovice, Czech Republic

HIGHLIGHTS

- Optimal predator foraging or optimal predator avoidance by prey creates a behavioral refuge for prey in predator–prey models.
- Such a behavioral refuge promotes predator–prey coexistence in the Gause predator–prey model.
- Predator avoidance by prey leads to a game that has two evolutionarily stable strategies at current population densities.
- The existence of these ESS leads to a hysteresis in prey behavior.

ARTICLE INFO

Available online 3 January 2013

Keywords:
Functional response
Hysteresis
Lotka–Volterra model
Population dynamics
Switching

ABSTRACT

The effects of a behavioral refuge caused either by the predator optimal foraging or prey adaptive antipredator behavior on the Gause predator–prey model are studied. It is shown that both of these mechanisms promote predator–prey coexistence either at an equilibrium, or along a limit cycle. Adaptive prey refuge use leads to hysteresis in prey antipredator behavior which allows predator–prey coexistence along a limit cycle. Similarly, optimal predator foraging leads to sigmoidal functional responses with a potential to stabilize predator–prey population dynamics at an equilibrium, or along a limit cycle.

1. Introduction

Presence of a refuge has been known to promote predator–prey coexistence for a long time. One of the first such experimental evidence was reported by Gause et al. (1936) who observed in experiments with protists and yeast that when at low densities, yeast formed into a sediment that was not accessible to protists staying in the water column. When at low density, the yeast was effectively in a refuge and protists and yeast densities fluctuated. Using a predator–prey model with exponentially growing prey and decelerating functional response these authors also showed that a refuge can promote predator–prey coexistence along a limit cycle (for a full analysis see Křivan, 2011). For the Lotka–Volterra predator–prey model Maynard Smith (1974) considered a refuge that protects either a fixed number of prey, or a constant fraction of prey. He concluded that refuges protecting a constant number of prey stabilize population dynamics more strongly than refuges protecting a proportion of prey.

The work mentioned so far assumes passive (non-adaptive) refuge use by prey: either a fixed number or a fixed proportion of prey stays in the refuge. However, using a refuge leads to a trade-off, because being in a refuge increases survival due to lower predation but decreases other components of prey fitness (e.g., food intake or mating opportunities). It has been clearly documented that under increasing predation risk prey reduce their activity or change their habitat adaptively (e.g.., Sih, 1980, 1986; Lima and Dill, 1990; Peacor and Werner, 2001; Brown and Kotler, 2004). Models of adaptive refuge use (reviewed in Křivan, 1998) were also studied in the literature (e.g., Ives and Dobson, 1987; Sih, 1987; Ruxton, 1995). These models assume that prey strategy is a function of predation risk. Křivan (1998) used a game theoretical approach to derive evolutionarily stable prey antipredator strategy as a function of predator density. For fitness functions based on the Lotka–Volterra population dynamics there were only two possibilities: below a critical predator density all prey were outside of the refuge while above the threshold they were in the refuge. The corresponding population dynamics then had a neutrally stable equilibrium at which either all prey were in the refuge, or out of the refuge. It was predicted that a similar behavior can be expected in the case where the linear functional response is replaced by the Holling type II functional response. In this paper I will study such a

---

[*] Correspondence address: Tel.: +420 387775365.
E-mail address: vlastimil.krivan@gmail.com

0022-5193/$ - see front matter © 2012 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.jtbi.2012.12.016

model and I will show that for the Holling type II functional response the situation is much more complex as the prey fitness depends not only on predator abundance but also on prey abundance. This makes the prey fitness frequency dependent, and the optimal prey strategy must be sought in the form of an evolutionarily stable strategy (ESS Hofbauer and Sigmund, 1998).

I will also survey how predator's optimal foraging (Oaten and Murdoch, 1975; Charnov, 1976a) can create a behavioral prey refuge. Both of these optimal foraging models predict that at low preferred prey densities the interaction strength between prey and predators sharply decreases because predators either switch to an alternative prey type, or include an alternative prey type to their diet. Such a behavior creates a refuge for the primary prey type. Although the effects of optimal foraging were studied extensively in the literature (e.g., Holt, 1983; Fryxell and Lundberg, 1994; Abrams and Matsuda, 1996; Fryxell and Lundberg, 1997; Křivan, 1997; Abrams, 1999; Křivan and Eisner, 2003; Ma et al., 2003) analysis in this paper allows me to compare effects of adaptive refuge use by prey with the refuge caused by predator's optimal foraging.

2. Adaptive refuge use by prey

In this paper I study the effect of refuges on the Gause predator–prey population dynamics

$$\frac{dR}{dt} = rR - Cf(R),$$
$$\frac{dC}{dt} = (g(R) - m)C \qquad (1)$$

and its variants. Here R is prey density, C is predator density, r is the per capita prey population growth rate, f is the functional response, g is the numerical response, and m is the predator mortality rate. The above model is not of the Kolmogorov type (Svirezhev and Logofet, 1983), because it assumes unlimited exponential prey growth. When the functional response is of the Holling type II ($f = \lambda R/(1+\lambda hR)$ where h is the handling time and λ is the predator search rate), predation alone cannot stabilize population dynamics at an equilibrium or along a limit cycle (Fig. 1A) (e.g., Gause et al., 1936; Hofbauer and Sigmund, 1998; Křivan, 2008) and predators cannot coexist with their prey.

A mechanism that was shown to lead to predator–prey coexistence is existence of a prey refuge that protects a fixed number of prey from predation (e.g., Gause et al., 1936; Maynard Smith, 1974). These models assume that prey prefer to be in the refuge, and only when the refuge is fully occupied, the surplus of prey moves outside. A Holling type II functional response that reflects such prey behavior is

$$f(R) = \begin{cases} 0 & \text{if } R < R_c, \\ \frac{\lambda(R-R_c)}{1+h\lambda(R-R_c)} & \text{if } R \geq R_c, \end{cases} \qquad (2)$$

(e.g., Ma et al., 2009), where R_c denotes the refuge size. Presence of a refuge changes the shape of the Holling type II functional response to an (extreme) sigmoid type (i.e., the Holling type III) functional response (Fig. 2A, solid line). In this case the Gause's equilibrium stability criterion $((df(R)/dR) > (f(R)/R)$; Gause et al., 1936) holds for prey densities that are smaller than $R_c + \sqrt{R_c/(h\lambda)}$ (see the vertical dotted line in Fig. 2A). The resource equilibrium density of model (1) with functional response (2), $R^* = R_c + m/(\lambda(e-hm))$ satisfies this stability condition provided the refuge size is large enough, i.e.,

$$R_c > \frac{hm^2}{\lambda(e-hm)^2},$$

(Fig. 1C). Numerical simulations show that for a smaller refuge size a locally stable limit cycle appears (Fig. 1B, D). This is because the prey isocline $C = rR(h + 1/(\lambda(R-R_c)))$ (the dashed curve in Fig. 1B), for prey population densities that are just above the refuge size R_c, is almost vertical and it effectively bounds the amplitude of predator–prey populations (Rosenzweig and MacArthur, 1963). However, neither this limit cycle nor the locally stable equilibrium are global phenomena. Depending on the handling time and initial population numbers there can be trajectories that completely escape predator regulation (Fig. 1B and C, bottom trajectories). Numerical simulations show that as the refuge size asymptotically

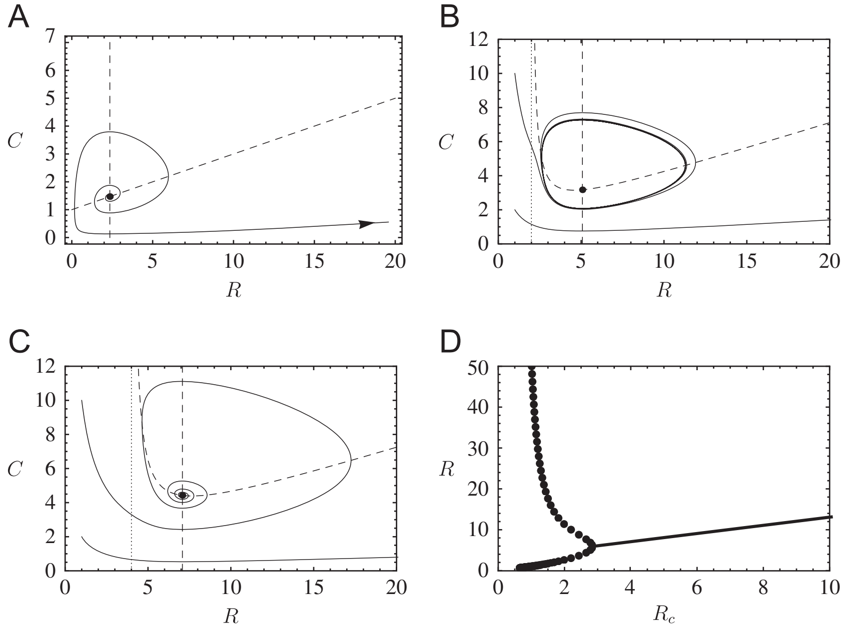

Fig. 1. Trajectories of model (1) with functional response (2). Panel A assumes no refuge (R_c=0), panel B assumes a small refuge (R_c=2, see the dotted vertical line) that leads to predator–prey coexistence along a limit cycle, and panel C assumes a large refuge size (R_c=4) which stabilizes predator–prey interactions at an equilibrium. There are also trajectories along which population densities tend to infinity (the bottom solid curves in B and C). Bifurcation diagram in panel D shows dependence of the amplitude of the locally stable limit cycle (solid dots) and the locally stable equilibrium (solid thick line) on the refuge size R_c. Other parameters: r=1, $\lambda = 1$, m=0.8, e=0.5, h=0.3.

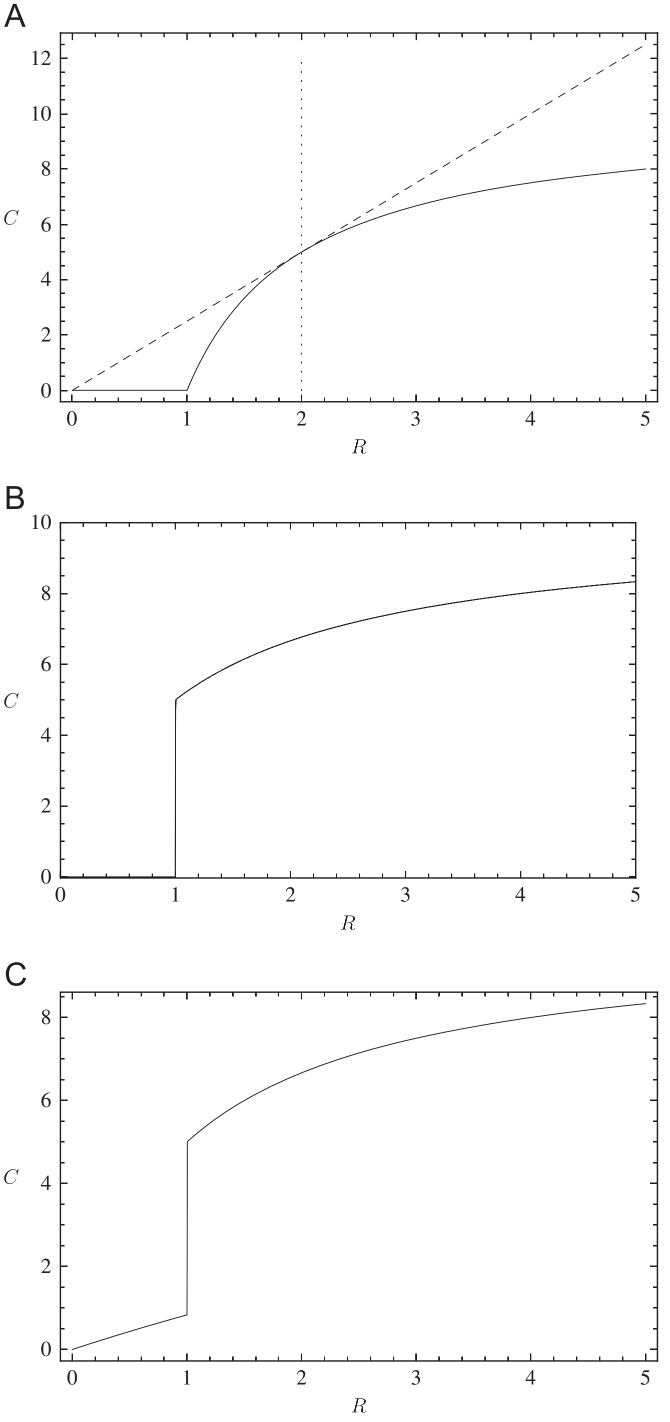

Fig. 2. Panel A shows functional response (2) with the refuge size $R_c = 1$. The dotted vertical line denotes the critical prey density below which the Gause equilibrium stability criterion holds and the functional response is stabilizing predator–prey population dynamics. Panel B shows functional responses (12). Panel C shows functional response for predators that follow predictions of the optimal foraging theory (9). The alternative resource density is set here to $R_a = 10$. Other parameters are the same in all three panels: $e = 1$, $e_a = 0.5$, $h = h_a = 0.1$, $\lambda = \lambda_a = 10$.

decreases to a critical value (about 0.5 in Fig. 1D), the amplitude of fluctuations increases to infinity and below the critical refuge size the limit cycle disappears and predator–prey coexistence is impossible. This analysis clearly shows that a refuge alone can lead to coexistence of predators and exponentially growing prey either at a population equilibrium, or along a limit cycle. No bottom-up regulation of prey growth is needed to achieve species coexistence. So far I have considered the situation where a prey used the refuge non-adaptively. Now I will consider the case where prey trade-off increased safety of refuges with decreased feeding rate and their preference for refuges depends on predation risk.

It is well known that when predators are present, prey often decrease their activity and/or change habitat to avoid predation risk (e.g., Werner and Gilliam, 1984; Holbrook and Schmitt, 1988; Brown and Alkon, 1990; Brown, 1998; Lima, 1998a, 1998b; Sih, 1998; Peacor and Werner, 2001; Preisser et al., 2005). Reduction in prey activity is an example of a behavioral refuge. However, whether prey reduce their activity, or move to a physical refuge leads to a trade-off, because being in a refuge (either behavioral or physical) increases survival due to lower predation but decreases other components of prey fitness (e.g., food intake or mating opportunities). To model this trade-off I consider the following variant of model (1):

$$\frac{dR}{dt} = r_1 u_1 R - C f(u_1 R) + r_2 u_2 R,$$

$$\frac{dC}{dt} = (e_1 f(u_1 R) - m) C. \tag{3}$$

Here u_1 is the proportion of prey lifetime spent out of the refuge so that u_2 is the proportion spent in the refuge ($u_1 + u_2 = 1$). I assume that being out of the refuge provides prey with a positive per capita intrinsic population growth rate ($r_1 > 0$) that is higher than the intrinsic population growth rate in the refuge (r_2). As the refuge may not provide enough resources to achieve a positive population growth rate there, r_2 can be negative. Model (3) does not describe mechanistically the transition process of moving in and out of the refuge. Instead, it assumes that this process occurs very fast when compared to demographic processes (e.g., if the refuge is physical it does not take too much time to reach it, or when the refuge is behavioral, it does not take too much time to change behavior). Provided that the refuge use by prey is a plastic trait, the question is what is the optimal prey strategy (u_1, u_2)? I remark that in the case of a monomorphic prey population, this strategy also defines the prey population distribution in and out of the refuge.

To answer this question I need to specify prey fitness as a function of prey strategy. If proportion u_1 of prey is out of the refuge, their payoff, expressed as the per capita prey population growth rate there is

$$V_1 = r_1 - \frac{\lambda_1 C}{1 + h_1 \lambda_1 u_1 R}.$$

As the proportion of prey outside the refuge (u_1) increases, payoff will increase, because the chance that a single prey will be captured by a predator decreases due to the risk dilution effect (e.g., Foster and Treherne, 1981). As I assume that prey in the refuge are completely protected from predation, the payoff in the refuge is $V_2 = r_2$ (possibly negative). Thus, fitness of a mutant prey (with strategy $\tilde{u} = (\tilde{u}_1, \tilde{u}_2)$) in a monomorphic resident population (with distribution $u = (u_1, u_2)$) is given by the mean payoff

$$W(\tilde{u}, u) = \tilde{u}_1 V_1 + \tilde{u}_2 V_2 = r_1 \tilde{u}_1 - \frac{\lambda_1 \tilde{u}_1 C}{1 + h_1 \lambda_1 u_1 R} + r_2 \tilde{u}_2. \tag{4}$$

Mutant fitness is not only density dependent but also frequency dependent, because it depends on the resident strategy.

Appendix A analyzes the evolutionarily stable strategy (ESS) as a function of population densities. Because fitness function (4) is non-linear, I use the local ESS definition (Hofbauer and Sigmund, 1998) that requires $W(u^*, u) > W(u, u)$ for all strategies $u \neq u^*$ in some neighborhood of the ESS u^*. It is proved in Appendix A that the evolutionarily stable strategy as a function of predator and prey numbers is

$$u_1^* = \begin{cases} 1 & \text{if } C < \frac{r_1-r_2}{\lambda_1}, \\ \{0,1\} & \text{if } \frac{r_1-r_2}{\lambda_1} < C < \frac{r_1-r_2}{\lambda_1}(1+h_1\lambda_1 R), \\ 0 & \text{if } C > \frac{r_1-r_2}{\lambda_1}(1+h_1\lambda_1 R). \end{cases} \quad (5)$$

For low predator densities ($C<(r_1-r_2)/\lambda_1$), predation risk out of the refuge is low too, and prey stay outside of the refuge ($u_1^*=1$) where they achieve a higher intrinsic per capita population growth rate that in the refuge (r_2). When predator density is high ($C>(r_1-r_2)/\lambda_1(1+h_1\lambda_1 R)$), predation risk out of the refuge is not compensated for by the higher intrinsic per capita population growth rate, because fitness out of the refuge (V_1) is lower than the fitness in the refuge ($V_2=r_2$). The best prey strategy is to be in the refuge ($u_1^*=0$). For intermediate predator densities three Nash equilibria exist. Besides the two boundary ESSs ($(u_1,u_2)=(1,0)$ and $(u_1,u_2)=(0,1)$) there exists an interior equilibrium $(v_1,v_2)=(v_1,1-v_1)$

$$v_1(R,C) = \frac{1}{\lambda_1 h_1 R}\left(\frac{\lambda_1 C}{r_1-r_2}-1\right).$$

However, this interior Nash equilibrium is not evolutionarily stable (Appendix A). Without considering some strategy dynamics it is impossible to predict which of the two boundary ESSs will get established in the population.

Several strategy dynamics were considered in the game theoretical literature. These include replicator dynamics (Taylor and Jonker, 1978), best response dynamics (Hofbauer and Sigmund, 1998), imitation dynamics (Schlag, 1998), adaptive dynamics (Abrams, 1999, 2003; Dieckmann and Law, 1996; Abrams and Matsuda, 2004; Abrams, 2006), Darwinian dynamics (Vincent and Brown, 2005), and dispersal dynamics (Cressman and Křivan, 2006). I will consider here the best response dynamics (Hofbauer and Sigmund, 1998)

$$\frac{du_1}{dt} = k(\beta(u,R,C)-u_1), \quad (6)$$

where $\beta(u,R,C)=\arg\max_{0\le\tilde{u}_1\le 1} W(\tilde{u},u)$ denotes the best strategy a mutant can play to the current resident strategy u. Appendix A shows that

$$\beta = \begin{cases} 1 & \text{if } u_1 > v_1(R,C), \\ [0,1] & \text{if } u_1 = v_1(R,C), \\ 0 & \text{if } u_1 < v_1(R,C), \end{cases} \quad (7)$$

i.e., β as a function of the resident strategy is a step-like function. Parameter k in (6) is an arbitrary positive constant that measures the speed with which individuals react to their environment. When this parameter is high, behavioral dynamics (6) converge quickly to either 1 or 0, which are the locally stable equilibria of (6) at current population numbers.

What interests us here is the feedback between behavioral dynamics (6) and population dynamics (3). Prey strategy influences population dynamics that, in turn, drive strategy dynamics. I remark that population dynamics (3) with prey strategy fixed at some value are unstable because predators cannot control prey exponential growth. The question here is whether prey behavioral dynamics (6) can make predator–prey coexistence possible. Numerical simulations as those shown in Fig. 3 suggest that this is indeed so, as adaptive refuge use by prey can lead to predator–prey coexistence along a limit cycle. Let us consider the trajectory in Fig. 3A. Initially, predators are in low numbers (below 1) and the only prey ESS is to be out of the refuge ($u_1=1$). The corresponding population dynamics follow a spiraling trajectory of model (3) (assuming the handling time is small) with $u_1=1$. At certain moment the predator population density reaches the lower threshold ($C=(r_1-r_2)/\lambda_1$, see the dashed horizontal line in Fig. 3A), but because all prey are out of the refuge, and payoff there is higher than payoff in the refuge due to risk dilution, the best strategy is to keep staying there until the trajectory reaches the upper threshold ($C=(r_1-r_2)/\lambda_1(1+h_1\lambda_1 R)$, see the dashed slanted line in Fig. 3A). At this moment predation risk is so high it cannot be compensated for by the higher intrinsic per capita population growth rate out of the refuge and the best prey strategy is to move to the refuge. Thus, following the best response dynamics (6), prey start to move to the refuge with speed given by parameter k ($k=1$ in panel A and $k=10$ in panel C). However, this will lead to a decrease in predator population growth rate and, eventually, predator population starts to decline. Assuming prey population growth rate in the refuge is negative (panels A–D), prey population will decrease too. Thus, in the prey–predator phase space the trajectory will, with some delay, start to move downwards and it will reach the slanted dashed line again. As some prey already moved to the refuge, the best prey strategy is to stay in the refuge, because due to the low prey density outside of the refuge, the risk dilution effect is weak and predation risk is high there. Thus, the best prey strategy is to keep staying in the refuge until the trajectory reaches the lower threshold (the horizontal line). At this moment predation risk is low and it pays off for prey to move out of the refuge which, in turn, leads to a positive predator population growth rate. Simulations as those given in Fig. 3A and C show that through this mechanism predator–prey population dynamics can converge to a limit cycle. In fact, along the predator–prey trajectory we observe a hysteresis in prey preferences (Fig. 3B, D). These panels show prey preference for staying outside of the refuge (dashed line) along the population limit cycle, and the best response along this limit cycle (solid line). As the relative speed of the best response dynamics with respect to population dynamics measured by parameter k increases (cf. panel B vs. panel D), prey strategy dynamics closely follow the best response strategy.

Numerical simulations for positive intrinsic per capita population growth rates in the refuge are shown in panels E–H. Even in this case population dynamics can converge on a limit cycle, although in this case faster behavioral dynamics lead to a larger amplitude population fluctuations (cf. panel E vs. panel G). Thus, large values of k in model (6) can be detrimental for species coexistence. Dependence of predator amplitude along the limit cycle on prey selectivity parameter k is shown in Fig. 4. Panel A corresponds to the case where the prey intrinsic per capita population growth rate in the refuge is negative, while panel B assumes a positive growth rate. These plots document the fact that for intermediate values of prey sensitivity parameter k, predators and prey can coexist along a limit cycle, when prey antipredator strategy is adaptive. Solid dots denote the locally stable limit cycle shown in Fig. 3, while the open dots show another unstable limit cycle (not shown in Fig. 3). Thus, the locally stable limit cycle exists for intermediate prey sensitivities k.

In this section I studied adaptive refuge use by prey. In the next section I will consider behavioral refuges due to predator adaptive foraging.

3. Refuges caused by predator foraging behavior

In this section I briefly review some consequences of predator optimal foraging behavior in the context of behavioral prey refuges. I will consider the optimal diet choice and prey switching models.

The diet choice model (Charnov, 1976b; Stephens and Krebs, 1986) assumes that predators rank potential prey types on the basis of their profitability measured by the ratio of energy gain over the handling time (i.e., e/h). Here I consider two prey types, a primary prey type (R) which is more profitable than an alternative prey type (R_a) (i.e., $e/h > e_a/h_a$). The optimal foraging theory then predicts that the primary prey type will be included in predators' diet upon each encounter, while the alternative prey type will be

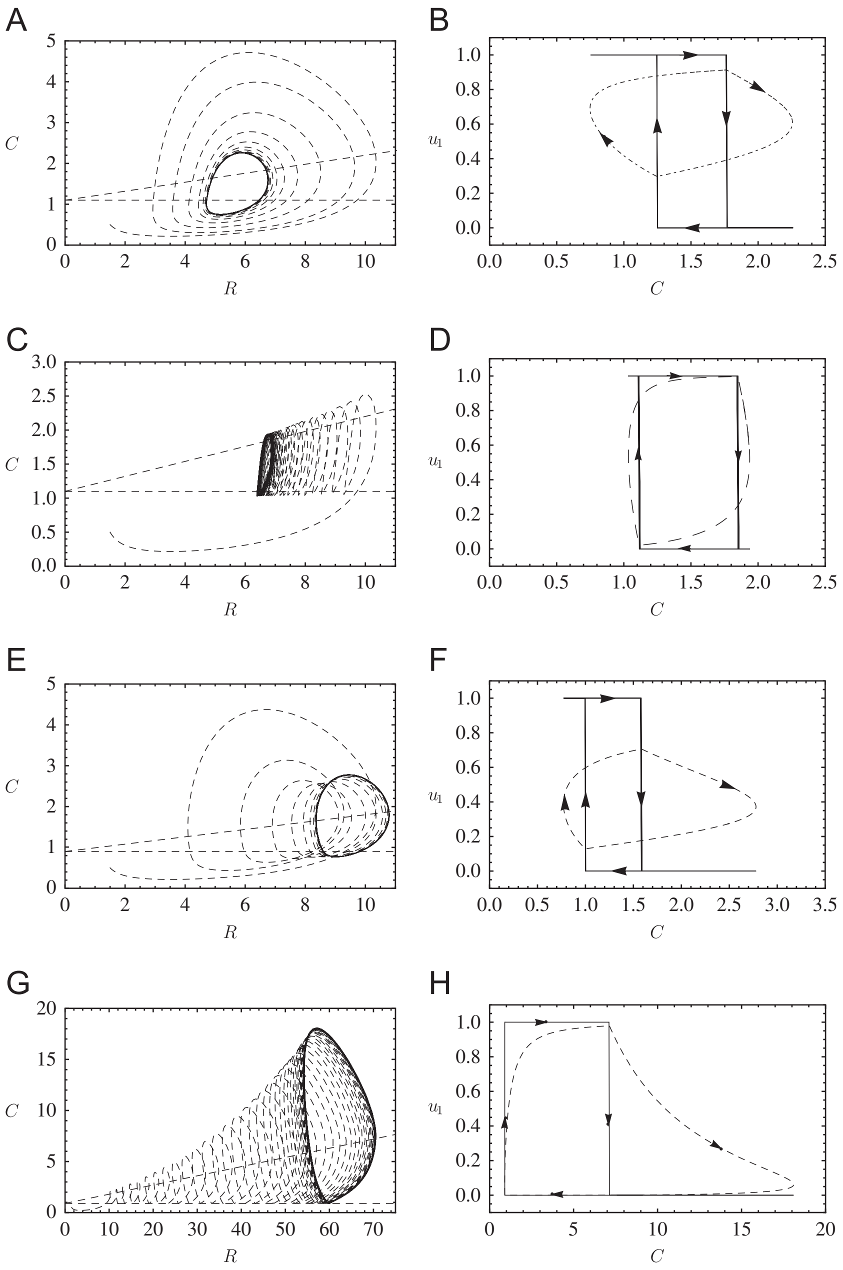

Fig. 3. Trajectories of model (3) with the best response behavioral dynamics (6). Panels A–D assume a negative prey population growth rate in the refuge ($r_2=-0.1$) while panels E–H assume a positive population growth rate in the refuge ($r_2=0.1$). Panels A, B, E, and F assume relatively low speed of behavioral dynamics ($k=1$) while panels C, D, G, and H assume that behavioral dynamics run on a fast time scale when compared to population dynamics ($k=10$). The left panels show predator–prey population dynamics, while the right panels show the prey preference for the open habitat as a function of predator density along the population limit cycle (dashed curve). The solid hysteresis loop shows the best response dynamics along the population limit cycle. Other parameters: $r_1=1$, $\lambda_1=1$, $m=2.6$, $e_1=1$, $h_1=0.1$.

fed upon only provided density of the primary prey type drops below the switching threshold

$$R_c=\frac{e_a}{\lambda(eh_a-e_ah)},\tag{8}$$

where λ is the predator search rate for the primary prey type (Stephens and Krebs, 1986). The corresponding Holling type II functional response for the primary prey type is then described by a piece-wise continuous function

$$f(R)=\begin{cases}\frac{\lambda R}{1+\lambda hR+h_aR_a} & \text{when } R<R_c,\\ \frac{\lambda R}{1+\lambda hR} & \text{when } R>R_c,\end{cases}\tag{9}$$

(Fig. 2C). This figure clearly shows that optimal foraging creates a partial behavioral refuge for the primary prey type; below the critical prey density R_c, predation on the primary prey decreases because predators include the alternative prey type in their diet. Thus the switching threshold R_c sets the effective refuge size in this model. Formula (8) shows that the behavioral refuge caused by optimal foraging increases with the quality of the alternative resource (i.e., with e_a). As e_a increases, the difference in profitability of the two resources decreases and predators will include the alternative prey type to their diet at a higher primary prey density. In fact, if density of the alternative prey (R_a) in the environment is high enough, feeding on the primary prey can be very negligible when $R<R_c$. The corresponding numeric

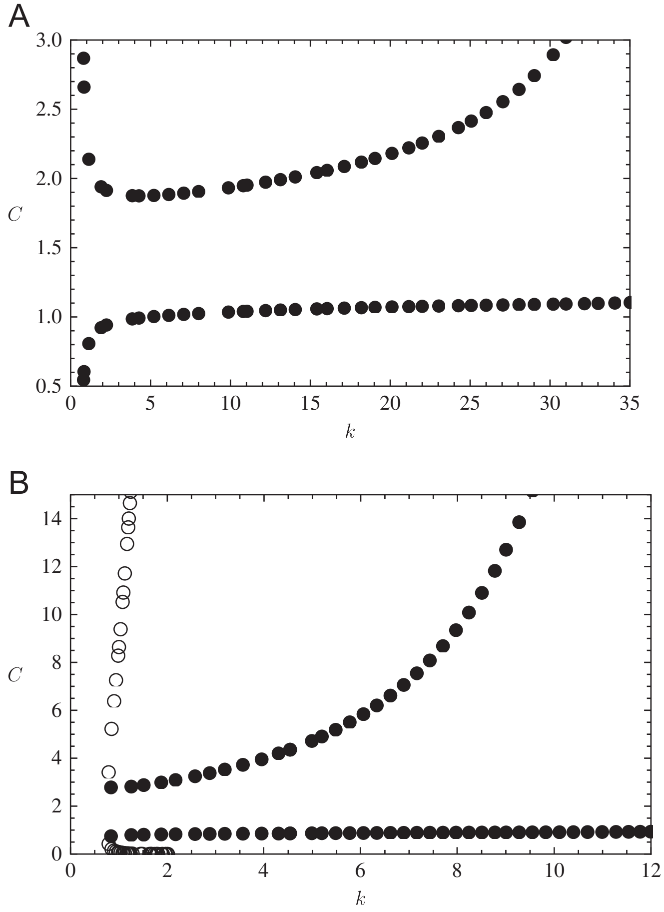

Fig. 4. Dependence of the amplitude of the stable (solid dots) and unstable (circles) limit cycles of predator–prey population dynamics (3) with prey strategy dynamics (6) on switching sensitivity k. Panel A assumes negative per capita prey population growth rate in the refuge ($r_2 = -0.1$) while panel B assumes a positive growth rate ($r_2 = 0.1$). Other parameters: $r_1 = 1$, $\lambda_1 = 1$, $e_1 = 1$, $h_1 = 0.1$, $m = 2.6$.

response is

$$g(R) = \begin{cases} \frac{e\lambda R + e_a \lambda_a R_a}{1 + h\lambda R + h_a \lambda_a R_a} & \text{when } R < R_c, \\ \frac{e\lambda R}{1 + h\lambda R} & \text{when } R > R_c. \end{cases} \tag{10}$$

Model (1) with functional response (9) and numerical response (10) was studied in detail by van Baalen et al. (2001) (for the case where both prey types undergo population dynamics see e.g., Holt, 1983; Fryxell and Lundberg, 1994; Abrams and Matsuda, 1996; Fryxell and Lundberg, 1997; Křivan, 1997; Abrams, 1999; Křivan and Eisner, 2003; Ma et al., 2003). It was shown that although prey and predators cannot coexist at an equilibrium, coexistence is possible along a limit cycle (Fig. 5). This is because a part of the prey isocline is vertical (see the vertical segment of the dashed line in Fig. 5A, B). Here I am interested in dependence of predator–prey population dynamics on the refuge size R_c. The results are given in Fig. 5. Panel A shows the case where the refuge (R_c) is small and the unstable predator–prey equilibrium is to the right of the vertical part of the prey isocline. As the refuge increases, the vertical part of the prey isocline (located at $R = R_c$) moves to the right which causes the amplitude of the limit cycle to shrink (Fig. 5C). When $R_c = m/(\lambda_1(e_1 - mh_1))$, the equilibrium is exactly on the vertical part of the prey isocline and it is locally asymptotically stable. Increasing R_c furthermore moves the predator–prey equilibrium to the left of the vertical part of the prey isocline (Fig. 5B) and the population oscillations increase again. Fig. 5C (solid dots) shows dependence of this limit cycle amplitude on the refuge size (R_c) given by formula (8). In this figure the solid dots correspond to the locally stable limit cycle shown in (5A, B) while the open circles denote the unstable large amplitude limit cycle (not shown in Fig. 5A, B). Both the stable and unstable limit cycle exists for intermediate refuge sizes.

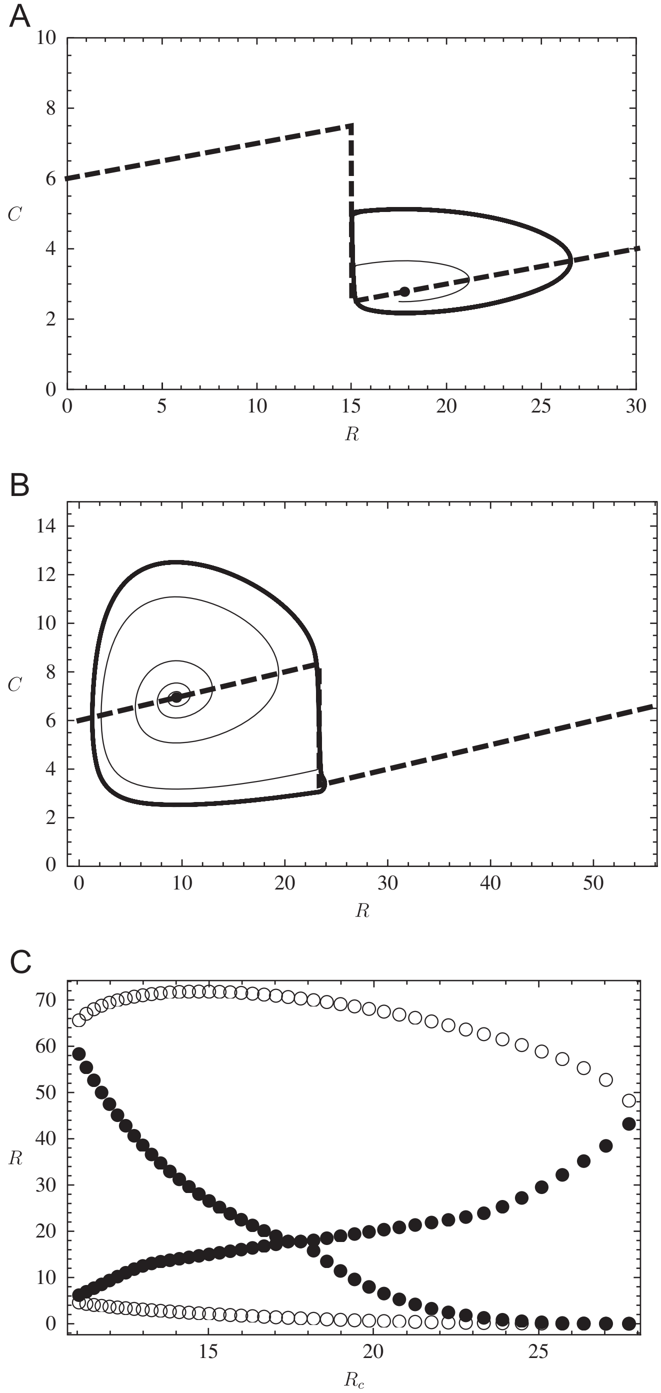

Fig. 5. This figure shows effects of behavioral refuge caused by optimal predator foraging on predator–prey population dynamics. The corresponding functional response is given by (9) and the numerical response by (10). Panel A assumes a small density of the alternative prey type (i.e., small behavioral refuge, $R_c = 15$, $e_a = 0.3$) so that the vertical part of the prey isocline is to the left of the equilibrium of model (1). Panel B assumes a larger behavioral refuge ($R_c = 23.3$, $e_a = 0.35$) and the corresponding equilibrium of the prey-predator model is to the left of the vertical part of the prey isocline. Bifurcation diagram in panel C shows dependence of the amplitude of the stable (solid dots) and unstable (circles) limit cycles on R_c. Other parameters: $r = 1$, $\lambda = \lambda_a = 1$, $e = 0.5$, $h = h_a = 0.1$, $m = 3.2$. $R_a = 50$.

Oaten and Murdoch (1975) examined how predator preference for prey might stabilize predator–prey population dynamics. They assumed that the proportion of prey in the predator's diet increases with increased prey proportion in the environment faster than linearly what they called switching. This happens, for example, when consumers exploit resources that are locally mixed but switching from one resource species to another requires some initial training or conditioning. The Holling type II functional response for the primary resource is (e.g., Holt, 1983; Abrams, 1999)

$$f(R)=\frac{u\lambda R}{1+h\lambda uR+h_a\lambda_a u_a R_a},\tag{11}$$

where u ($u_a=1-u$) is the predator preference for the primary (alternative) prey type R (R_a). At an extreme case where predators forage on the more abundant species only functional response (11) is piece-wise continuous (Fig. 2B)

$$f(R)=\begin{cases}0 & \text{when } R<R_a,\\ \frac{\lambda R}{1+h\lambda R} & \text{when } R>R_a\end{cases}\tag{12}$$

and the corresponding numerical response is

$$g(R)=\begin{cases}\frac{e_a\lambda_a R_a}{1+h_a\lambda_a R_a} & \text{when } R<R_a,\\ \frac{e\lambda R}{1+h\lambda R} & \text{when } R>R_a.\end{cases}\tag{13}$$

Once again the alternative prey density sets the refuge size because when primary prey density decreases below R_a, primary prey are not consumed at all. Model (1) with functional response (12) and numerical response (13) is analyzed in Appendix B. Depending on the refuge size (R_a) there are three qualitative cases. First, when refuge size is so small that $R_a<R^*$ (where $R^*=m/(\lambda(e-mh))$ is the prey equilibrium of model (1) when predators feed on primary prey only) a limit cycle along which predator and prey population densities periodically fluctuate exists (Fig. 6A). Second, if the refuge size is intermediate, $R^*<R_a<m/(\lambda_a(e_a-h_a m))$, there exists an interior equilibrium

$$E=(R^*,C^*)=\left(R_a,\frac{rR_a(e(\lambda+h_aR_a\lambda\lambda_a)-e_a(1+hR_a\lambda)\lambda_a)}{\lambda(m+(h_am-e_a)R_a\lambda_a)}\right),$$

with prey density equal to the refuge size (i.e., to the alternative prey density) (Fig. 6B). As the alternative resource density approaches $m/(\lambda_a(e_a-h_a m))$ the predator equilibrium tends to infinity. When R_a crosses this upper bound (i.e., $R_a>m/(\lambda_a(e_a-h_a m))$), no equilibrium exists along the vertical line $R=R_a$ and trajectories of the model once they fall on this line move along it to infinity. This is a consequence of the fact that the alternative resource density, which is not depleted, supports positive predator population growth. As it is unrealistic to assume that the alternative prey could reach such a high density and still be not influenced by predation or competition, these results are limited to alternative prey densities that do not allow for such unlimited predator growth. Fig. 6C shows dependence of the equilibrium and the amplitude of the limit cycle (solid dots denote the locally stable limit cycle) on the refuge size R_a.

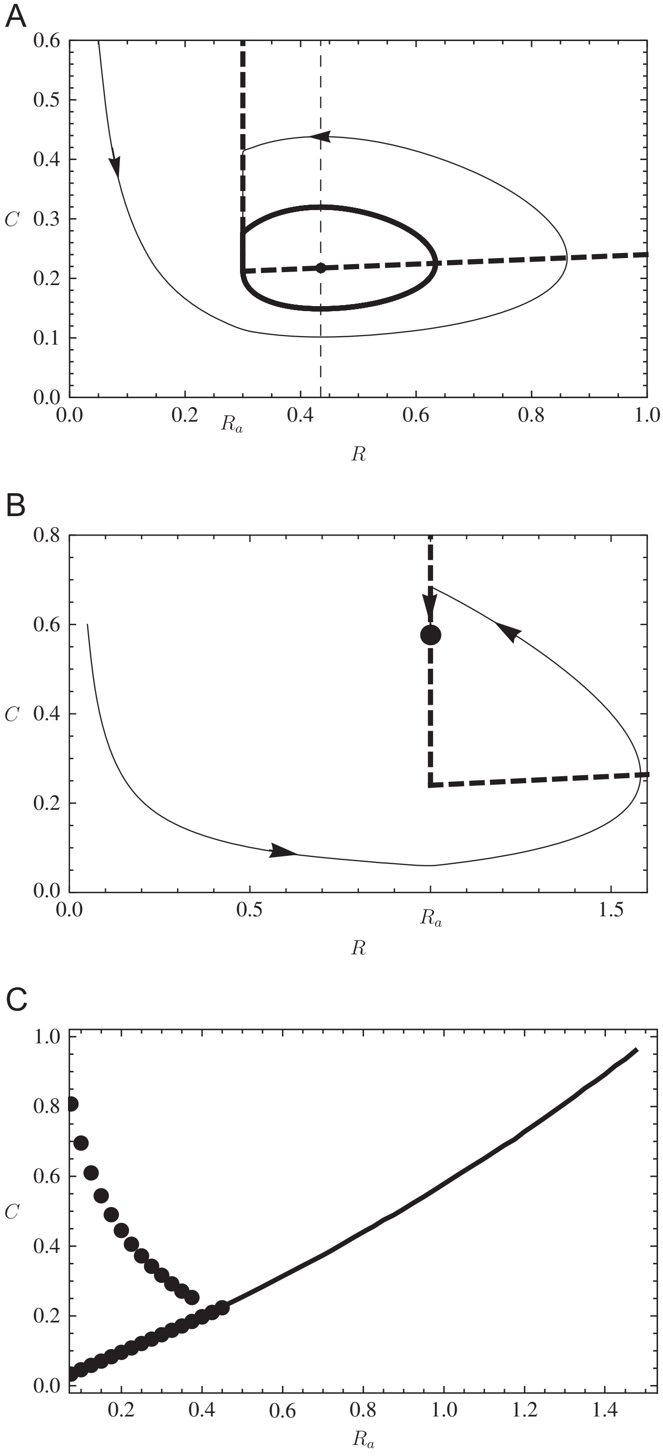

Fig. 6. This figure document effects of behavioral refuge caused by prey switching (12) on predator–prey population dynamics. Panel A assumes a small behavioral refuge when density of the alternative prey type (R_a=0.3) is smaller than the equilibrium prey density of model (1). In this case the behavioral refuge leads to a limit cycle. For an intermediate refuge size (R_a=1, panel B) refuge can stabilize predator prey population dynamics at an equilibrium. Panel C shows a bifurcation diagram with respect to R_a. Solid dots denote predator maxima and minima along the limit cycle and the solid line shows the locally stable interior equilibrium. Other parameters: $r=0.2$, $r_a=0.1$, $\lambda=\lambda_a=1$, $m=0.2$, $e=0.5$, $e_a=0.05$, $h=0.2$, h_a=0.1.

4. Discussion

In this paper, effects of a refuge on the Gause predator–prey model are studied. Two types of adaptive prey or predator behavior are studied in detail. First, I consider the effect of adaptive refuge use by prey. In this case the prey fitness is frequency dependent and I analyzed the corresponding prey ESS as a function of prey and predator numbers. Due to the risk dilution effect (e.g., Foster and Treherne, 1981) caused by the Holling type II functional response (i.e., the decrease in predation risk per an individual prey when the number of conspecifics increases) adaptive refuge use by prey leads to a bi-stable situation where for some predator and prey population densities two alternative ESSs exist (prey are either in the refuge or out of the refuge). Which of these two will be attained depends on the strategy dynamics. In this paper I consider the best response strategy dynamics that assume prey strategy evolves towards an ESS (Hofbauer and Sigmund, 1998). When the inherently unstable and impermanent Gause predator–prey population dynamics are combined with the adaptive prey refuge use, the resulting population dynamics converge on a limit cycle. It is interesting that existence of the two alternative ESSs leads to hysteresis in the prey preference for the refuge along the predator–prey population dynamics (Fig. 3). This shows that a behavioral refuge can cause coexistence between predators and their prey in models, where such coexistence without refuge is impossible. However, such coexistence is possible only for intermediate reaction speeds with which prey adjust their antipredator behavior to changes in population densities (Fig. 4). These results extend those given in Křivan (1998) where a similar model with linear functional response was considered. The optimal prey strategy there was much simpler, because prey fitness function (4) was independent of the prey density as the handling time was set to zero. For predator densities below a certain threshold the optimal prey strategy was to be out of the refuge while above that threshold all prey were in the refuge. Thus, there was no bi-stability in prey strategy. Predator–prey population dynamics oscillated around a neutrally stable equilibrium similarly to the classic Lotka–Volterra predator–prey model. Adaptive refuge use limited the maximum amplitude of predator–prey oscillations there. My hypothesis was that when the linear functional response was replaced by the Holling type II functional response the effect on population persistence would be similar and predators and their prey would coexist along a limit cycle. Present analysis shows that this is indeed so, but population dynamics are more complicated than those shown in Fig. 6 in Křivan (1998).

Second, I reviewed behavioral refuges caused either by predator optimal foraging (Charnov, 1976a), or by prey switching (Murdoch, 1969). Both these foraging behavior create a behavioral refuge for the preferred prey type because due to predator behavior the interaction strength with the preferred prey type decreases when at low densities. As a consequence of these foraging behaviors, the corresponding functional responses are of the sigmoidal Holling type III with possibly a steep (in its extreme form even vertical) part (Fig. 2B, C). Such functional responses cause prey isoclines to have a vertical (or almost vertical) part. Models with such isoclines were graphically analyzed in the seminal paper by Rosenzweig and MacArthur (1963) who recognized their potential to bound the amplitude of predator and prey oscillations. However, these authors did not provide explicit mechanistic models where this occurs. It is also well known that sigmoidal functional responses have a stabilizing effect on predator–prey population dynamics (Gause et al., 1936). An important observation for population ecology is that refuges whether they are physical or behavioral promote such shape of isoclines, thus predator–prey coexistence. Although this has already been observed by many authors (e.g., Rosenzweig and MacArthur, 1963; Hassell and May, 1973; Maynard Smith, 1974; Murdoch and Oaten, 1975; Sih, 1987; McNair, 1986; Ives and Dobson, 1987; Ruxton, 1995; Hochberg and Holt, 1995; Křivan, 1998; Ma et al., 2009) most of these models also include other stabilizing mechanisms (e.g., prey negative density dependent growth) that can mask the stabilizing effect of refuges per se. The Gause predator–prey model which assumes exponential prey growth is thus very suitable for disentangling the effect of refuges from other possibly stabilizing mechanisms. The only two mechanisms that operate in models considered in this paper are the refuge size and predation. A small refuge size leads to predator–prey persistence along a limit cycle, while a large refuge size has the potential to stabilize population dynamics at an equilibrium, but this depends on model details. For example, predictions for non-adaptive refuge use by prey and for the behavioral refuge caused by predator switching behavior lead to qualitatively similar predictions (cf. Fig. 1D vs. Fig. 6C). When refuge is small, predator–prey coexistence is achieved along a limit cycle, while for larger refuges, coexistence is at a locally stable equilibrium. In these cases increased refuge size effectively stabilizes predator–prey population dynamics. This contrast with adaptive prey refuge use (Fig. 4) and a refuge caused by predator's optimal foraging (Fig. 5), where predator–prey coexistence is achieved along a limit cycle (except at a single refuge size in Fig. 5C where predators and prey coexist at an equilibrium). This shows that non-adaptive refuge use and the refuge caused by prey switching have a stronger stabilizing effect on predator–prey population dynamics when compared with prey adaptive refuge use or a refuge caused by predator optimal foraging. In the context of predator's optimal foraging species coexistence is a consequence of decreased predation pressure at low prey densities. Optimal foraging weakens the interaction strength at low prey densities and leads either to an equilibrium or to a limit cycle in population dynamics. This shows that weak interactions are important for maintaining species coexistence (McCann et al., 1998).

The results of this paper are based on some important assumptions. First, in real populations, there will always be some prey negative density dependent growth that will further promote species coexistence. On the other hand, refuges considered in this paper assumed complete protection of prey. This can be the case of a physical refuge, but when a refuge is behavioral (either due to changes in prey antipredator behavior, or predator optimal foraging) this is unlikely to be the case. In the latter case it is more likely that the refuge will provide prey only a partial protection from predation. Results for the Lotka–Volterra predator–prey dynamics with a partial prey refuge (Křivan, 1998) suggest that as protectiveness (measured as the inverse of interaction strength between predators and prey in the refuge) will decrease, predator–prey population dynamics will tend to get destabilized.

Acknowledgment

I thank two anonymous reviewers for their thoughtful suggestions. This work was partly conducted while the author was a Sabbatical Fellow at the Mathematical Biosciences Institute, an Institute sponsored by the National Science Foundation under Grant DMS 0931642 and at the National Institute for Mathematical and Biological Synthesis, an Institute sponsored by the National Science Foundation, the US Department of Homeland Security, and the US Department of Agriculture through NSF Award EF-0832858, with additional support from the University of Tennessee, Knoxville. Support provided by the Institute of Entomology (AV0Z50070508, RVO60077344) is acknowledged.

Appendix A. ESS for adaptive prey refuge use

First I compute, for each resident prey strategy $0 \le u_1 \le 1$ the corresponding best response strategy $\beta(u_1,R,C)$ that maximizes prey fitness $W(\tilde{u},u)$ given by (4) at current population densities. I remark that for

$$v_1(R,C) = \frac{1}{\lambda_1 h_1 R}\left(\frac{\lambda_1 C}{r_1 - r_2} - 1\right),$$

$\partial W(\tilde{u},v)/\partial \tilde{u}_1 = 0$. When $u_1 > v_1(R,C)$, the best response strategy is to stay out of the refuge (i.e., $\beta(u_1,R,C) = 1$), while if $u_1 < v_1$ the best response strategy is to be in the refuge (i.e., $\beta(u_1,R,C) = 0$). If $u_1 = v_1$ then the best strategy is not uniquely defined ($\beta(v_1,R,C) = [0,1]$) and any strategy between 0 and 1 provides the same fitness

$W(\tilde{u}_1,v_1)=r_2$. Because for

$$C>\frac{r_1-r_2}{\lambda_1}(1+\lambda_1 h_1 R),$$

$v_1>1$, the best response strategy is $\beta(u_1,R,C)=0$. For low predator abundance satisfying

$$C<\frac{r_1-r_2}{\lambda_1},$$

$v_1<0$, and the best response strategy is $\beta(u_1,R,C)=1$. For predator and prey abundances that satisfy

$$\frac{r_1-r_2}{\lambda_1}<C<\frac{r_1-r_2}{\lambda_1}(1+\lambda_1 h_1 R),$$

the best response strategy depends on the resident strategy

$$\beta(u_1,R,C)=\begin{cases}1 & \text{if } u_1>v_1(R,C),\\ [0,1] & \text{if } u_1=v_1(R,C),\\ 0 & \text{if } u_1<v_1(R,C).\end{cases} \tag{A.1}$$

The Nash equilibria are defined as the rest points of the best response map, i.e., $u_1\in\beta(u_1,R,C)$, (Nash, 1951). Thus, there are three Nash equilibria: $u_1=0$, $u_1=1$, and $u_1=v_1$. The two boundary equilibria 0 and 1 are strict Nash equilibria and therefore they are evolutionarily stable. The interior equilibrium is not evolutionarily stable, because

$$W(v_1,u_1)-W(u_1,u_1)=-\frac{(r_2+h_1 r_2 u_1 R\lambda_1+C\lambda_1-r_1(1+h_1 u_1 R\lambda_1))^2}{h_1(r_1-r_2)R\lambda_1(1+h_1 u_1 R\lambda_1)}<0$$

and the local stability condition (Hofbauer and Sigmund, 1998) $W(v_1,u_1)>W(u_1,u_1)$ for every u_1 in a neighborhood of v_1 does not hold.

Appendix B. Analysis of predator–prey dynamics with prey switching

Here I analyze model (1) with functional response (11) and numerical response (13). For prey population densities below the threshold ($R<R_a$) population dynamics are

$$\begin{aligned}\frac{dR}{dt}&=rR,\\ \frac{dC}{dt}&=\left(\frac{e_a\lambda_a R_a}{1+h_a\lambda_a R_a}-m\right)C.\end{aligned} \tag{B.1}$$

Thus, at each point of the prey–predator density phase space to the left of the critical prey density $R=R_a$, prey exponentially increase and predators increase (when $e_a\lambda_a R_a/(1+h_a\lambda_a R_a)>m$), or decrease (when $e_a\lambda_a R_a/(1+h_a\lambda_a R_a)<m$).

For prey population densities above the threshold ($R>R_a$), population dynamics (1) are given by the Lotka–Volterra model with the Holling type II functional response

$$\begin{aligned}\frac{dR}{dt}&=rR-C\frac{\lambda R}{1+h\lambda R},\\ \frac{dC}{dt}&=\left(\frac{e\lambda R}{1+h\lambda R}-m\right)C.\end{aligned} \tag{B.2}$$

In the vicinity and to the right of the vertical line $R=R_a$, the prey population decreases provided predator density is high enough, i.e.,

$$C>C_c=\frac{r}{\lambda}(1+\lambda h R_a).$$

Here the point (R_a,C_c) corresponds to the intersection of the prey isocline of model (B.2) with the switching line $R=R_a$. Similarly, to the left of this line, the prey population increases. It is clear that above the critical predator density C_c trajectories of model (1) are pushed from both sides to the line $R=R_a$ and they cannot leave this line. Thus, trajectories of model (1) cannot cross the critical line $R=R_a$ above the point C_c. To fully analyze model (1) with functional response (11) and numerical response (13) we need to know population dynamics along the vertical part of the prey isocline. For $R=R_a$ population dynamics are

$$\begin{aligned}\frac{dR}{dt}&=rR-\frac{u\lambda RC}{1+h\lambda uR+h_a\lambda_a u_a R_a},\\ \frac{dC}{dt}&=\left(\frac{eu\lambda R+e_a u_a\lambda_a R_a}{1+h\lambda uR+h_a\lambda_a u_a R_a}-m\right)C,\end{aligned} \tag{B.3}$$

where u is any number from interval $[0,1]$ and $u_a=1-u$. Because trajectories cannot leave the switching line $R=R_a$ when predator density is higher than C_c, the corresponding preference u can be calculated from equation $dR/dt=0$. This gives

$$u=\frac{r(1+h_a R_a\lambda_a)}{C\lambda+rR_a(h_a\lambda_a-h\lambda)}.$$

Substituting this u in predator growth equation leads to the following population dynamics along the vertical part of the prey isocline:

$$\begin{aligned}\frac{dR}{dt}&=0,\\ \frac{dC}{dt}&=e\frac{R_a(-e_a(r-C\lambda+hrR_a\lambda)\lambda_a+er\lambda(1+h_a R_a\lambda_a))}{\lambda(1+h_a R_a\lambda_a)}-mC.\end{aligned} \tag{B.4}$$

These dynamics have the following equilibrium:

$$E^F=(R^F,C^F)=\left(R_a,\frac{rR_a(e\lambda(1+h_a R_a\lambda_a)-e_a\lambda_a(1+hR_a\lambda))}{\lambda(m+(h_a m-e_a)R_a\lambda_a)}\right), \tag{B.5}$$

for model (B.4) which is also an equilibrium of model (1), provided this point is on the vertical part of the prey isocline, i.e., when $C^F>C_c$. This holds whenever the prey critical density satisfies

$$\frac{m}{\lambda_a(e_a-h_a m)}>R_a>\frac{m}{\lambda(e-mh)}=R^*, \tag{B.6}$$

i.e., when the predator isocline of model (B.2) is to the left of the prey critical line $R=R_a$, or, in other words, if the refuge size (R_a) is large enough.

References

Abrams, P.A., 1999. The adaptive dynamics of consumer choice. Am. Nat. 153, 83–97.

Abrams, P.A., 2003. Effects of altered resource consumption rates by one consumer species on a competitor. Ecol. Lett. 6, 550–555.

Abrams, P.A., 2006. The effects of switching behavior on the evolutionary diversification of generalist consumers. Am. Nat. 168, 645–659.

Abrams, P.A., Matsuda, H., 1996. Fitness minimization and dynamic instability as a consequence of predator–prey coevolution. Evol. Ecol. 10, 167–186.

Abrams, P.A., Matsuda, H., 2004. Consequences of behavioral dynamics for the population dynamics of predator–prey systems with switching. Popul. Ecol. 46, 13–25.

Brown, J.S., 1998. Game theory and habitat selection. In: Dugatkin, L.A., Hudson, K.R. (Eds.), Game Theory & Animal Behavior. Oxford University Press, New York, NY, USA, pp. 188–220.

Brown, J.S., Alkon, P.A., 1990. Testing values of crested porcupine habitats by experimental food patches. Oecologia 83, 512–518.

Brown, J.S., Kotler, B.P., 2004. Hazardous duty pay and the foraging cost of predation. Ecol. Lett. 7, 999–1014.

Charnov, E.L., 1976a. Optimal foraging: attack strategy of a mantid. Am. Nat. 110, 141–151.

Charnov, E.L., 1976b. Optimal foraging: the marginal value theorem. Theor. Popul. Biol. 9, 129–136.

Cressman, R., Křivan, V., 2006. Migration dynamics for the ideal free distribution. Am. Nat. 168, 384–397.

Dieckmann, U., Law, R., 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. J. Math. Biol. 34, 579–612.

Foster, W.A., Treherne, J.E., 1981. Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. Nature 293, 466–467.

Fryxell, J.M., Lundberg, P., 1994. Diet choice and predator–prey dynamics. Evol. Ecol. 8, 407–421.

Fryxell, J.M., Lundberg, P., 1997. Individual Behavior and Community Dynamics. Chapman & Hall, London, UK.

Gause, G.F., Smaragdova, N.P., Witt, A.A., 1936. Further studies of interaction between predators and prey. J. Anim. Ecol. 5, 1–18.

Hassell, M.P., May, R.M., 1973. Stability in insect host-parasite models. J. Anim. Ecol. 42, 693–736.

Hochberg, M.E., Holt, R., 1995. Refuge evolution and the population dynamics of coupled host-parasitoid associations. Evol. Ecol. 9, 633–661.

Hofbauer, J., Sigmund, K., 1998. Evolutionary Games and Population Dynamics. Cambridge University Press, Cambridge.

Holbrook, S.J., Schmitt, R.J., 1988. The combined effects of predation risk and food reward on patch selection. Ecology 69, 125–134.

Holt, R.D., 1983. Optimal foraging and the form of the predator isocline. Am. Nat. 122, 521–541.

Ives, A.R., Dobson, A.P., 1987. Antipredator behaviour and the population dynamics of simple predator–prey systems. Am. Nat. 130, 431–447.

Křivan, V., 1997. Dynamic ideal free distribution: effects of optimal patch choice on predator–prey dynamics. Am. Nat. 149, 164–178.

Křivan, V., 1998. Effects of optimal antipredator behavior of prey on predator–prey dynamics: role of refuges. Theoretical Population Biology 53, 131–142.

Křivan, V., 2008. Prey-predator models. In: Jorgensen, S.E., Fath, B.D. (Eds.), Encyclopedia of Ecology, vol. 4. Elsevier, Oxford, pp. 2929–2940.

Křivan, V., 2011. On the gause predator–prey model with a refuge: a fresh look at the history. J. Theor. Biol. 274, 67–73.

Křivan, V., Eisner, J., 2003. Optimal foraging and predator–prey dynamics III. Theor. Popul. Biol. 63, 269–279.

Lima, S.L., 1998a. Nonlethal effects in the ecology of predator–prey interactions. Bioscience 48, 25–34.

Lima, S.L., 1998b. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Stress Behav. 27, 215–290.

Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68, 619–640.

Ma, B., Abrams, P., Brassil, C., 2003. Dynamic versus instantaneous models of diet choice. Am. Nat. 162, 668–684.

Ma, Z., Li, W., Zhao, Y., Wang, W., Zhang, H., Li, Z., 2009. Effects of prey refuges on a predator–prey model with a class of functional responses: the role of refuges. Math. Bio. 218, 73–79.

Maynard Smith, J., 1974. Models in Ecology. Cambridge University Press Cambridge, UK.

McCann, K., Hastings, A., Huxel, G.R., 1998. Weak trophic interactions and the balance of nature. Nature 395, 794–798.

McNair, J.N., 1986. The effects of refuges on predator–prey interactions: a reconsideration. Theor. Popul. Biol. 29, 38–63.

Murdoch, W.W., 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. Ecol. Monogr. 39, 335–354.

Murdoch, W.W., Oaten, A., 1975. Predation and population stability. In: MacFadyen, A. (Ed.), Advances in Ecological Research. Academic Press, pp. 1–131.

Nash, J., 1951. Non-cooperative games. Ann. Math. 54, 286–295.

Oaten, A., Murdoch, W.W., 1975. Switching, functional response, and stability in predator–prey systems. Am. Nat. 109, 299–318.

Peacor, S.D., Werner, E.E., 2001. The contribution of trait-mediated indirect effects to the net effects of a predator. In: Proceedings of the National Academy of Sciences of the USA, vol. 98, pp. 3904–3908.

Preisser, E.L., Bolnick, D.I., F., B.M., 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. Ecology 86, 501–509.

Rosenzweig, M.L., MacArthur, R.H., 1963. Graphical representation and stability conditions of predator–prey interactions. Am. Nat. 97, 209–223.

Ruxton, G.D., 1995. Short term refuge use and stability of predator–prey models. Theor. Popul. Biol. 47, 1–17.

Schlag, K.H., 1998. Why imitate, and if so, how? A boundedly rational approach to multi-armed bandits. J. Econ. Theory 78, 130–156.

Sih, A., 1980. Optimal behavior: can foragers balance two conflicting demands? Science 210, 1041–1043.

Sih, A., 1986. Antipredator responses and the perception of danger by mosquito larvae. Ecology 67, 434–441.

Sih, A., 1987. Prey refuges and predator–prey stability. Theor. Popul. Biol. 31, 1–12.

Sih, A., 1998. Game theory and predator–prey response races. In: Dugatkin, L.A., Hudson, K.R. (Eds.), Game theory & Animal Behavior. Oxford University Press, New York, NY, USA, pp. 221–238.

Stephens, D.W., Krebs, J.R., 1986. Foraging Theory. Princeton University Press, Princeton, NJ, USA.

Svirezhev, Y.M., Logofet, D.O., 1983. Stability of Biological Communities. Mir Publishers, Moscow, USSR.

Taylor, P.D., Jonker, L.B., 1978. Evolutionary stable strategies and game dynamics. Math. Biosci. 40, 145–156.

van Baalen, M., Křivan, V., van Rijn, P.C.J., Sabelis, M., 2001. Alternative food switching predators, and the persistence of predator–prey systems. Am. Nat. 157, 512–524.

Vincent, T.L., Brown, J.S., 2005. Evolutionary Game Theory, Natural Selection, and Darwinian Dynamics. Cambridge University Press.

Werner, E.E., Gilliam, J.F., 1984. The ontogenetic niche and species interactions in size-structured populations. Annu. Rev. Ecol. Syst. 15, 393–425.