

Effects of Optimal Antipredator Behavior of Prey on Predator–Prey Dynamics: The Role of Refuges

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The influence of optimal antipredator behavior of prey on predator–prey dynamics in a two-patch environment is studied. One patch represents an open habitat while the other is a refuge for prey. It is assumed that prey maximize their fitness measured by the instantaneous per capita growth rate. In each patch population dynamics is described by the Lotka–Volterra time continuous model. The refuge is characterized by its protectiveness which is inversely related to the predation risk for prey, and the dependence of population dynamics on protectiveness is studied. It is shown that adaptive behavior of prey changes qualitative properties of the underlying Lotka–Volterra model due to the appearance of a bounded attractor. Adaptive prey behavior does not lead to a stable equilibrium but to the reduction of population fluctuations. Dynamic consequences of a limited carrying capacity of the refuge are also considered. Low refuge carrying capacity leads to stability of predator–prey dynamics while stability is lost when the carrying capacity of the refuge is high. Lastly, it is shown that optimal antipredator behavior of prey leads to persistence and reduction of oscillations in population densities.

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INTRODUCTION

Most of the theoretical work on population dynamics of refugia lead to the conclusion that refugia have a stabilizing effect on predator–prey interactions (Rosenzweig and MacArthur, 1963; Hassel and May, 1973; Maynard Smith, 1974; Murdoch and Stewart-Oaten, 1975; Hassell, 1978; Sih, 1987b; Ives and Dobson, 1987; Ruxton, 1995; Hochberg and Holt, 1995). Two types of refugia have been considered in the literature: those that protect a constant fraction and those that protect a constant number of prey. The consequences of refuge type for stability of predator–prey interactions then depends on the underlying model, but the general conclusion from these studies is that refugia which protect a constant

number of prey lead to a stable equilibrium and have a stronger stabilizing effect on population dynamics than refugia which protect a constant proportion of prey. However, McNair (1986) and Collings (1995) showed that such a simplistic interpretation of the stabilizing role of refugia may not be correct, since for more complex models refugia may exert a locally destabilizing effect due to the emergence of a stable limit cycle. Applicability of these models seems to be reduced by the fact that “neither a constant number nor a constant proportion of prey refuges has been reported” (Sih, 1987b). However, in Hochberg and Holt (1995) it was suggested, based on empirical evidence, that for most host–parasitoid systems part of the host population is in a constant proportion refuge. In experimental tests with red scale no stabilizing

effect of a refuge on population dynamics was observed (Murdoch, Luck, Swarbrick, Walde, Yu, and Reeve, 1995; Murdoch, Swarbrick, Luck, Walde, and Yu, 1996).

Since refugia are safe but rarely offer feeding or mating opportunities, prey must balance energy gain against the risk of predation in deciding where to feed. One of the major components of risk is the time spent in the open habitat where the probability of an encounter with a predator is high. When prey are mobile and a spatial refuge exists, prey may avoid predators via a habitat shift by moving to the refuge (Diehl and Eklöv, 1995; Fraser and Gilliam, 1987; Fraser and Gilliam, 1992; Fraser, Gilliam and Yip-Hoi, 1995; Gilliam and Fraser, 1987; Gilliam and Fraser, 1988; Lima and Dill, 1990; Mittelbach and Chesson, 1987; Sih, 1980; Sih, 1986; Sih, 1987a; Sih, 1987b; Werner, Gilliam, Hall, and Mittelbach, 1983; Werner and Gilliam, 1984).

In Ives and Dobson (1987) effects of optimal anti-predator behavior of prey on a continuous-time population model were studied. Prey investment in antipredator behavior was modeled by a parameter. They showed that adaptive change of the parameter speeds the convergence of trajectories to an equilibrium. Sih (1987b) showed that if the proportion of prey in refugia is decreasing with increasing prey abundance, or increasing with both increasing predator density and increasing predation pressure than the corresponding ecological equilibrium is locally stable. Ruxton (1995) derived a continuous-time predator-prey model under the assumption that the rate prey move to a refuge is proportional to predator density. It was shown that antipredator behavior has a stabilizing effect.

Colombo and Křivan (1993) developed a mathematical framework for modelling effects of optimal behavioral decisions of animals on predator-prey population dynamics. This general framework was then used in Křivan (1997) to study population dynamic consequences of optimal patch choice assuming that only predators move between patches and they maximize per capita instantaneous growth rate, or both predators and prey are free to move between patches and both maximize their instantaneous growth rates. In this paper I will study effects of optimal antipredator behavior of prey on population dynamics described by Lotka-Volterra differential equations assuming optimal choice of the patch by prey only. I consider two types of patches where one is a refuge for prey and the other not. A patch may be a refuge for two reasons: either there are fewer (or no) predators in this patch, or the predators are less effective. I characterize a refuge by its "protectiveness" which is inversely related to the product of the attack rate of predators in the refuge and the probability that a

predator will stay in the refuge. Thus, higher protectiveness means lower predation. If protectiveness is infinity then the refuge is complete. This happens if either the attack rate is zero in the refuge or the refuge is predator free. I begin with a model that does not include other stabilizing mechanisms such as prey density dependence or passive diffusion of prey between patches that alone could lead to a stable equilibrium (Comins and Blatt, 1974; Holt, 1983; Holt, 1985; Holt, 1987). I analyze the effects of protectiveness of the refuge on stability of the Lotka-Volterra model. I next extend this basic model by including the effect of limited carrying capacity of the refuge. The main question of this paper is: Do refuges promote persistence or stability of predator-prey dynamics provided prey behave optimally? I show that even for the simplest Lotka-Volterra type of dynamics the answer is not straightforward, since the amplitude of maximal possible fluctuations in population densities is not a monotone function of protectiveness of the refuge.

POPULATION DYNAMICS

I will consider a system consisting of two habitats: an open habitat (patch 1) and a spatial refuge (patch 2). First, I derive a general model for a refuge that is not complete, and I consider the associated dynamics. In my model, antipredator behavior of prey consists of moving to the refuge. If the per capita intrinsic growth rate in the refuge is lower than in the open habitat then this leads to a classic trade-off dilemma for prey: stay in a safer but less profitable refuge, or move to more profitable but riskier open habitat? If, on average, a prey stays in patch i for T_i time units within its lifetime T , then the probability it will be in this patch is

$$v_i = \frac{T_i}{T}.$$

The residence time T_i is a major determinant of the risk of being preyed upon, and, consequently, it will depend on the predator abundance in patch i . I assume that prey are omniscient and they move between patches infinitely fast and I note that

$$v_1 + v_2 = 1.$$

The assumption on the infinitely fast movement is realistic if the two patches have a common boundary, for example in aquatic environments where the open habitat is clear water while the refuge is the vegetated bottom

(Diehl and Eklöv, 1995). I assume that population dynamics is described by the following system of the Lotka–Volterra equations

$$\begin{aligned} x' &= (a_1 - \lambda_1 p_1 y) v_1 x + (a_2 - \lambda_2 p_2 y) v_2 x, \\ y' &= (e\lambda_1 v_1 x - m_1) p_1 y + (e\lambda_2 v_2 x - m_2) p_2 y. \end{aligned} \quad (1)$$

Here x and y are total prey and predator abundances, respectively, and a_i and m_i are instantaneous per capita growth and mortality rates of prey population in patch i , respectively. I assume that the intrinsic growth rate in the refuge (patch 2) is smaller than in the open habitat (patch 1) and I have $a_1 > a_2$. While I assume that $a_1 > 0$, a_2 may also be negative. This occurs if the background mortality rate in the refuge is higher than the natality rate due to the lack of resources, mating opportunities, etc. Parameter e is the efficiency with which predators convert consumed prey into new predators, and λ_i is the attack rate of predators in patch i . I assume that predators move between patches at random, and p_i is a fixed number that models preferences of predators for patch i . Because in the refuge either the attack rate λ_2 or predator preference p_2 to remain in the refuge are small relative to the open habitat, I assume that

$$\lambda_1 p_1 > \lambda_2 p_2.$$

A complete refuge is characterized either by $p_2 = 0$ or $\lambda_2 = 0$. In both cases prey in a complete refuge are not being preyed upon. I assume that prey fitness is measured by the instantaneous per capita growth rate x'/x . If prey behave to maximize their fitness this assumption leads to

$$\max_{(v_1, v_2)} ((a_1 - \lambda_1 p_1 y) v_1 + (a_2 - \lambda_2 p_2 y) v_2). \quad (2)$$

The optimal antipredator strategy of prey is the set of controls (v_1, v_2) that maximize criterion (2) for given predator abundance y . Because the optimal strategy depends on predator density y , it is not constant over time, and I split the $x > 0$, $y > 0$ space into two parts according to the values of the optimal strategy. Since expression (2) is a linear function of v_1 and v_2 , it follows that

(a) Prey aggregate in patch 1 ($v_1 = 1$, $v_2 = 0$) if $a_1 - \lambda_1 p_1 y > a_2 - \lambda_2 p_2 y$ which occurs if predator abundance is below

$$y^* = \frac{a_1 - a_2}{\lambda_1 p_1 - \lambda_2 p_2}, \quad (3)$$

because the risk of predation in the open patch is low (predator density is low), while the prey growth rate is high there.

(b) Prey aggregate in the refuge ($v_1 = 0$, $v_2 = 1$) if $a_1 - \lambda_1 p_1 y < a_2 - \lambda_2 p_2 y$. This occurs if predator abundance is greater than y^* , since in this case the risk of predation in open habitat is high.

(c) Prey fitness is the same in both patches if $a_1 - \lambda_1 p_1 y = a_2 - \lambda_2 p_2 y$, i.e., (v_1, v_2) are not uniquely determined, which happens when $y = y^*$.

The above defined strategy leads to the classical ideal free distribution of prey between patches, in which no prey can increase its fitness by moving to the other patch. In cases (a) and (b) prey play pure strategy (i.e., the probability of being in a patch is either zero or one) while in case (c) prey play mixed strategies (i.e., the probability of being in a patch is between zero and one). This later case leads to the emergence of partial preferences of prey for habitats. The line $y = y^*$ is the switching line since the behavior of prey switches when predator density crosses this line.

I study the qualitative behavior of (1) with controls (v_1, v_2) given by the optimal strategy. When predator density is below y^* , the corresponding dynamics is obtained from (1) by substituting the optimal strategy $v_1 = 1$, $v_2 = 0$. This gives

$$\begin{aligned} x' &= (a_1 - \lambda_1 p_1 y) x, \\ y' &= (e\lambda_1 p_1 x - m_1 p_1 - m_2 p_2) y. \end{aligned} \quad (4)$$

If predator density is above y^* , the corresponding dynamics driven by the optimal strategy $v_1 = 0$, $v_2 = 1$ is

$$\begin{aligned} x' &= (a_2 - \lambda_2 p_2 y) x, \\ y' &= (e\lambda_2 p_2 x - m_1 p_1 - m_2 p_2) y. \end{aligned} \quad (5)$$

Note that since optimal prey strategy is not uniquely defined if predator density equals y^* , the right handside of (1) is set-valued. Despite this non-uniqueness the model has uniquely defined solution for every initial density of predators and prey, see Appendix A. Both (4) and (5) are the classical Lotka–Volterra equations with a neutrally stable equilibrium surrounded by cycles. The equilibria of (4) and (5) are

$$\begin{aligned} E^4 &= \left(\frac{m_1 p_1 + m_2 p_2}{e\lambda_1 p_1}, \frac{a_1}{\lambda_1 p_1} \right), \\ E^5 &= \left(\frac{m_1 p_1 + m_2 p_2}{e\lambda_2 p_2}, \frac{a_2}{\lambda_2 p_2} \right), \end{aligned}$$

respectively. If the solution of (1) falls on the line $y = y^*$, there are two possibilities. The solution may either move along this line for some positive time or it may cross the line transversally. The part of the switching line where trajectories of (1) cannot leave the line is called the partial preference domain. Movement in this part of the line leads to partial preferences for habitats, i.e., the probability that a prey will stay in patch i is strictly between zero and one. On the population level this means that prey will spread between the two patches in the ratio v_1/v_2 . The partial preference domain is the part of the line $y = y^*$ between x^1 and x^2 where

$$x^1 = \frac{m_1 p_1 + m_2 p_2}{e \lambda_1 p_1},$$

$$x^2 = \frac{m_1 p_1 + m_2 p_2}{e \lambda_2 p_2},$$

see Appendix A. If a solution of (1) driven by the optimal strategy reaches the partial preference domain, the proportion of prey in each patch can be explicitly computed (see Appendix A):

$$v_1 = \frac{m_1 p_1 + m_2 p_2 - e \lambda_2 p_2 x}{e x (\lambda_1 p_1 - \lambda_2 p_2)}, \quad (6)$$

$$v_2 = \frac{e \lambda_1 p_1 x - m_1 p_1 - m_2 p_2}{e x (\lambda_1 p_1 - \lambda_2 p_2)}.$$

Inserting (6) into (1) gives the following system of differential equations that govern the dynamics in the partial preference domain:

$$x' = \frac{a_2 \lambda_1 p_1 - a_1 \lambda_2 p_2}{\lambda_1 p_1 - \lambda_2 p_2} x, \quad (7)$$

$$y' = 0.$$

I consider the behavior of trajectories of (1) driven by the optimal strategy. First I assume that

$$\frac{a_1}{\lambda_1 p_1} < \frac{a_2}{\lambda_2 p_2}. \quad (8)$$

The inequality (8) can only hold if the intrinsic prey growth rate in the refuge is positive. If the predator initial density is below y^* , all prey are in the open habitat, and the corresponding population dynamics follows a Lotka–Volterra cycle of (4). After some time predator

density reaches the critical threshold y^* , because E^4 is above the switching line $y = y^*$ due to the assumption (8). If at this moment the prey density is between x^1 and x^2 (i.e., in the partial preference domain such as in Fig. 1A) then prey start to move to the refuge. Predator density is constant and equal to y^* until prey density reaches x^2 due to (7). At this moment all prey are in the refuge and the trajectories follow the Lotka–Volterra cycle of (5), which passes through the point (x^2, y^*) , see Fig. 1A. Using a Lyapunov function (see Appendix B) it can be proved that the set bounded by this cycle is the

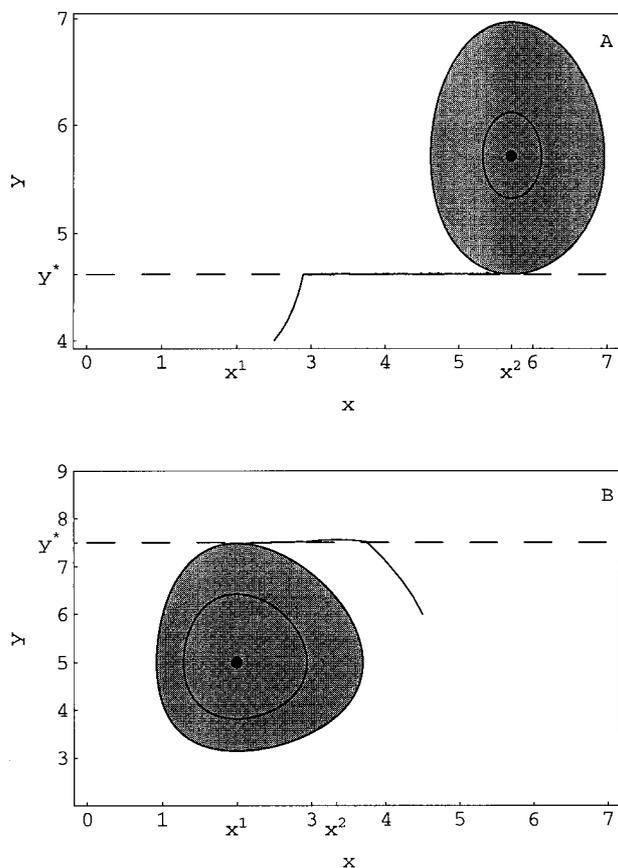


FIG. 1. Solutions of (1) driven by the optimal antipredator strategy. All trajectories converge to a global attractor (the shaded area). On the attractor, trajectories follow the Lotka–Volterra cycles. The amplitude of these cycles is constrained by the switching line $y = y^*$ (dashed line) along which switching in the behavior of prey occurs. In Fig. 1A condition $a_2 \lambda_1 p_1 > a_1 \lambda_2 p_2$ holds and both equilibria are above the line $y = y^*$. In the long term run all prey will aggregate in the refuge. Parameters: $a_1 = 2.5$, $a_2 = 1$, $m_1 = m_2 = 1$, $e = 1$, $\lambda_1 = 1$, $\lambda_2 = 0.35$, $p_1 = p_2 = 0.5$. In Fig. 1B, $a_2 \lambda_1 p_1 < a_1 \lambda_2 p_2$ and both equilibria are below the line $y = y^*$. All prey will aggregate in the open habitat. Parameters: $a_1 = 2.5$, $a_2 = 1$, $m_1 = m_2 = 1$, $e = 1$, $\lambda_1 = 1$, $\lambda_2 = 0.6$, $p_1 = p_2 = 0.5$.

global attractor of (1) (shown as the shaded region in Fig. 1) driven by the optimal strategy. Thus, all trajectories that start outside the attractor are converging to the attractor. The dynamics inside the attractor is described by the Lotka–Volterra system (5) and trajectories in the attractor follow the Lotka–Volterra cycles. Thus, if (8) holds, all prey will aggregate in the refuge and predator–prey dynamics will follow a Lotka–Volterra cycle constrained from below by the line $y = y^*$. The reason why all prey will be in the refuge is due to the fact that predator densities will never decrease below the critical value y^* at which switching behavior of prey occurs.

If

$$\frac{a_1}{\lambda_1 p_1} > \frac{a_2}{\lambda_2 p_2}, \tag{9}$$

then the equilibria E^4, E^5 are below the line $y = y^*$, see Fig. 1B. Inequality (9) holds, for example, when per capita prey growth rate in the refuge is negative (e.g., due to the lack of feeding or mating opportunities). In the long term run (Fig. 1B) all prey will aggregate in open habitat and predator–prey population dynamics will be described by the Lotka–Volterra cycles of (4) which are constrained from above by the line $y = y^*$. Thus, in the long term run there are only two possibilities for prey: Either all prey will be in the open habitat (if (9) holds) or they will be in the refuge (if (8) holds) and no partial preferences for habitats appear.

Next I explore the effect of protectiveness P of the refuge defined by

$$P = \frac{1}{p_2 \lambda_2}$$

on population dynamics. I measure this effect by the distance of the equilibrium E^5 from the line $y = y^*$ if (8) holds and by the distance of E^4 from this line if (9) holds. Since these distances are proportional to the amplitude of the largest fluctuations in predator–prey dynamics, my measure gives an estimate of the largest possible amplitude of fluctuations in population densities. The distance is for $a_2 \geq 0$ given by

$$d(P) = \begin{cases} \frac{a_1/P - a_2 \lambda_1 p_1}{\lambda_1 p_1 (\lambda_1 p_1 - 1/P)} & \text{if } \frac{1}{\lambda_1 p_1} < P \leq \frac{a_1}{a_2 \lambda_1 p_1}, \\ \frac{a_2 \lambda_1 p_1 P - a_1}{\lambda_1 p_1 - 1/P} & \text{if } P > \frac{a_1}{a_2 \lambda_1 p_1}, \end{cases} \tag{10}$$

(Fig. 2) and for $a_2 < 0$ by

$$d(P) = \frac{a_1/P - a_2 \lambda_1 p_1}{\lambda_1 p_1 (\lambda_1 p_1 - 1/P)} \quad \text{for } P > 1/(\lambda_1 p_1). \tag{11}$$

First I consider the case $a_2 \geq 0$. For $1/(\lambda_1 p_1) < P < a_1/(a_2 \lambda_1 p_1)$ the distance d is a decreasing function of P since for increasing protectiveness equilibrium E^4 moves toward the line $y = y^*$ (Fig. 2). For $P = a_1/(a_2 \lambda_1 p_1)$ both equilibria E^4 , and E^5 are on the line $y = y^*$ and $d(P) = 0$. In this singular case all points in the partial preference domain (on the line $y = y^*$ between the points x^1 and x^2) are equilibria, i.e., when a solution of (1) driven by the optimal strategy reaches any point in the partial preference domain it will stay there forever and partial preferences for habitats appear. For $P > a_1/(a_2 \lambda_1 p_1)$ the attractor is above the line $y = y^*$ and the distance $d(P)$ increases to infinity for increasing protectiveness since the distance of E^5 from this line tends to infinity. For $a_2 < 0$ equilibrium E^4 will always be below the line $y = y^*$ and all prey will aggregate in the open habitat. As protectiveness of the refuge increases, E^4 moves toward this line and the limit cycle will shrink. Thus, a refuge with higher protectiveness leads to smaller oscillations in predator–prey fluctuations for $a_2 < 0$. Note that protectiveness of the refuge influences dynamics in the open habitat even in the case there are no prey in the refuge.

I may compare the case of optimal patch use with the case where prey migrate between patches at random which corresponds to fixed values of v_i . In this case (1), it is the classical Lotka–Volterra system that has a neutrally stable equilibrium surrounded by cycles. Thus,

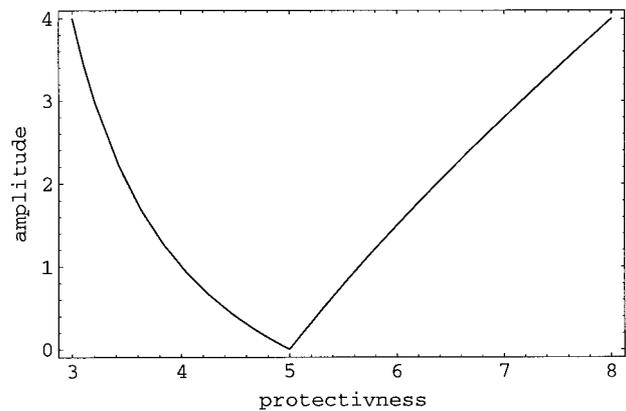


FIG. 2. The dependence of the amplitude of the largest Lotka–Volterra cycle on protectiveness of the refuge when no carrying capacity is assumed. Parameters $a_1, a_2, m_1, m_2, e, \lambda_1, p_1$ are the same as in Fig. 1A.

the global attractor is the whole positive quadrant and fluctuations of any amplitude may appear in population dynamics. Therefore, optimal prey behavior leads to partial stabilization of predator–prey population dynamics in the sense that fluctuations in population densities are bounded.

COMPLETE REFUGE

Now I will consider the case where the second patch is a complete refuge for prey. A complete refuge is either predator free or the attack rate of predators is zero. This amounts to $P = \infty$ or, equivalently, $\lambda_2 p_2 = 0$. System (1) becomes

$$\begin{aligned} x' &= (a_1 - \lambda_1 p_1 y) v_1 x + a_2 v_2 x, \\ y' &= (e \lambda_1 v_1 x - m_1) p_1 y - m_2 p_2 y. \end{aligned} \quad (12)$$

Optimal antipredator strategy of prey is in the case of complete refuge as follows. If predator density is below $y^* = (a_1 - a_2) / (\lambda_1 p_1)$ (see (3)) then prey will stay in the open habitat where they achieve a higher growth rate. If the predator population is above y^* then it pays off for prey to move to the refuge to avoid high predation in the open habitat. The dynamics in the open habitat is given by (4) while the dynamics in the refuge is described by:

$$\begin{aligned} x' &= a_2 x, \\ y' &= -y(m_1 p_1 + m_2 p_2). \end{aligned}$$

Partial preferences do arise along the line $y = y^*$ for $x > x^1$ since $x^2 = \infty$. Let us consider the case where predator density is below y^* . All prey are in the open habitat and predator–prey dynamics follows a Lotka–Volterra cycle of (4). When predator density reaches a critical level y^* then prey start to move to the refuge. If $a_2 > 0$ then the population of prey in the refuge will grow exponentially since they are not being preyed upon. Predator abundance will be constant and equal to y^* . Thus, trajectories are unbounded for $a_2 > 0$ and the prey population will split between both patches. The ratio of prey in the open habitat and the refuge will be (see (6)):

$$\frac{v_1}{v_2} = \frac{m_1 p_1 + m_2 p_2}{e x \lambda_1 p_1 - m_1 p_1 - m_2 p_2}.$$

As prey abundance increases this ratio will decrease, i.e., prey will aggregate in the refuge.

If $a_2 < 0$, then trajectories when reaching the partial preference domain move to the left and after reaching the point (x^1, y^*) they move along the corresponding Lotka–Volterra cycle of (4) as in Fig. 1B. I note that for $P = \infty$ the distance E^4 from the line $y = y^*$ is given by

$$-\frac{a_2}{\lambda_1 p_1} > 0$$

that determines the amplitude of the largest possible fluctuations in the predator–prey dynamics. Thus, for $a_2 < 0$ no partial preferences for a habitat arise since after some time all prey will stay in the open habitat. If $a_2 = 0$ then each trajectory when reaching the partial preference domain stays at that point forever. This means that the entire partial preference domain consists of equilibria.

The assumption of unlimited growth of prey in the refuge is not realistic. As predation risk increases more prey will move to the refuge which results in increasing competition for resources, leading to density dependence in the refuge. In the next section I consider the effect of limited carrying capacity of the refuge on dynamics (1).

REFUGES WITH LIMITED CARRYING CAPACITY

Model (1) shows that for refuges of high protectiveness with a positive intrinsic growth rate a_2 , prey abundance in the refuge may be very high and as protectiveness tends to infinity it may also tend to infinity. It would mean that the refuge itself is unlimited, which is not a reasonable assumption. In general, due to the size of the refuge (as in the case of the vegetated part of a lake) or due to the limited resources in the refuge there will be a maximum prey abundance that the refuge can support. This abundance is described by the carrying capacity of the refuge denoted by K . Predation risk can create significant competition between prey in the refuge (Mittelbach and Chesson, 1987). I will assume that if prey abundance in the refuge is K , no other prey are allowed to move into the refuge even if this would be the optimal antipredator strategy. In this section I analyze the effect of limited carrying capacity of the refuge on predator–prey dynamics described by (1), provided prey behave optimally. I do not impose any constraint on the prey growth rate in the open habitat. To model the limited carrying capacity of the refuge I add a constraint to system (1), namely

$$v_2 \leq \frac{K}{x}, \quad (13)$$

which constrains prey abundance in the refuge. This constraint together with the optimality principle (2) leads to the following optimal strategy of prey:

(i) If $x \leq K$, constraint (13) is not active and the optimal strategy for prey is the same as in the unconstrained case.

(ii) If $x > K$ then there are the following possibilities:

(α) If $y > y^*$ the optimal strategy is $v_1 = 1 - K/x$, $v_2 = K/x$. Note that partial preferences for habitats do appear in this case since v_i is between zero and one.

(β) If $y < y^*$ the optimal strategy is the same as in the unconstrained case.

(γ) If $y = y^*$ then $0 \leq v_2 \leq 1 - K/x$, $v_1 = 1 - v_2$ and the optimal strategy is not uniquely determined.

Population dynamics for predator density below y^* is described by (4) while population dynamics for predator density above y^* is described by (5) only if $x \leq K$. If $x > K$ substituting the optimal strategy (α) into (1) gives the following dynamics:

$$\begin{aligned} x' &= (a_1 - \lambda_1 p_1 y)(x - K) + K(a_2 - \lambda_2 p_2 y), \\ y' &= (e\lambda_1(x - K) - m_1) p_1 y + (e\lambda_2 K - m_2) p_2 y. \end{aligned} \quad (14)$$

System (14) has one ecological equilibrium:

$$E^{14} = \left(\frac{eK(\lambda_1 p_1 - \lambda_2 p_2) + m_1 p_1 + m_2 p_2}{e\lambda_1 p_1}, \frac{eK(a_2 \lambda_1 p_1 - a_1 \lambda_2 p_2) + a_1(m_1 p_1 + m_2 p_2)}{\lambda_1 p_1(m_1 p_1 + m_2 p_2)} \right).$$

Note that E^{14} belongs to the part of the space where $x > K$ and $y > y^*$ if $a_2 \lambda_1 p_1 > a_1 \lambda_2 p_2$ and

$$K < \frac{m_1 p_1 + m_2 p_2}{e\lambda_2 p_2}. \quad (15)$$

Under the above conditions E^{14} is positive and locally asymptotically stable for dynamics described by (14) (see Appendix C).

Now I consider the behavior of trajectories of (1) which are governed by the optimal strategy given by (i) and (ii). First, I determine the partial preference domain (see Appendix A). To this end I define

$$x^3 = \frac{eK(\lambda_1 p_1 - \lambda_2 p_2) + m_1 p_1 + m_2 p_2}{e\lambda_1 p_1}.$$

Note that if (15) holds then $x^3 > x^2 > K$. The partial preference domain consists of two parts now: a part of the line $y = y^*$ between the points x^1 and x^3 and the part of the space where $x > K$ and $y > y^*$. Any trajectory of (1) driven by the optimal antipredator strategy that reaches at a certain time the line $y = y^*$ between the points x^1 and x^3 will move along this line until it reaches the point (x^3, y^*) where it enters the region $x > K$, $y > y^*$. In this way trajectories converge to equilibrium E^{14} (Fig. 3A). Note that at equilibrium E^{14} prey population will split between both patches in the ratio

$$\frac{v_1}{v_2} = \frac{m_1 p_1 + m_2 p_2 - eK\lambda_2 p_2}{eK\lambda_1 p_1}. \quad (16)$$

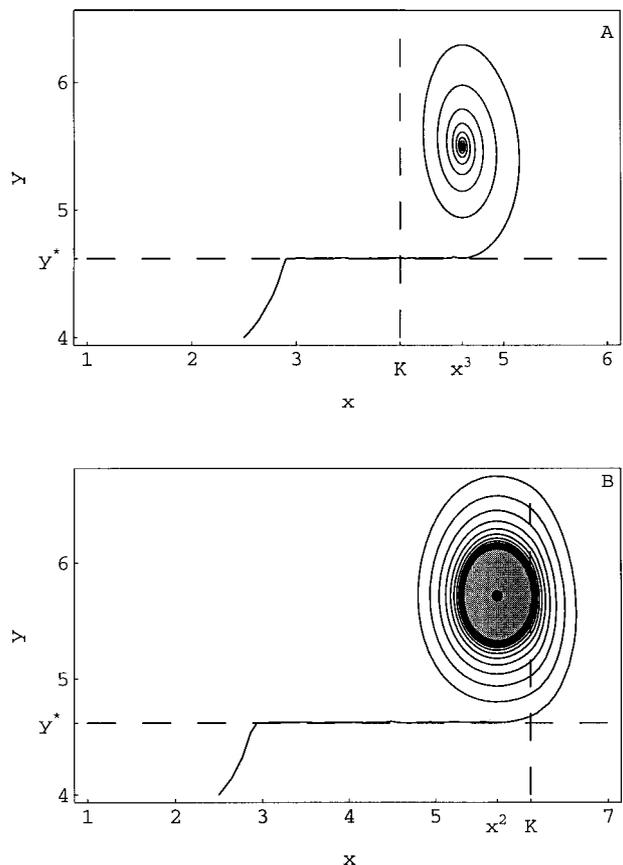


FIG. 3. Solutions of (1) driven by optimal antipredator strategy when the refuge is limited. If carrying capacity of the refuge is low ($K=4$ in Fig. 3A) trajectories converge to E^{14} . If carrying capacity is high ($K=6.1$ in Fig. 3B) then trajectories converge to a Lotka–Volterra cycle which is above the line $y = y^*$ and to the left of the line $x = K$. Other parameters are the same as in Fig. 1A.

If (15) does not hold, the carrying capacity K is higher than x^2 and trajectories leave the line $y = y^*$ before prey abundance reaches the carrying capacity of the refuge. They enter the part of the space where $y > y^*$ where they start to follow the corresponding Lotka–Volterra cycle. In this case, there are two possibilities. If this cycle does not intersect with the line $x = K$ then trajectories behave qualitatively in the same way as in the unconstrained case (Fig. 1A) and no partial preferences appear. This happens if K is large enough. For smaller K the Lotka–Volterra cycle will intersect the line $x = K$ that decreases fluctuations in predator–prey dynamics (Fig. 3B). Thus, a small carrying capacity of the refuge leads to a stable equilibrium in predator prey dynamics and partial preferences for habitats. When K is large enough, i.e.,

$$K \geq \frac{m_1 p_1 + m_2 p_2}{e \lambda_2 p_2}$$

then a limit cycle appears and all prey will be in the refuge. However, the amplitude of this limit cycle is smaller than in the case of unlimited refuges since it is constrained not only by the distance of E^5 from the line $y = y^*$ but also from the line $x = K$. As K increases, this distance will also increase and at a certain moment the distance of E^5 from the line $x = K$ will be the same as the distance of E^5 from the line $y = y^*$. For higher values of K the amplitude of the limit cycle measured by the distance of E^5 from the line $y = y^*$ is an increasing function of K . The dependence of the amplitude of the largest possible fluctuations in predator–prey dynamics on the carrying capacity K is plotted in Fig. 4.

We may also study the dependence of the amplitude of largest fluctuations on protectiveness of the refuge

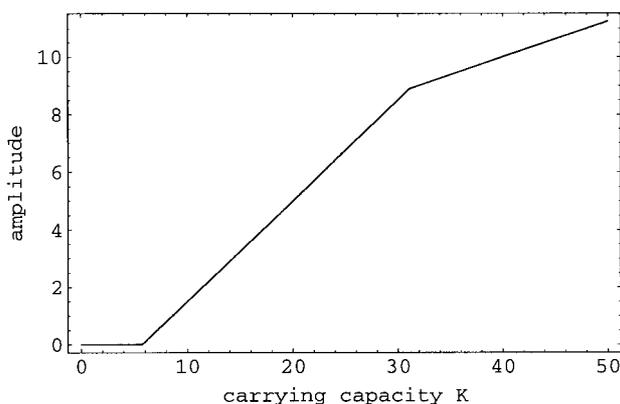


FIG. 4. The dependence of the amplitude of largest fluctuations in population abundances on the carrying capacity of the refuge. Parameters $a_1, a_2, m_1, m_2, e, \lambda_1, p_1$ are the same as in Fig. 1A.

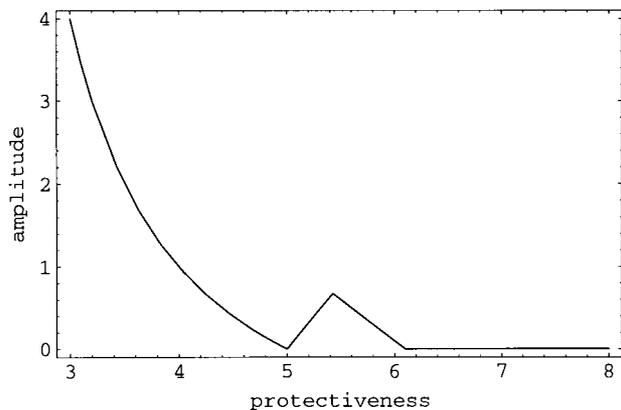


FIG. 5. The dependence of the amplitude of the largest Lotka–Volterra cycle on protectiveness of the refuge when the refuge has a fixed carrying capacity. Parameters $a_1, a_2, m_1, m_2, e, \lambda_1, p_1, K$ are the same as in Fig. 1A.

(Fig. 5). To study this dependence I assume that $m_1 = m_2 = m$ because this assumption allows us to express the distance of E^{14} from the lines $y = y^*$ and $x = K$ as a function of protectiveness P as in the case of unconstrained refugia. When protectiveness is small, the shape of the curve is the same as in the unconstrained case. As protectiveness increases the effect of limited carrying capacity will strongly influence the shape of the curve. For high values of protectiveness the system will converge to E^{14} , since (15) will be satisfied and the amplitude of fluctuations is zero.

When the refuge is complete ($P = \infty$) then E^{14} always belongs to the part of the (x, y) -space where $x > K$ and $y > y^*$ and every trajectory governed by the optimal antipredator strategy tends to E^{14} .

DISCUSSION

In this paper a system consisting of two patches—open habitat and refuge—occupied by predators and prey was studied. I assumed that prey use the refuge in order to maximize their fitness measured by instantaneous per capita growth rate. I showed that the optimal antipredator behavior of prey has a strong influence on the Lotka–Volterra population dynamics. First, without considering prey density dependence, I proved that in the long term run prey will aggregate either in the open habitat or in the refuge depending on the model parameters. If prey instantaneous growth rate in the refuge is positive and the protectiveness of the refuge is high (i.e., $a_1/\lambda_1 p_1 < a_2/\lambda_2 p_2$) then all prey will aggregate

in the refuge. If prey intrinsic growth rate in the refuge is low (or negative), or if protectiveness of the refuge is low (i.e., $a_1/\lambda_1 p_1 > a_2/\lambda_2 p_2$) then prey will aggregate in the open habitat. This result qualitatively agrees with the “minimize death per unit energy” rule (Gilliam and Fraser, 1987; Gilliam and Fraser, 1988; Werner and Gilliam, 1984). This rule suggests that prey should move to the patch where the mortality rate to energy intake rate ratio is minimized. In my model prey are in the patch in which the instantaneous mortality rate to instantaneous per capita growth rate is minimized. We also mention that present model does not support the idea of constant number or constant proportion refugia, provided prey develop an antipredator strategy.

It is well known that for prey moving between patches at random the Lotka–Volterra model (1) has a neutrally stable equilibrium surrounded by cycles. The amplitude of population fluctuations then depends on initial predator and prey abundances only. Optimal antipredator behavior of prey leads to a qualitatively different picture. All trajectories are converging to a bounded set, called attractor (shaded area in Fig. 1). Inside the attractor, trajectories follow Lotka–Volterra cycles. Thus, optimal antipredator behavior of prey may decrease fluctuations in population densities compared with the model where prey choose habitat at random. In Fig. 2 the dependence of the amplitude of the largest possible cycle is plotted versus protectiveness of the refuge ($a_2 > 0$). This relationship is not monotone; for both low and high protectiveness of the refuge fluctuations in population densities may be high. There is an optimal protectiveness that leads to stabilization of population dynamics. It is interesting to stress that the population dynamics in the open habitat is influenced by the protectiveness of the refuge, even in the case there are no prey in the refuge. If intrinsic mortality rate is higher than intrinsic natality rate in the refuge (i.e., growth rate parameter a_2 is negative), then population oscillations are decreasing for increasing protectiveness of the refuge. In this case existence of a refuge has a stabilizing effect on population dynamics. When the refuge protects its habitants completely, the population of prey will spread (for $a_2 > 0$) between both habitats due to the emergence of partial preferences of prey for habitats. Because prey population in the refuge grows exponentially overall prey abundance will also grow exponentially while predator abundance will be fixed. Due to the fact that no population can grow indefinitely, I also analyzed the case where the refuge has a limited carrying capacity. This assumption greatly affects population dynamics, since a stable equilibrium and partial preferences of prey for habitats appear for small carrying capacities (Fig. 3A). As refuge carrying

capacity increases, oscillations in population densities do appear (Figs. 3B, 4). This possible phenomenon should be taken into account when experimentally testing effects of refugia on population dynamics. Refuge hypothesis (Murdoch *et al.*, 1996) states that stability of predator–prey interactions results from the existence of a refuge. Thus, when decreasing the refuge size one might expect that fluctuations in population densities should increase. Refuge hypothesis was tested by Murdoch *et al.* (1995) and Murdoch *et al.* (1996), but removal of the refuge in these experiments did not provide supporting evidence for this hypothesis. The results of this paper suggest that the relationship between the refuge size and population dynamics may be quite complex when prey behavior is adaptive and dynamics is described by the Lotka–Volterra system. Reducing (but not removing) the refuge size even promotes the stability in the predator–prey dynamics. A similar behavior was also observed by McNair (1986). McNair (1986) assumes that both open habitat and refuge are limited and he shows that for low density dependence in the refuge a limit cycle appears. Murdoch *et al.* (1996) suggested that in their experimental system McNair’s mechanism is probably not operating because the observed prey density dependence in the refuge was high. The difference between my model and McNair’s model is that I do not consider density dependence in the open habitat and the system becomes stable due to strong density dependence in the refuge. The presence of a limited refuge may also lead to the emergence of partial preferences of prey for habitats for low refuge carrying capacities.

The results of this paper may be compared with those obtained by Křivan (1997), where both predators and prey were assumed to move between patches in order to maximize their per capita growth rates. It was assumed there that the optimal decisions of both predators and prey lead to the Nash equilibrium at which no individual can unilaterally increase its fitness by changing its strategy. Predator–prey dynamics was described by the Lotka–Volterra model (1) with both p ’s and v ’s taken as control parameters. The results there are qualitatively similar to the case considered in this paper where only prey behave optimally. However, when only prey behave optimally, in a long term run no partial preferences for habitats occur for the unlimited refuge, while if both predators and prey behave optimally partial preferences appear (Křivan, 1997).

The effect of refuges on continuous-time dynamics was studied in Sih (1987b). The analysis given there assumes that the prey mortality rate is a continuous (and differentiable) function. I showed that the assumption on the optimal antipredator behavior leads naturally to

discontinuous prey mortality rates for the Lotka–Volterra dynamics, i.e.,

$$\text{prey mortality rate} = \begin{cases} \lambda_1 p_1 y & \text{if } y < y^* \\ \lambda_2 p_2 y & \text{if } y > y^*. \end{cases} \quad (17)$$

Discontinuous prey mortality rates were suggested in Gilliam and Fraser (1988). Note that in my model the proportion of prey in the refuge is zero when predators are rare ($y < y^*$) while it is positive if predators are abundant ($y > y^*$). Thus the use of the refuge is increasing with increasing predator density which seems to be the pattern observed in nature (Sih, 1987b). When prey density dependence is included into my model, prey mortality rate will become a continuous function.

In Ives and Dobson (1987) it was argued that “as the efficiency of antipredator behavior increases, the density of the prey population always increases and the ratio of predator to prey densities always decreases.” In the case of no limitation of prey in the refuge it is true that abundance of prey at equilibrium is increasing for increasing protectiveness of the refuge. However, this equilibrium is not asymptotically stable (Fig. 1) and the ratio of predator to prey abundance is constant. For a limited carrying capacity of the refuge prey abundance at equilibrium also increases as the efficiency of antipredator behavior increases (i.e., when attack rate of predators decreases) but the ratio of predator to prey abundance is increasing.

Since the Lotka–Volterra model is known to be structurally unstable one may ask what happens if I substitute the Holling type I functional response in (1) by the more realistic Holling type II functional response which leads to non-persistence for prey moving between patches at random. System (1) becomes

$$\begin{aligned} x' &= \left(a_1 - \frac{\lambda_1 p_1 y}{1 + h_1 \lambda_1 v_1 x} \right) v_1 x + \left(a_2 - \frac{\lambda_2 p_2 y}{1 + h_2 \lambda_2 v_2 x} \right) v_2 x, \\ y' &= \left(\frac{e \lambda_1 v_1 x}{1 + h_1 \lambda_1 v_1 x} - m_1 \right) p_1 y \\ &\quad + \left(\frac{e \lambda_2 v_2 x}{1 + h_2 \lambda_2 v_2 x} - m_2 \right) p_2 y. \end{aligned} \quad (18)$$

It can be seen in Fig. 6 that the optimal antipredator behavior of prey (i.e., switching) may lead to persistence of (18). In this case a limit cycle appears. Since this limit cycle is partly formed by the switching curve, partial preferences for habitats arise as a consequence of positive handling times. Detailed analysis of the predator–prey

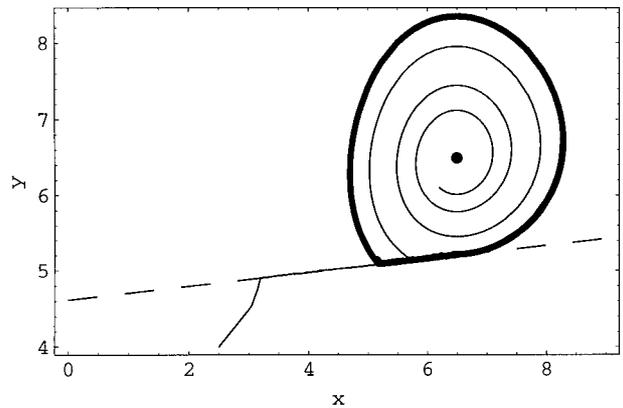


FIG. 6. Solutions of (18) driven by the optimal antipredator strategy. This figure shows that optimal antipredator behavior of prey may lead to persistence of the predator–prey system even if non-zero handling times are considered. Trajectories converge to a limit cycle which is partly formed by the switching curve. The handling times $h_1 = 0.02$, $h_2 = 0.06$, and other parameters are the same as in Fig. 1A.

dynamics with the Holling second type functional response will be given elsewhere.

APPENDIX A: BEHAVIOR OF THE MODEL ALONG THE LINE $y = y^*$

By $n = (0, 1)$ I denote the normal vector to the line $y = y^*$. Denoting the right hand-side of (4) by f^4 and similarly for (5) and (14) we get ($\langle \cdot, \cdot \rangle$ stands for the scalar product)

$$\begin{aligned} \langle f^4, n \rangle &> 0 & \text{if } x > x^2 = \frac{m_1 p_1 + m_2 p_2}{e \lambda_1 p_1}, \\ \langle f^5, n \rangle &< 0 & \text{if } x < x^1 = \frac{m_1 p_1 + m_2 p_2}{e \lambda_2 p_2}, \\ \langle f^{14}, n \rangle &< 0 & \text{if } x < x^3 = \frac{eK(\lambda_1 p_1 - \lambda_2 p_2)}{e \lambda_1 p_1} \\ & & + \frac{m_1 p_1 + m_2 p_2}{e \lambda_1 p_1}. \end{aligned}$$

Note that $x^1 < x^2 < x^3$. The above inequalities imply existence and uniqueness of trajectories of (1) driven by the optimal strategy (Colombo and Křivan, 1993) both for limited and unlimited refuge. For unlimited refuge it follows that trajectories of (1) driven by the optimal strategy cross the line $y = y^*$ upward if $x > x^2$ and downward if $x < x^1$. In the segment of the line $y = y^*$ with end points x^1 and x^2 trajectories cannot leave the

line, i.e., $y' = 0$ and, consequently, it is possible to compute the optimal strategy of prey

$$v_1 = \frac{m_1 p_1 + m_2 p_2 - e \lambda_2 p_2 x}{e x (\lambda_1 p_1 - \lambda_2 p_2)}.$$

If the refuge is limited and (15) holds than the trajectories of (1) move along the switching line between points x^1 and x^3 .

APPENDIX B: QUALITATIVE ANALYSIS OF (1)

I construct the Lyapunov function for (1) driven by the optimal antipredator strategy assuming that $a_1 \lambda_2 p_2 < a_2 \lambda_1 p_1$. Let

$$V(x, y) =$$

$$\begin{cases} e \lambda_2 p_2 \left(x - \frac{m_1 p_1 + m_2 p_2}{e \lambda_2 p_2} \ln(x) \right) \\ + \lambda_2 p_2 \left(y - \frac{a_2}{\lambda_2 p_2} \ln(y) \right) & \text{for } y > y^*, \\ e \lambda_2 p_2 x - (m_1 p_1 + m_2 p_2) \ln(x) \\ + \lambda_1 p_1 y - a_1 \ln(y) \\ + (a_1 - a_2) \left(\ln \left(\frac{a_1 - a_2}{\lambda_1 p_1 - \lambda_2 p_2} \right) - 1 \right) & \text{for } y \leq y^*. \end{cases} \quad (19)$$

The above function is continuous along the line $y = y^*$. Denoting f^4 and f^5 the right handside of (4) and (5), respectively we get

$$\langle V', f^4 \rangle = e x (\lambda_2 p_2 - \lambda_1 p_1) (a_1 - \lambda_1 p_1 y) < 0$$

$$\text{for } y \leq y^*$$

$$\langle V', f^5 \rangle = 0 \quad \text{for } y > y^*.$$

Due to the LaSalle theorem, trajectories of (1) driven by the optimal antipredator strategy converge to a global attractor which is bounded by the largest Lotka–Volterra cycle which is above the line $y = y^*$. If $a_1 \lambda_2 p_2 > a_2 \lambda_1 p_1$ existence of a global attractor can be proved analogously.

APPENDIX C: STABILITY OF E^{14}

The characteristic polynomial corresponding to E^{14} is:

$$\begin{aligned} \sigma^2 + \frac{eK(a_2 \lambda_1 p_1 - a_1 \lambda_2 p_2)}{m_1 p_1 + m_2 p_2} \sigma \\ + eK(a_2 \lambda_1 p_1 - a_1 \lambda_2 p_2) + a_1(m_1 p_1 + m_2 p_2). \end{aligned}$$

Under the assumption $a_2 \lambda_1 p_1 > a_1 \lambda_2 p_2$ all coefficients of the characteristic polynomial are positive and the Routh–Hurwitz criterion implies local stability of E^{14} .

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REFERENCES

- Collings, J. B. 1995. Bifurcation and stability analysis of a temperature-dependent mite predator–prey interaction model incorporating a prey refuge, *Bull. Math. Biology* **57**, 63–76.
- Colombo, R., and Křivan, V. 1993. Selective strategies in food webs, *IMA J. Math. Appl. Med. Biol.* **10**, 281–291.
- Comins, H. N., and Blatt, D. W. E. 1974. Prey–predator models in spatially heterogeneous environments, *J. Theor. Biol.* **48**, 75–83.
- Diehl, S., and Eklöv, P. 1995. Effects of piscivore-mediated habitat use on resources, diet, and growth of perch, *Ecology* **76**, 1712–1726.
- Fraser, D. F., and Gilliam, J. F. 1987. Feeding under predation hazard: response of the guppy and hart's rivulus from sites with contrasting predation hazard, *Behav. Ecol. Sociobiol.* **21**, 203–209.
- Fraser, D. F., and Gilliam, J. F. 1992. Nonlethal impacts of predator invasion: Facultative suppression of growth and reproduction, *Ecology* **73**, 959–970.
- Fraser, D. F., Gilliam, J. F., and Yip-Hoi, T. 1995. Predation as an agent of population fragmentation in a tropical watershed, *Ecology* **76**, 1461–1472.
- Gilliam, J. F., and Fraser, D. F. 1987. Habitat selection under predation hazard: Test of a model with foraging minnows, *Ecology* **68**, 1856–1862.
- Gilliam, J. F., and Fraser, D. F. 1988. Resource Depletion and Habitat Segregation by Competitors under Predation Hazard, in “Size-Structured Populations” (B. Ebenman and L. Perrson, Eds.), Springer-Verlag, Berlin/New York.
- Hassel, M. P., and May, R. M. 1973. Stability in insect host-parasite models, *J. An. Ecol.* **42**, 693–725.
- Hassell, M. P. 1978. “The Dynamics of Arthropod Predator–Prey Systems,” Princeton Univ. Press, Princeton, NJ.
- Hochberg, M. E., and Holt, R. D. 1995. Refuge evolution and the population dynamics of coupled host-parasitoid associations, *Evol. Ecol.* **9**, 633–661.

- Holt, R. D. 1983. Optimal foraging and the form of the predator isocline, *Am. Naturalist* **122**, 521–541.
- Holt, R. D. 1985. Population dynamics in two-patch environments: Some anomalous consequences of an optimal habitat distribution, *Theor. Popul. Biol.* **28**, 181–208.
- Holt, R. D. 1987. Prey communities in patchy environments, *Oikos* **50**, 276–290.
- Ives, A. R., and Dobson, A. P. 1987. Antipredator behavior and the population dynamics of simple predator–prey systems, *Am. Naturalist* **130**, 431–447.
- Křivan, V. 1997. Dynamic ideal free distribution: Effects of optimal patch choice on predator–prey dynamics, *Am. Naturalist* **149**, 164–178.
- Lima, S. L., and Dill, L. M. 1990. Behavioral decisions made under the risk of predation: A review and prospectus, *Can. J. Zool.* **68**, 619–640.
- Maynard Smith, J. 1974. “Models in Ecology,” Cambridge Univ. Press, Cambridge, UK.
- McNair, J. N. 1986. The effects of refuges on predator–prey interactions: A reconsideration, *Theor. Popul. Biol.* **29**, 38–63.
- Mittelbach, G. G., and Chesson, P. L. 1987. Predation risk: Indirect effects on fish populations, in “Predation” (W. C. Kerfoot and A. Sih, Eds.), Univ. press of New England, Hanover.
- Murdoch, W. W., and Stewart-Oaten, A. 1975. Predation and population stability, *Adv. Ecol. Res.* **9**, 1–131.
- Murdoch, W. W., Luck, R. F., Swarbrick, S. L., Walde, S., Yu, D. S., and Reeve, J. D. 1995. Regulation of an insect population under biological control, *Ecology* **76**, 206–217.
- Murdoch, W. W., Swarbrick, S. L., Luck, R., Walde, S., and Yu, D. S. 1996. Refuge dynamics and metapopulation dynamics: An experimental test, *Am. Naturalist* **147**, 424–444.
- Rosenzweig, M. L., and MacArthur, R. H. 1963. Graphical representation and stability conditions of predator–prey interactions, *Am. Naturalist* **97**, 209–223.
- Ruxton, G. D. 1995. Short term refuge use and stability of predator–prey models, *Theor. Popul. Biol.* **47**, 1–17.
- Sih, A. 1980. Optimal behavior: Can foragers balance two conflicting demands?, *Science* **210**, 1041–1043.
- Sih, A. 1986. Antipredator responses and the preception of danger by mosquito larvae, *Ecology* **67**, 434–441.
- Sih, A. 1987a. Predators and prey lifestyles: An evolutionary overview, in “Predation” (W. C. Kerfoot and A. Sih, Eds.), Univ. Press of New England, Hanover.
- Sih, A. 1987b. Prey refuges and predator–prey stability, *Theor. Popul. Biol.* **31**, 1–12.
- Werner, E. E., and Gilliam, J. F. 1984. The ontogenetic niche and species interactions in size-structured populations, *Ann. Rev. Ecol. Syst.*
- Werner, E. E., Gilliam, J. F., Hall, D. J., and Mittelbach, G. G. 1983. An experimental test of the effects of predation risk on habitat use in fish, *Ecology* **64**, 1540–1548.