

Optimal Foraging and Predator–Prey Dynamics, II

Vlastimil Křivan and Asim Sikder

Department of Theoretical Biology, Institute of Entomology, Academy of Sciences of the Czech Republic, and Faculty of Biological Sciences USB, Branišovská 31, 370 05 České Budějovice, Czech Republic
E-mail: krivan@entu.cas.cz

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In this paper we consider one-predator–two-prey population dynamics described by a control system. We study and compare conditions for permanence of the system for three types of predator feeding behaviors: (i) specialized feeding on the more profitable prey type, (ii) generalized feeding on both prey types, and (iii) optimal foraging behavior. We show that the region of parameter space leading to permanence for optimal foraging behavior is smaller than that for specialized behavior, but larger than that for generalized behavior. This suggests that optimal foraging behavior of predators may promote coexistence in predator–prey systems. We also study the effects of the above three feeding behaviors on apparent competition between the two prey types. © 1999 Academic Press

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INTRODUCTION

In Křivan (1996) a two-prey–one-predator population dynamic model with optimal predator foraging behavior was considered. This model assumes that predators forage according to optimal foraging theory (Charnov, 1976; Stephens and Krebs, 1986), which predicts that the more profitable prey type is always included in the predator diet while the less profitable (i.e., alternative) prey type is included with probability one only if the density of the more profitable prey type falls below a critical threshold. Therefore, the optimal foraging model does not predict the emergence of partial preferences for the alternative prey type which is either completely included or excluded from predators' diet. The predictions of optimal foraging theory were compared with several experimental and field studies in Stephens and Krebs (1986) (see also Richardson and Verbeek (1992)). These studies support the idea that the diet choice is based on food profitability although the inclusion of the less

profitable prey type is more gradual than predicted by optimal foraging theory.

Křivan (1996) showed that optimal foraging leads naturally to a more general class of population dynamical systems which are described by differential inclusions (i.e., by differential equations with multivalued right-hand sides), and to the emergence of partial preferences for the alternative prey type as a consequence of population dynamics. The multivaluedness in the model description is due to the non-uniqueness of optimal foraging strategy when the more profitable prey type reaches the critical threshold. It was shown that the interplay among behavioral ecology and population dynamics is twofold: optimal foraging influences population dynamics, which, in turn, affects optimal prey diet. Analysis given in Křivan (1996) focused mainly on local stability of the ecological equilibrium and analytical results given there were only for a special case in which both prey types had the same intrinsic per capita growth rate. The reason for this limitation was due to the fact that even local stability

analysis for the general case gives very complex expressions which cannot be efficiently analyzed. On the numerical evidence it was conceived there that optimal foraging may lead to permanence in the one-predator–two-prey model; i.e., all three populations can coexist indefinitely. Optimal foraging can also reduce amplitude of fluctuations in population densities when compared with generalist predator behavior.

In this paper we study analytically the effect of optimal foraging on permanence of the one-predator–two-prey system introduced in Křivan (1996). We show that the conditions for permanence are a great deal simpler and more efficiently tractable than those for local asymptotic stability. To conclude that all populations can coexist, permanence theory (Hofbauer and Sigmund, 1984; Butler and Waltman, 1986; Hutson and Schmitt, 1992) does not require consideration of the complicated behavior of interior (i.e., all populations present) orbits of the model found in Křivan (1996). Permanence means that there is a lower positive bound such that in a long term run all population densities (initially positive) will be above this bound and no population density tends to infinity. In Butler and Waltman (1986) the results concerning permanence are given for continuous dynamical systems, i.e., for systems in which trajectories depend continuously on initial data. Since the system studied in Křivan (1996) is described by differential inclusions which define a continuous dynamical system, we can use the results of Butler and Waltman (1986) to study its permanence.

We consider the effects of three types of predator foraging behaviors: (i) predators specialize on the more profitable prey type only, (ii) predators are generalists and they feed on both prey types, and (iii) predators forage adaptively following rules of optimal foraging theory. We derive and compare permanence conditions for the system incorporating the above three predator foraging behavior types. We show that the region of the parameter space for which permanence holds for adaptive foragers is larger than that for non-adaptive generalist foragers, but smaller than that for specialist foragers which feed only on the more profitable prey type.

We do not consider any direct competition among the two prey types. Therefore, in the predator absence both prey populations coexist at their equilibrium levels. When predators are introduced, predator-mediated apparent competition (Holt, 1977) among prey populations may drive on prey type to extinction. For generalist predators the indirect effects of predation on competition among the two prey types were studied by Holt (1977). In this paper we extend this study to the case where

predators follow optimal diet choice and predator–prey population dynamics is of the Rosenzweig–MacArthur type.

POPULATION DYNAMICS

In this part we survey the model introduced in Křivan (1996) where more details can be found. We consider predators foraging on two prey types. Predator density is denoted by x_3 , and prey densities are x_1 and x_2 , respectively. Population dynamics is described by a system of differential equations

$$\begin{aligned}x'_1 &= a_1 x_1 \left(1 - \frac{x_1}{K_1}\right) - \frac{u_1 \lambda_1 x_1 x_3}{1 + u_1 h_1 \lambda_1 x_1 + u_2 h_2 \lambda_2 x_2} \\x'_2 &= a_2 x_2 \left(1 - \frac{x_2}{K_2}\right) - \frac{u_2 \lambda_2 x_2 x_3}{1 + u_1 h_1 \lambda_1 x_1 + u_2 h_2 \lambda_2 x_2} \quad (1) \\x'_3 &= \frac{u_1 e_1 \lambda_1 x_1 x_3 + u_2 e_2 \lambda_2 x_2 x_3}{1 + u_1 h_1 \lambda_1 x_1 + u_2 h_2 \lambda_2 x_2} - m x_3.\end{aligned}$$

Here u_i denotes the probability that a predator will attack the prey type i , λ_i is the search rate of a predator for the i th prey type, e_i is the expected net energy gained from the i th prey type, and h_i is the expected handling time spent with the i th prey type. In what follows we assume that either u_1 and u_2 are fixed if predators show fixed preferences for their prey or they are chosen according to the optimal diet model. Maximization of the net energy intake rate which is used as the fitness measure in optimal foraging theory (Stephens and Krebs, 1986; Křivan, 1996) is equivalent to maximization of the instantaneous per capita predator growth rate x'_3/x_3 . We remark that model (1) does not consider any direct competition between the two prey populations, but the two prey types are in apparent competition through the shared predation (Holt, 1977). Of course, this apparent competition appears only provided that both prey types are included in predators' diet.

Throughout the paper we will assume that the first prey type is more profitable for predators than the second alternative prey type, by which we mean that

$$\frac{e_1}{h_1} > \frac{e_2}{h_2}.$$

If predators follow optimal diet choice, the optimal strategy of a predator when encountering a prey depends on the density of the more profitable prey type which is

always attacked upon an encounter, i.e., $u_1 = 1$. The alternative prey type is attacked with probability one ($u_1 = 1$) if the density of the more profitable prey type is below the critical threshold

$$x_1^* = \frac{e_2}{\lambda_1(e_1 h_2 - e_2 h_1)}.$$

If the first prey type density is above x_1^* then the alternative prey type is not attacked upon an encounter ($u_2 = 0$) since it pays off for predators to search for the more profitable prey type. Following Murdoch and Oaten (1975) we call x_1^* the switching density because predators switch their behavior at this prey density. If the first prey type density equals x_1^* then optimal predator strategy is not uniquely defined by maximization of x'_3/x_3 , i.e., $0 \leq u_2 \leq 1$. Thus, control u_2 as a function of the more profitable prey type density is a step-like function and (1) which is driven by optimal predator foraging strategy is not a differential equation but a differential inclusion (Aubin and Cellina, 1984; Filippov, 1988) because the right-hand side of (1) is not uniquely defined for $x_1 = x_1^*$.

By $\mathbf{R}_+^3 = \{(x_1, x_2, x_3) \mid x_1 \geq 0, x_2 \geq 0, x_3 \geq 0\}$, we denote the non-negative octant which we split in three parts:

$$G^1 = \{x \in \mathbf{R}_+^3 \mid x_1 < x_1^*\},$$

$$G^2 = \{x \in \mathbf{R}_+^3 \mid x_1 > x_1^*\},$$

$$G^0 = \{x \in \mathbf{R}_+^3 \mid x_1 = x_1^*\}.$$

System (1) driven by optimal predator foraging strategy is defined on each set G^i ($i=0, 1, 2$) separately. In the region G^1 the more profitable prey type density is low, the alternative prey type is always included into the predator diet ($u_2 = 1$), and system (1) becomes

$$\begin{aligned} x'_1 &= a_1 x_1 \left(1 - \frac{x_1}{K_1}\right) - \frac{\lambda_1 x_1 x_3}{1 + h_1 \lambda_1 x_1 + h_2 \lambda_2 x_2} \\ x'_2 &= a_2 x_2 \left(1 - \frac{x_2}{K_2}\right) - \frac{\lambda_2 x_2 x_3}{1 + h_1 \lambda_1 x_1 + h_2 \lambda_2 x_2} \\ x'_3 &= \frac{e_1 \lambda_1 x_1 x_3 + e_2 \lambda_2 x_2 x_3}{1 + h_1 \lambda_1 x_1 + h_2 \lambda_2 x_2} - m x_3. \end{aligned} \quad (2)$$

In G^2 the more profitable prey type density is high, the alternative prey type is excluded from the predator diet ($u_2 = 0$), and the corresponding dynamics is

$$\begin{aligned} x'_1 &= a_1 x_1 \left(1 - \frac{x_1}{K_1}\right) - \frac{\lambda_1 x_1 x_3}{1 + h_1 \lambda_1 x_1} \\ x'_2 &= a_2 x_2 \left(1 - \frac{x_2}{K_2}\right) \\ x'_3 &= \frac{e_1 \lambda_1 x_1 x_3}{1 + h_1 \lambda_1 x_1} - m x_3. \end{aligned} \quad (3)$$

Note that the equation for x_2 in (3) is independent of the other two equations.

In G^0 the right-hand side of (1) is not uniquely defined since $0 \leq u_2 \leq 1$. However, it was shown in Křivan (1996) that in the subregion of G^0 described by

$$\begin{aligned} &\frac{a_1}{\lambda_1} \left(1 - \frac{x_1^*}{K_1}\right) (1 + h_1 \lambda_1 x_1^*) \\ &< x_3 < \frac{a_1}{\lambda_1} \left(1 - \frac{x_1^*}{K_1}\right) (1 + h_1 \lambda_1 x_1^* + h_2 \lambda_2 x_2) \end{aligned}$$

trajectories of (1) cannot leave G^0 . This region was called the partial preference domain, since partial preferences (i.e., u_2 is strictly between zero and one) for the alternative prey type arise in this area. These partial preferences can be uniquely computed along the partial preference domain since in the partial preference domain $x'_1 = 0$, which gives

$$\begin{aligned} u_2 &= \frac{e_1}{\lambda_2 x_2 (e_2 h_1 - e_1 h_2)} \\ &+ \frac{K_1 \lambda_1^2 x_3 (e_2 h_1 - e_1 h_2)}{a_1 \lambda_2 h_2 x_2 (e_2 + \lambda_1 K_1 (e_2 h_1 - e_1 h_2))}; \end{aligned}$$

for details see Křivan (1996). Substituting this expression for u_2 in (1) the dynamics in the partial preference region is described by

$$\begin{aligned} x'_1 &= 0 \\ x'_2 &= x_2 a_2 \left(1 - \frac{x_2}{K_2}\right) \\ &\quad - \frac{1}{h_2 \lambda_1} \left(\lambda_1 x_3 - a_1 (1 + h_1 \lambda_1 x_1^*) \left(1 - \frac{x_1^*}{K_1}\right)\right) \\ x'_3 &= x_3 \left(\frac{e_2}{h_2} - m\right). \end{aligned}$$

We want to study permanence of (1) for various predator foraging behaviors. Permanence is a weaker notion than stability because it says only that there is a positive lower and upper bound for population densities but it does not give any information regarding qualitative

behavior of trajectories. For deriving conditions for the permanence of three-dimensional systems it is enough to study the behavior of trajectories of (1) with one population missing. This simplifies the analysis, by reducing the dimensionality of the problem. Butler and Waltman (1986) derived the necessary and sufficient conditions for permanence of a dynamical system. The conditions require that trajectories of the system depend continuously on initial data, trajectories of the system are uniformly bounded, all boundary invariant sets repel interior trajectories, there are no cycles formed by subsets of boundary invariant sets, and all boundary invariant sets are isolated. For Gause-type models such as those described by (2) the dynamics when one population is missing are simple. The two-dimensional $x_i - x_3$ ($i = 1, 2$) predator-prey dynamics when one prey type is missing has one equilibrium which either is globally asymptotically stable or is unstable and then a globally asymptotically stable limit cycle around this equilibrium exists (Hofbauer and Sigmund, 1984; Kuang and Freedman, 1988). If the equilibrium is not feasible (by feasible we mean that all coordinates are positive), then due to a high mortality rate predator population is eliminated from the two-dimensional system. When the predator population is missing then the two-prey system has one equilibrium (K_1, K_2) which is globally asymptotically stable. The conditions ensuring permanence for three-dimensional Gause-type models reduce to verify that the boundary equilibria are repelling interior trajectories if the boundary limit cycles do not appear, since other conditions of the Butler and Waltman theorem are satisfied. We remark that the conditions ensuring repellence of boundary equilibria are also called invasibility conditions, because they imply that if the one-prey-one-predator subsystem is in equilibrium and the missing prey is introduced in a small quantity then it will invade the community (Holt, 1977, Hofbauer and Sigmund, 1984).

Verification of boundary limit cycle repellence, if it exists, is a cumbersome problem as we do not know the analytical description of the limit cycle and thus we cannot compute the Floquet multipliers which determine limit cycle repellence. Throughout this paper we will assume that if a boundary limit cycle exists then it repels interior trajectories. This condition can be verified numerically for each set of parameters.

PERMANENCE FOR GENERALIST PREDATORS

Here we assume that predators are generalists and they forage on every prey encountered ($u_2 = 1$), regardless of

its profitability measured by the ratio e_i/h_i . Population dynamics are described by system (2) which has the following boundary equilibria (i.e., equilibria at which at least one population is missing): $E_0 = (0, 0, 0)$, $E_1 = (K_1, 0, 0)$, $E_2 = (0, K_2, 0)$, $E_{12} = (K_1, K_2, 0)$,

$$E_{13} = \left(\frac{m}{\lambda_1(e_1 - h_1 m)}, 0, \frac{a_1 e_1 (e_1 K_1 \lambda_1 - (1 + h_1 K_1 \lambda_1) m)}{K_1 \lambda_1^2 (e_1 - h_1 m)^2} \right),$$

$$E_{23} = \left(0, \frac{m}{\lambda_2(e_2 - h_2 m)}, \frac{a_2 e_2 (e_2 K_2 \lambda_2 - (1 + h_2 K_2 \lambda_2) m)}{K_2 \lambda_2^2 (e_2 - h_2 m)^2} \right).$$

We will call E_{12} , E_{13} , and E_{23} planar equilibria. Since

$$\frac{e_i K_i \lambda_i}{1 + h_i K_i \lambda_i} < \frac{e_i}{h_i},$$

equilibrium E_{i3} ($i = 1, 2$) is feasible (i.e., i th and third coordinates are positive) if

$$m < \frac{e_i K_i \lambda_i}{1 + h_i K_i \lambda_i}, \quad i = 1, 2. \quad (4)$$

Condition (4) is more likely to be satisfied for large values of carrying capacity K_i . If the predator mortality rate is higher than the prey profitability measured by e_i/h_i , then E_{i3} is not feasible.

System (2) has one interior equilibrium

$$E^{(2)} = \left(\frac{K_1(a_2 \lambda_1 m - K_2 \lambda_2 (a_2 \lambda_1 - a_1 \lambda_2)(e_2 - h_2 m))}{a_2 K_1 \lambda_1^2 (e_1 - h_1 m) + a_1 K_2 \lambda_2^2 (e_2 - h_2 m)}, \frac{K_2(a_1 \lambda_2 m + K_1 \lambda_1 (a_2 \lambda_1 - a_1 \lambda_2)(e_1 - h_1 m))}{a_2 K_1 \lambda_1^2 (e_1 - h_1 m) + a_1 K_2 \lambda_2^2 (e_2 - h_2 m)}, (e_1 K_1 \lambda_1 + e_2 K_2 \lambda_2 - (1 + h_1 K_1 \lambda_1 + h_2 K_2 \lambda_2) m) \right. \\ \left. (a_1 a_2 (a_1 K_2 \lambda_2^2 (e_2 + e_2 h_1 K_1 \lambda_1 - e_1 h_2 K_1 \lambda_1) + a_2 K_1 \lambda_1^2 (e_1 - e_2 h_1 K_2 \lambda_2 + e_1 h_2 K_2 \lambda_2))) \right) \\ \left. (a_2 K_1 \lambda_1^2 (e_1 - h_1 m) + a_1 K_2 \lambda_2^2 (e_2 - h_2 m))^2 \right).$$

If predators are missing then equilibrium E_{12} is always feasible and globally asymptotically stable for the two-prey system because densities of both prey types converge to their carrying capacities. If one of the two prey

types is missing and the corresponding Rosenzweig–MacArthur predator–prey system has a feasible equilibrium E_{i3} ($i=1, 2$) then this equilibrium is globally asymptotically stable provided that

$$m \geq \frac{e_i(K_i\lambda_i h_i - 1)}{h_i(K_i\lambda_i h_i + 1)} \quad (5)$$

(Hofbauer and Sigmund, 1984). If the opposite inequality holds in (5), then there is a unique globally asymptotically stable limit cycle around E_{i3} (Kuang and Freedman, 1988). In what follows we will assume that either no boundary limit cycle exists (which happens if either E_{13} and E_{23} are not feasible or (5) holds for $i=1, 2$) or if a boundary limit cycle exists then it repels interior trajectories. Under this assumption permanence for (2) holds if all feasible boundary equilibria are repelling interior orbits; i.e., when one population is missing and the corresponding two-dimensional system is in equilibrium, then the missing population will invade the community when introduced in small quantity; see Appendix A. Predators will invade the two-prey community which is at equilibrium E_{12} if

$$m < \frac{e_1 K_1 \lambda_1 + e_2 K_2 \lambda_2}{1 + h_1 K_1 \lambda_1 + h_2 K_2 \lambda_2}. \quad (6)$$

If opposite inequality holds in (6) then predators will be always driven to extinction due to a high mortality rate. Note that since the first prey type is more profitable than the second prey type the following inequality is satisfied

$$\frac{e_2 K_2 \lambda_2}{1 + h_2 K_2 \lambda_2} < \frac{e_1 K_1 \lambda_1 + e_2 K_2 \lambda_2}{1 + h_1 K_1 \lambda_1 + h_2 K_2 \lambda_2}, \quad (7)$$

which implies that feasibility of equilibrium E_{23} automatically implies that predators will invade the community of the two prey types. If E_{13} is feasible then the second prey type will invade the equilibrium community consisting of the first prey type and predators if

$$a_2 \lambda_1 - a_1 \lambda_2 > -\frac{m a_1 \lambda_2}{(e_1 - m h_1) K_1 \lambda_1} \quad (8)$$

and, similarly, if E_{23} is feasible then the first prey type will invade the equilibrium community consisting of the second prey type and predators if

$$a_2 \lambda_1 - a_1 \lambda_2 < \frac{m a_2 \lambda_1}{(e_2 - m h_2) K_2 \lambda_2}. \quad (9)$$

Invasibility condition (8) can be rewritten as

$$\lambda_1 \left(\frac{a_2 \lambda_1}{a_1 \lambda_2} - 1 \right) > -\frac{m}{(e_1 - m h_1) K_1} \quad (10)$$

and condition (9) as

$$\lambda_2 \left(1 - \frac{a_1 \lambda_2}{a_2 \lambda_1} \right) < \frac{m}{(e_2 - m h_2) K_2}. \quad (11)$$

The prey type with higher ratio a_i/λ_i is called the keystone species (Paine, 1969; Holt, 1977; Vandermeer and Maruca, 1998). It follows that the keystone prey type will always invade the equilibrium community consisting of the other prey type and predators. For example, if the first prey type is the keystone species ($a_1/\lambda_1 > a_2/\lambda_2$) then it will always invade the system consisting of the second prey type and predators because condition (11) will hold. Under the same assumption condition (10) constrains the possibility for the second prey type to invade the community consisting of the first prey type and predators. If, for example, the predator mortality rate m is low or carrying capacity K_1 is high the second prey type cannot invade. This implies that in this case the second prey type is in higher danger of being eliminated from the community when environmental productivity increases, or predator mortality rate decreases. If $a_1/\lambda_1 = a_2/\lambda_2$, which is the case considered in Křivan (1996), then invasibility conditions (10) and (11) are automatically satisfied. Invasibility conditions with handling times set to zero (i.e., population dynamics is described by the Lotka–Volterra model) are discussed in detail in Holt (1977).

It is known that permanence implies automatically feasibility (densities of all populations are positive) of the interior equilibrium $E^{(2)}$ (Hofbauer and Sigmund, 1984). In our case this can be easily verified directly. Indeed, repellence of the boundary equilibria E_{13} and E_{23} implies positivity of both prey densities in equilibrium $E^{(2)}$. Positivity of the predator equilibrium density follows from the repellence conditions and condition (4). Local stability analysis of $E^{(2)}$ leads to very complex expressions which do not seem to be readily interpretable.

To get permanence for (2) we have the following cases with respect to the predator mortality rate; see Appendix A:

(a)

$$0 < m < \min \left\{ \frac{e_1 K_1 \lambda_1}{1 + h_1 K_1 \lambda_1}, \frac{e_2 K_2 \lambda_2}{1 + h_2 K_2 \lambda_2} \right\}.$$

This is the case in which both predator–prey systems with one prey type missing do coexist because both planar equilibria E_{13} and E_{23} are feasible (Fig. 1A). Due to (7) equilibrium E_{12} repels interior trajectories, and E_{13} and E_{23} repel interior orbits if

$$-\frac{ma_1\lambda_2}{(e_1 - mh_1)K_1\lambda_1} < a_2\lambda_1 - a_1\lambda_2 < \frac{ma_2\lambda_1}{(e_2 - mh_2)K_2\lambda_2}. \quad (12)$$

Note that if prey type 2 is the keystone species ($a_2/\lambda_2 > a_1/\lambda_1$), condition (12) can be satisfied only if K_2 is not too large, and, similarly, if prey type 1 is the keystone species then K_1 cannot be large. This means that in order to satisfy invasibility condition (12), the keystone prey type cannot have high carrying capacity, or it cannot strongly dominate the other prey type in the sense that the two a/λ ratios do not differ too much. When $a_1/\lambda_1 \neq a_2/\lambda_2$ and both K_1 and K_2 are large enough, then (12) will never hold and (2) will not be permanent.

(b)

$$\frac{e_2K_2\lambda_2}{1 + h_2K_2\lambda_2} < m < \min \left\{ \frac{e_1K_1\lambda_1}{1 + h_1K_1\lambda_1}, \frac{e_1K_1\lambda_1 + e_2K_2\lambda_2}{1 + h_1K_1\lambda_1 + h_2K_2\lambda_2} \right\}.$$

In this case the only feasible planar equilibria are E_{12} and E_{13} (Fig. 1B). E_{12} repels interior trajectories due to (6) and E_{13} repels interior trajectories if (8) holds. For example, this will be the case if the second prey type is the keystone species.

(c)

$$\frac{e_1K_1\lambda_1}{1 + h_1K_1\lambda_1} < m < \frac{e_2K_2\lambda_2}{1 + h_2K_2\lambda_2}.$$

In this case the only feasible planar equilibria are E_{12} and E_{23} (Fig. 1C). E_{12} repels interior orbits due to (7) and E_{23} repels interior orbits if (9) holds which happens, for example, if the first prey type is the keystone species.

(d)

$$\max \left\{ \frac{e_1K_1\lambda_1}{1 + h_1K_1\lambda_1}, \frac{e_2K_2\lambda_2}{1 + h_2K_2\lambda_2} \right\} < m < \frac{e_1K_1\lambda_1 + e_2K_2\lambda_2}{1 + h_1K_1\lambda_1 + h_2K_2\lambda_2}.$$

In this case neither E_{13} nor E_{23} is feasible, E_{12} repels interior trajectories, and no additional assumptions are needed to have permanence of (2) (Fig. 1D).

The above results can be interpreted from the community ecology point of view. The case (a) considers the situation in which predators can coexist with each of the two prey types alone. Introduction of the missing prey will result in permanence if (12) is satisfied which is possible only if the two prey types do not differ too much in their a/λ value, or in other words, if the carrying capacity of the keystone prey type is low. Cases (b) and (c) describe the situation in which predators can coexist with one prey type alone, but they cannot coexist with the other prey type alone. Conditions which allow the missing prey type to invade the predator–prey system are less restrictive than those for case (a). For example, in case (b) the three-dimensional system will be permanent if the second prey type is the keystone species. If the first prey type is the keystone species then the system with generalist predators will be permanent only provided that a_1/λ_1 is not too much higher than a_2/λ_2 , i.e., when the keystone species is not strongly dominant over the other prey type. Case (d) describes the situation in which predators cannot coexist with any of the two prey types alone, but coexistence is possible when both prey types are in the community. Thus we see that conditions which ensure permanence of the three-dimensional system depend strongly on the predator mortality rate. For higher predator mortality rates (case (d)) the conditions are less restrictive than those for low mortality rates (case (a)); see Fig. 2. We remark that parameters used in Fig. 2 are such that (5) is satisfied; i.e., no population cycles appear in predator–prey dynamics if one prey type is missing.

The shape of the set of parameters that lead to permanence for generalist predators depends on the relation between the carrying capacities of the two prey types. First assume that

$$\frac{e_1K_1\lambda_1}{1 + h_1K_1\lambda_1} < \frac{e_2K_2\lambda_2}{1 + h_2K_2\lambda_2},$$

which happens if the carrying capacity of the first prey type is low, namely

$$K_1 < \frac{e_2K_2\lambda_2}{\lambda_1(e_1 + K_2\lambda_2(e_1h_2 - e_2h_1))}. \quad (13)$$

Because

$$\frac{e_2K_2\lambda_2}{\lambda_1(e_1 + K_2\lambda_2(e_1h_2 - e_2h_1))} < x_1^*,$$

it follows that (13) can be satisfied only if the carrying capacity of the more profitable prey type is lower than the switching density, i.e., $K_1 < x_1^*$. The parameter region leading to permanence looks as in Fig. 2A.

Now assume that

$$\frac{e_2 K_2 \lambda_2}{1 + h_2 K_2 \lambda_2} < \frac{e_1 K_1 \lambda_1}{1 + h_1 K_1 \lambda_1} < \frac{e_1 K_1 \lambda_1 + e_2 K_2 \lambda_2}{1 + h_1 K_1 \lambda_1 + h_2 K_2 \lambda_2}.$$

This is satisfied if

$$\frac{e_2 K_2 \lambda_2}{\lambda_1 (e_1 + K_2 \lambda_2 (e_1 h_2 - e_2 h_1))} < K_1 < x_1^*. \quad (14)$$

The parameter region leading to permanence looks as in Fig. 2B.

If the carrying capacity of the more profitable prey type is higher than the switching density then

$$\frac{e_1 K_1 \lambda_1}{1 + h_1 K_1 \lambda_1} > \frac{e_1 K_1 \lambda_1 + e_2 K_2 \lambda_2}{1 + h_1 K_2 \lambda_1 + h_2 K_2 \lambda_2}$$

and the region of the parameter space where permanence holds is shown in Fig. 2C.

PERMANENCE FOR SPECIALIST PREDATORS

Here we consider the case in which predators specialize only on the more profitable prey type and the alternative prey type is excluded from predator diet ($u_2 = 0$). Population dynamics is then described by system (3), which has two planar equilibria E_{12} and E_{13} . These two equilibria are the same as those for system (2). Again, we assume that if the boundary limit cycle exists then it repels interior trajectories. If E_{13} is feasible then it always repels interior orbits, and E_{12} repels interior trajectories if

$$m < \frac{e_1 \lambda_1 K_1}{1 + h_1 \lambda_1 K_1}; \quad (15)$$

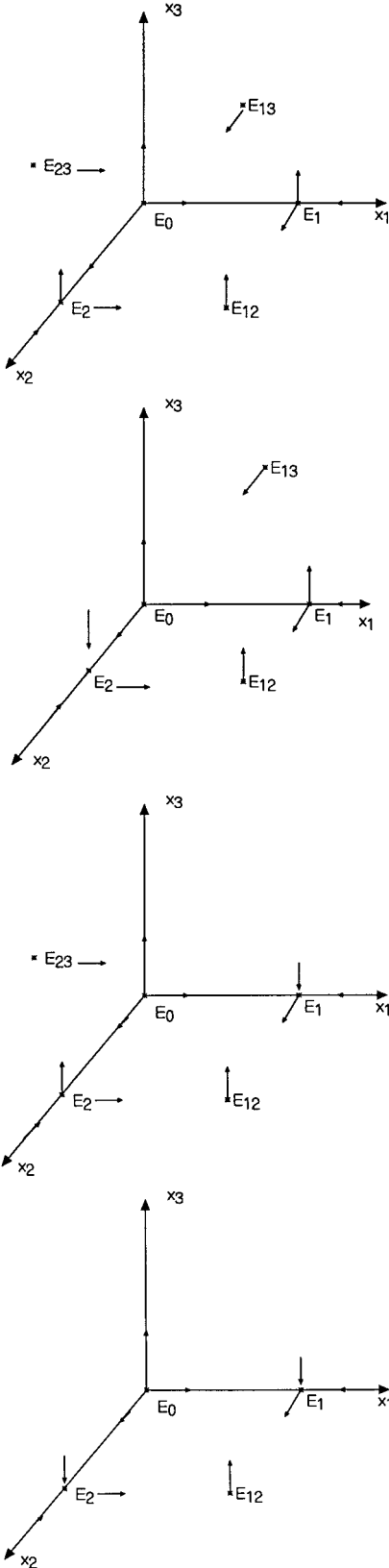
FIG. 1. This figure shows four possible scenarios that lead to permanence of (2). In order for (2) to be permanent all planar equilibria must repel interior orbits. In (A) the three planar equilibria E_{12} , E_{13} , and E_{23} are feasible and they are repelling interior trajectories. In (B) and (C) only one of the two planar equilibria E_{13} and E_{23} is feasible and repelling. In (D) E_{13} and E_{23} do not exist. In all cases it is trivial to see that boundary equilibria are acyclic.

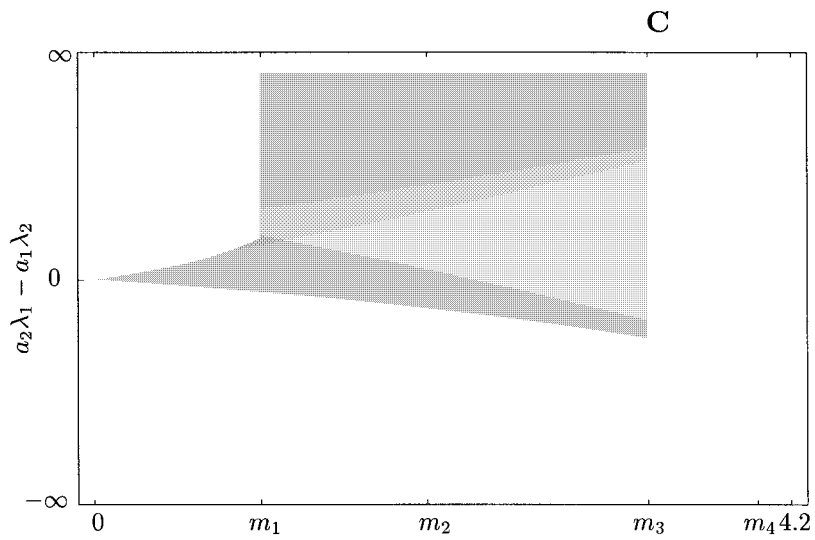
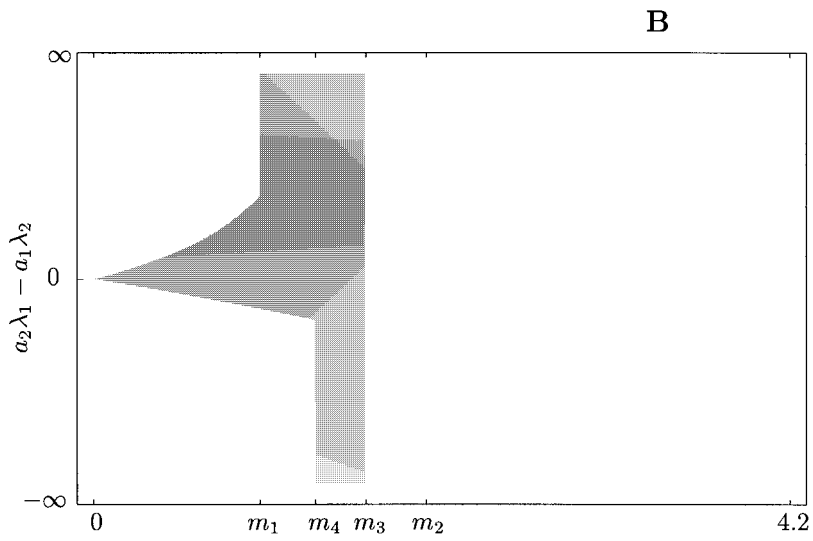
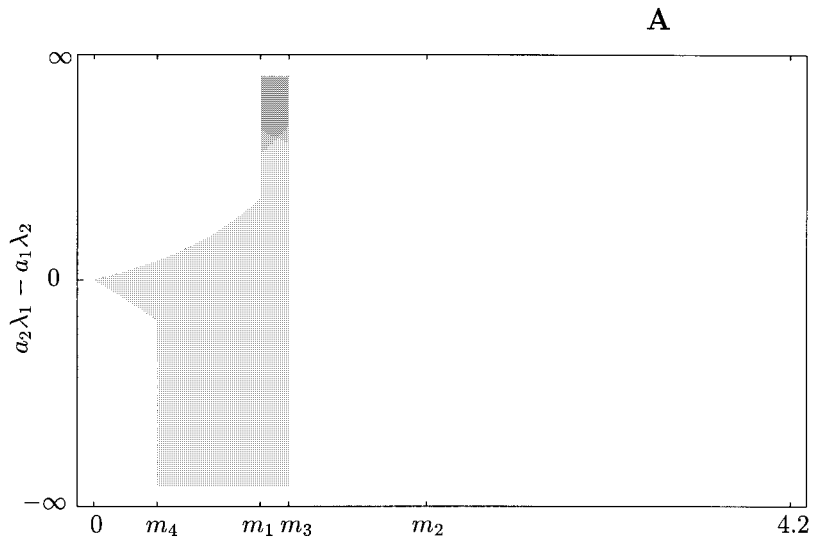
A

B

C

D





see Appendix B. Since (15) is equivalent with feasibility of E_{13} , it follows that (3) is permanent if and only if E_{13} is feasible. Note that feasibility of E_{13} is equivalent with the existence of a feasible interior equilibrium

$$E^{(3)} = \left(\frac{m}{\lambda_1(e_1 - h_1 m)}, K_2, \frac{a_1 e_1 (e_1 K_1 \lambda_1 - (1 + h_1 K_1 \lambda_1) m)}{K_1 \lambda_1^2 (e_1 - h_1 m)^2} \right).$$

Since x_2 is independent of x_1 and x_3 and it converges to K_2 , every trajectory of (3) converges to a plane described by $x_2 = K_2$. In this plane the dynamics of (3) is described by a two-dimensional system for the first prey and predator. Thus, the system in which predators specialize on the more profitable prey type is permanent only if (15) holds. If the mortality rate m is large (i.e., when opposite inequality in (15) holds) then the prey population cannot support the predator population, which will die out. Compared with generalist predators we see that conditions that imply permanence for specialist predators are much less restrictive. In Fig. 3 the region of the parameter space where permanence holds when predators specialize on the more profitable prey type is shown for the same set of parameters as in Fig. 2C.

PERMANENCE FOR OPTIMALLY FORAGING PREDATORS

Now we consider the case in which predators follow optimal prey choice. We show that the parameter space that leads to permanence of (1) driven by optimal foraging strategy is larger than for the case in which predators are generalists and they choose their diet in a non-adaptive way.

As in the previous parts we assume that if a boundary limit cycle exists then it repels interior trajectories. The key observation is the fact that system (3), which describes the dynamics when predators feed only on the more profitable prey type, has only two planar equilibria E_{12} and E_{13} , and the alternative prey type, not being

eaten, can always invade the community. We will consider two cases depending on the position of the switching threshold x_1^* with respect to the carrying capacity K_1 of the more profitable prey type. First we assume that $K_1 < x_1^*$, which happens if the carrying capacity of the more profitable prey type is low, or prey types do not differ too much in their profitability which leads to high values of the switching threshold. Since the density of the more profitable prey type is bounded by K_1 , predators will never switch to exclude the alternative prey type from their diet and will always behave as generalists. Thus, the results concerning system permanence driven by optimal foraging strategy will be the same as those for the case of generalist predators discussed earlier.

Next we assume that $K_1 > x_1^*$. This condition is likely to be satisfied provided that either the profitability of the two prey types differs one from another significantly (e_1/h_1 is sufficiently larger than e_2/h_2), or the carrying capacity K_1 for the more profitable prey type is high. Since condition $K_1 > x_1^*$ implies that E_{12} belongs to G^2 where predators behave as specialists, E_{12} repels interior trajectories provides that (15) holds. Further, condition $K_1 > x_1^*$ leads to the occurrence of switching in predator behavior, and, moreover, it implies the ordering

$$\begin{aligned} \frac{e_2 K_2 \lambda_2}{1 + h_2 K_2 \lambda_2} &< \frac{e_2}{h_2} < \frac{e_1 K_1 \lambda_1 + e_2 K_2 \lambda_2}{1 + h_1 K_1 \lambda_1 + h_2 K_2 \lambda_2} \\ &< \frac{e_1 K_1 \lambda_1}{1 + h_1 K_1 \lambda_1} < \frac{e_1}{h_1}. \end{aligned} \quad (16)$$

In turn, this ordering implies the occurrence of the following cases which lead to permanence; see Appendix C:

(Aa)

$$0 < m < \frac{e_2 K_2 \lambda_2}{1 + h_2 K_2 \lambda_2}.$$

In this case E_{13} and E_{23} are feasible and E_{13} belongs to G^1 . E_{12} always repels interior orbits and (1) is permanent

FIG. 2. In this figure the regions of parameter space that lead to permanence for generalist predators are shown for various values of carrying capacities. Here $m_1 = e_2 K_2 \lambda_2 / (1 + h_2 K_2 \lambda_2)$, $m_2 = e_2 / h_2$, $m_3 = (e_1 K_1 \lambda_1 + e_2 K_2 \lambda_2) / (1 + h_1 K_1 \lambda_1 + h_2 K_2 \lambda_2)$, and $m_4 = e_1 K_1 \lambda_1 / (1 + h_1 K_1 \lambda_1)$, where for this plot the following values of parameters were chosen: $a_1 = 1$, $a_2 = 2$, $e_1 = 4$, $e_2 = 1$, $h_1 = h_2 = 0.5$, and $\lambda_1 = \lambda_2 = 2$. This choice of parameters satisfies condition (5); i.e., no predator-prey cycles appear when one prey type is missing. In (A) carrying capacities satisfy (13) ($K_1 = 0.05$, $K_2 = 1$). In (B) carrying capacities satisfy (14) ($K_1 = 0.2$, $K_2 = 1$), and in (C) the more profitable prey type carrying capacity is above the switching threshold; i.e., $K_1 > x_1^*$ ($K_1 = 1$, $K_2 = 1$).

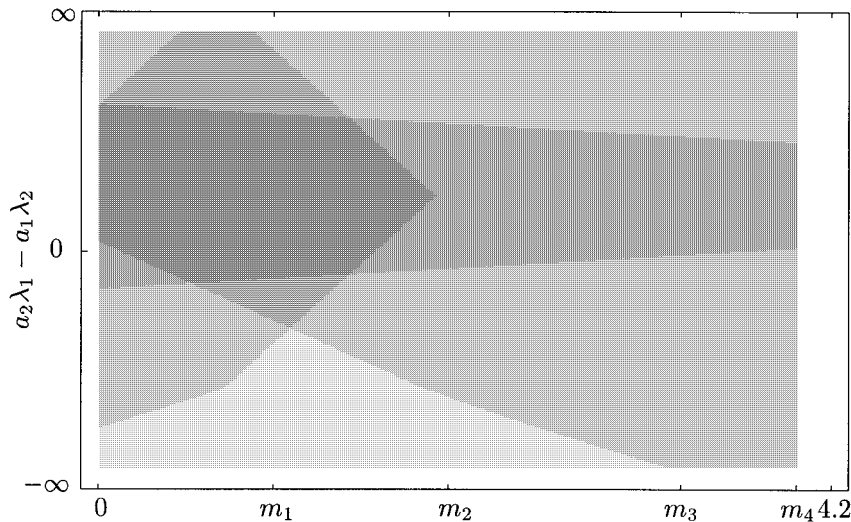


FIG. 3. In this figure the region of parameter space that leads to permanence for specialist predators is shown for the same parameters that are used in Fig. 2C.

provided that E_{13} and E_{23} repel interior orbits, which happens if (12) holds (Fig. 4A).

(Ab)

$$\frac{e_2 K_2 \lambda_2}{1 + h_2 K_2 \lambda_2} < m < \frac{e_2}{h_2}.$$

In this case E_{23} is not feasible and E_{13} is in G^1 . E_{12} repels interior trajectories and (1) is permanent if (8) holds (Fig. 4B).

(Ac)

$$\frac{e_2}{h_2} < m < \frac{e_1 K_1 \lambda_1}{1 + h_1 K_1 \lambda_1}.$$

In this case E_{23} is not feasible and E_{13} is in G^2 . In G^2 dynamics of (1) driven by optimal foraging strategy is described by (3), for which E_{13} always repels interior orbits. Therefore, no additional constraints are necessary to ensure permanence of (1) driven by optimal foraging strategy (Fig. 4C).

In Fig. 5 the region of parameter space in which the permanence of (1) when driven by optimal foraging strategy is shown for the case $K_1 > x_1^*$. We see that compared to generalist predators (see Fig. 2C) the parameter space leading to permanence is larger for optimally foraging predators, but smaller than that for specialist predators (see Fig. 3). When the predator mortality rate is lower than $m_2 = e_2/h_2$, the ordering of (16) implies that the conditions for permanence for optimal foragers (Aa) and (Ab) are the same as are the conditions (a) and (b)

for permanence for generalist predators. These conditions ensure that neither of the two prey types will be driven to extinction by predation. When predator mortality rate is above m_2 , for optimally foraging predators planar equilibrium E_{23} is not feasible and E_{13} always repels interior trajectories. This means that neither of the two prey types can be driven to extinction due to predation and the situation is qualitatively the same as that for predators which specialize on the more profitable prey type. Thus, the set of parameters that lead to permanence for optimally foraging predators is obtained as a combination of these parameters for generalist (for $m < m_2$) and specialist predators (for $m > m_2$). The reason optimal foraging behavior of predators enlarges the region of parameter space that leads to permanence is that for predator mortality rates which are higher than the profitability of the second prey type (case (Ac)) neither of the two prey populations can be driven to extinction by predation. Indeed, for

$$\frac{e_2}{h_2} < m < \frac{e_1 K_1 \lambda_1}{1 + h_1 K_1 \lambda_1}$$

and due to the ordering given by (16) persistence for generalist predators is given by (b) while that for optimally foraging predators, by (Ac). Thus, in order to have permanence for generalist predators the alternative prey type must be able to invade the community consisting of the first prey type and predators. This is so if, for example, the alternative prey type is the keystone species. However, under the above assumptions, for optimally foraging predators the alternative prey type can always

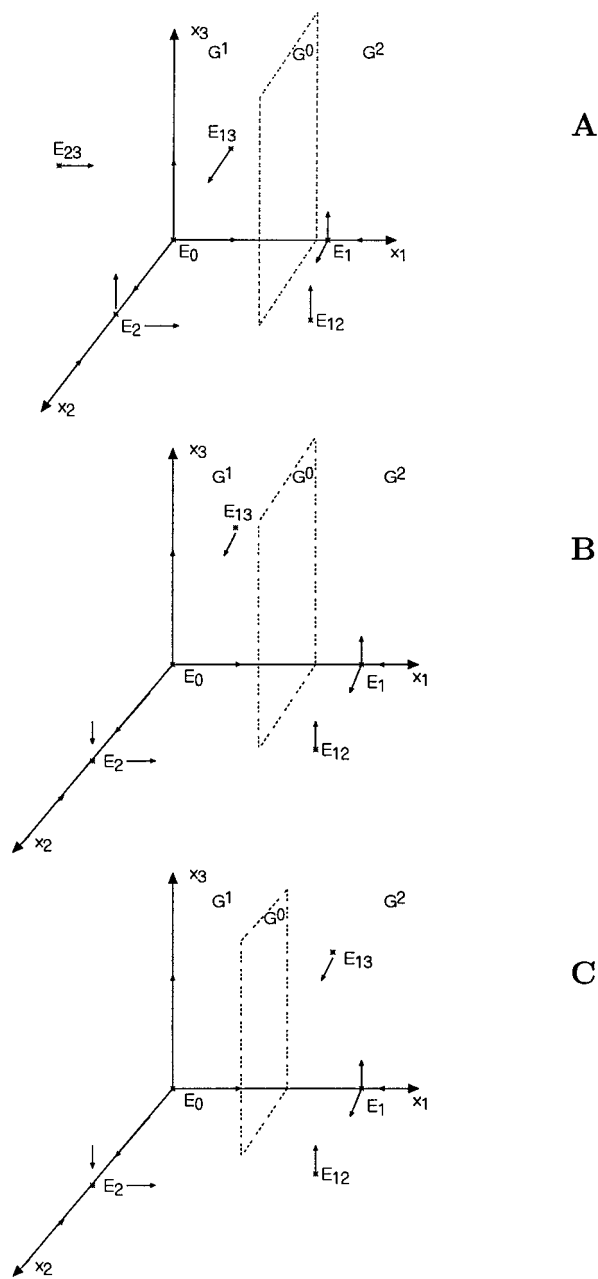


FIG. 4. This figure shows the acyclicity of the boundary equilibria and permanence of system (1) driven by optimal foraging strategy. In all cases E_{12} is in G^2 . In (A) E_{13} and E_{23} exist in G^1 . If E_{23} does not exist, then we get two cases: E_{13} exists in G^1 (B) or E_{13} exists in G^2 (C).

invade when the system consisting of the first prey type and predators is at E_{13} equilibrium because at this equilibrium predators do not feed on the less profitable prey type. This is because as the more profitable prey type becomes abundant, predators exclude the alternative prey type from their diet which then recovers until it is included again in the predator diet.

DISCUSSION

In this paper we studied the effects of three types of predator behavior on the permanence of one-predator–two-prey population dynamics. These types of behavior were: (i) predators specialize only on the more profitable prey type; (ii) predators are non-adaptive generalists—they feed on every encountered prey; and (iii) predators are adaptive generalists—they behave as optimal foragers. For all three types of behavior we compared the set of parameters that leads to permanence of all three populations. The largest region of parameter space that leads to permanence is for predators that specialize on the more profitable prey type (Fig. 3). This is because, in this case, the alternative prey type not being preyed upon grows logistically and therefore it will always be present. Thus, permanence of a three-dimensional system reduces to permanence of a system which consists of the more profitable prey type and predators only. This model is the Rosenzweig–MacArthur predator–prey model which has one equilibrium. This equilibrium, if positive (see condition (15)), either is stable or a stable limit cycle exists due to the paradox of enrichment. In both cases predators coexist indefinitely with prey and the model is therefore permanent. If predators behave as generalists and they include the alternative prey type in their diet, this gives more restrictive conditions for permanence of the model (Fig. 2). Such more restrictive conditions are due to the fact that we have to ensure that predators do not drive any of the two prey types to extinction. Holt (1977) showed that by including an alternative prey type in predators’ diet the predator equilibrium density increases and the original prey type suffers heavier predation. This leads to lower equilibrium density of the original prey type, or even to exclusion of the original prey type. This indirect effect of one prey type on the other prey species is called predator-mediated apparent competition. The shape of the parameter set that leads to permanence depends on the environmental productivity. If productivity is low, i.e., if the carrying capacity of the more profitable prey type is below the switching threshold, then the set of parameters for which the two-prey–one predator system is permanent is shown in Figs. 2A and 2B. If the carrying capacity for the more profitable prey type is above the switching threshold, then the set of parameters leading to permanence is given in Fig. 2C.

If predators follow the optimal diet rule then we show (Fig. 5) that when the carrying capacity of the more profitable prey type is above the switching threshold then the region of parameter space that leads to permanence for optimal predators is larger than that for generalist predators (Fig. 2C) but smaller than that for specialist

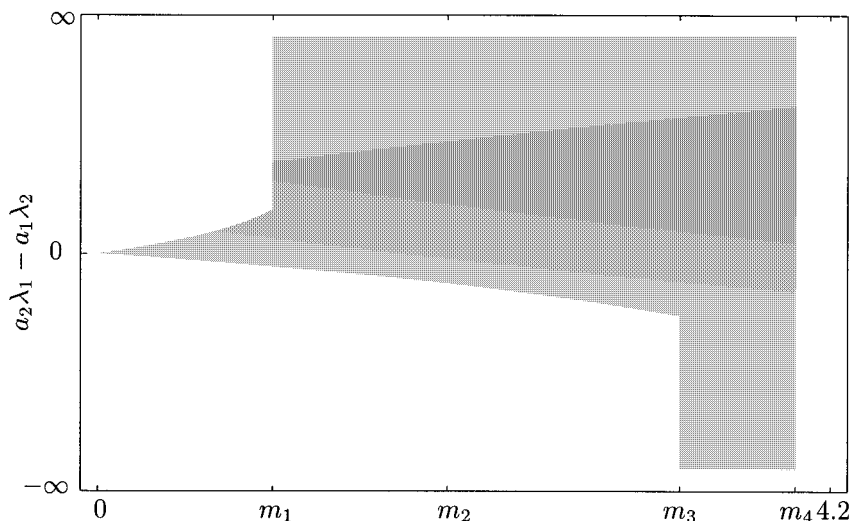


FIG. 5. In this figure the region of parameter space that leads to permanence for optimal predators is shown for the same parameters that are used in Fig. 3C.

predators (Fig. 3). This is because for predator mortality rates which are lower than the profitability of the alternative prey type the set of parameters leading to permanence for optimal predators is the same as that for generalist predators while for higher predator mortality rates the set of parameters leading to permanence for optimal foragers is the same as that for specialist predators. This is due to the fact that for low predator mortality rates ($m < e_2/h_2$) the conditions that lead to permanence are the same for both generalist and optimal predators. However, for higher predator mortality rates the alternative prey type cannot be driven to extinction because when the more profitable prey type is abundant, predators exclude the alternative prey type from their diet. This reduces predation pressure on the alternative prey type which can survive in the community.

The results of this paper suggest that adaptive (i.e., optimal) behavior which maximizes fitness, measured by instantaneous per capita growth rate, may be an important mechanism maintaining high biodiversity. A similar conclusion was also obtained in some other papers that analyzed the effects of various adaptive animal behaviors on population dynamics within the predator-prey and host-parasitoid models: optimal foraging of predators (Fryxell and Lundberg, 1994; Křivan, 1996; Schmitz *et al.*, 1997), optimal patch use (Colombo and Křivan, 1993; van Baalen and Sabelis, 1993; Křivan, 1997a), adaptive host-feeding (Yamamura and Yano, 1988; Kidd and Jervis, 1989, 1991; Briggs *et al.*, 1995; Křivan, 1997b), adaptive superparasitism (Sirot and Křivan, 1997), adaptive searching for food versus parasitizing (Křivan and Sirot, 1997), and adaptive use of refuges by

prey (Ives and Dobson, 1987; Sih, 1987; Ruxton, 1995; Křivan, 1998). For example, Fryxell and Lundberg (1994) assumed a gradual change in profitability of inclusion of the less profitable prey type. However, this gradual change described by a sigmoidal function leads to expressions in permanence analysis which are very difficult to analyze. Our approach, based on the direct use of the step function, allows us to obtain simple conditions ensuring permanence.

In predator-prey models with Holling type II functional response limit cycles occur. Numerical simulations such as those given in Křivan (1996) show that such fluctuations in population densities may occur also in the two-prey-one-predator system considered in this paper. If there are fluctuations with large amplitude, the system is still permanent from a mathematical point of view, but in reality extinction has to be expected. It was shown in Křivan (1996) that optimal foraging reduces the amplitude of fluctuations that occur for generalist predators.

The key condition under which optimal foraging increases permanence is that the carrying capacity of the more profitable prey type is above the switching density. This condition is more likely to be satisfied, if, for example, the profitability of the alternative prey type is sufficiently lower than the profitability of the better prey type, or the carrying capacity of the more profitable prey type is sufficiently high.

In applications of permanence results dynamical systems are typically assumed to be described by differential equations with smooth right-hand sides (Hutson and Schmitt, 1992; Sikder and Roy, 1994) for which continuous dependence of trajectories on initial data

automatically holds. This condition allowed us to apply the permanence results of Butler and Waltman and we showed that this theory is a useful tool in some models that are described by differential inclusions. Such models arise naturally when the effects of optimal adaptive behavior on population dynamics are studied.

We remark that the model considered in this paper is purely deterministic. Permanence in this setting means only that population densities are bounded and they will be larger than some positive quantity which is not explicitly specified. Therefore, this lower positive bound can be rather small and stochastic effects (e.g., demographic noise) may lead to population extinction. For stochastic systems the concept of permanence is called stochastic boundedness (Chesson, 1978).

Stochastic boundedness means that for every positive probability ε there is an upper and lower bound such that the average densities of populations are within these bounds with probability at least $1 - \varepsilon$. Thus, for deterministic systems these two definitions give the same notion of permanence.

The permanence analysis given in this paper does not provide any detailed insight into the behavior of interior trajectories. However, for the purposes of community ecology which focuses on species composition rather than on details of dynamics this may suffice.

In this paper we assumed that both prey populations grow in the absence of predators logistically. If the prey population grows exponentially, then still we get that the indefinite coexistence of all three populations is possible, but due to the exponential growth the alternative prey type will grow to infinity. We remark that due to such unboundedness of trajectories application of the Butler–Waltman theorem is impossible. The Butler–Waltman permanence theory can also be applied to more general Gause or Kolmogorov two-prey–one-predator models. For these models prey isoclines may not be unimodal and multiple steady states in the predator–prey subsystems might appear. However, this is not an obstacle for applying the permanence theory, although invasibility conditions may become more complicated.

APPENDIX A: PERMANENCE OF (2)

PROPOSITION 1. *Assume that if a boundary limit cycle of (2) exists then it repels interior trajectories. System (2) is permanent if one of the following conditions holds:*

(a)

$$m < \min \left\{ \frac{e_1 K_1 \lambda_1}{1 + h_1 K_1 \lambda_1}, \frac{e_2 K_2 \lambda_2}{1 + h_2 K_2 \lambda_2} \right\} \quad (17)$$

and

$$-\frac{ma_1 \lambda_2}{(e_1 - mh_1) K_1 \lambda_1} < a_2 \lambda_1 - a_1 \lambda_2 < \frac{ma_2 \lambda_1}{(e_2 - mh_2) K_2 \lambda_2}. \quad (18)$$

(b)

$$\frac{e_2 K_2 \lambda_2}{1 + h_2 K_2 \lambda_2} < m < \min \left\{ \frac{e_1 K_1 \lambda_1}{1 + h_1 K_1 \lambda_1}, \frac{e_1 K_1 \lambda_1 + e_2 K_2 \lambda_2}{1 + h_1 K_1 \lambda_1 + h_2 K_2 \lambda_2} \right\}, \quad (19)$$

and

$$-\frac{ma_1 \lambda_2}{(e_1 - mh_1) K_1 \lambda_1} < a_2 \lambda_1 - a_1 \lambda_2. \quad (c)$$

$$\frac{e_1 K_1 \lambda_1}{1 + h_1 K_1 \lambda_1} < m < \frac{e_2 K_2 \lambda_2}{1 + h_2 K_2 \lambda_2},$$

and

$$a_2 \lambda_1 - a_1 \lambda_2 < \frac{ma_2 \lambda_1}{(e_2 - mh_2) K_2 \lambda_2}.$$

(d)

$$\max \left\{ \frac{e_1 K_1 \lambda_1}{1 + h_1 K_1 \lambda_1}, \frac{e_2 K_2 \lambda_2}{1 + h_2 K_2 \lambda_2} \right\} < m < \frac{e_1 K_1 \lambda_1 + e_2 K_2 \lambda_2}{1 + h_1 K_1 \lambda_1 + h_2 K_2 \lambda_2}.$$

Proof. First we note that the trajectories of (2) are uniformly bounded in the set

$$\{(x_1, x_2, x_3) \in \mathbf{R}^3 \mid e_1 x_1 + e_2 x_2 + x_3 \leq M\},$$

where we take M larger than K_1/e_1 and K_2/e_2 . Now the proof consists in verifying the three conditions of the theorem of Butler and Waltman (1986) which we recall here. The first condition requires that the stable manifold of any boundary invariant set has an empty intersection with the positive octant. The second condition requires

that all boundary invariant sets form an acyclic sequence; i.e., no subset of these sets forms a cycle. The last condition is that all boundary invariant sets are isolated, which is automatically satisfied if they are hyperbolic (i.e., all eigenvalues have non-zero real parts in the case of equilibria). By Π_i ($i=1, 2, 3$) we denote the part of the boundary of \mathbf{R}_+^3 for which the i th population is missing, i.e., $x_i=0$ ($i=1, 2, 3$). Since we assume that if boundary limit cycles exist then they repel interior trajectories, we have to study only the repelling properties of boundary equilibria. $E_{12} \in \Pi_3$ is always feasible and it is also globally asymptotically stable in the plan Π_3 . Moreover, since

$$\frac{e_2 K_2 \lambda_2}{1 + h_2 K_2 \lambda_2} < \frac{e_1 K_1 \lambda_1 + e_2 K_2 \lambda_2}{1 + h_1 K_1 \lambda_1 + h_2 K_2 \lambda_2}$$

it follows that the condition

$$m < \frac{e_1 K_1 \lambda_1 + e_2 K_2 \lambda_2}{1 + h_1 K_1 \lambda_1 + h_2 K_2 \lambda_2},$$

which implies that x'_3/x_3 evaluated at E_{12} is positive, holds in all cases. Thus, E_{12} repels interior trajectories. E_0 is locally unstable along the x_1 and x_2 directions but locally stable along the x_3 direction. By M we denote the set of all feasible boundary equilibria. Since

$$\left. \frac{x'_3}{x_3} \right|_{E_i} = \frac{e_i \lambda_i K_i}{1 + h_i \lambda_i K_i} - m, \quad i=1, 2$$

it follows that if E_{i3} is feasible then E_i repels boundary trajectories along the x_3 direction. Moreover, E_1 always repels boundary trajectories in the x_2 direction and similarly for E_2 . Thus, all the boundary equilibria are isolated.

(a) From inequality (17) it follows that

$$M = \{E_0, E_1, E_2, E_{12}, E_{13}, E_{23}\};$$

see Fig. 1A. Since E_{13} and E_{23} are feasible, equilibrium E_i ($i=1, 2$) repels orbits locally along the x_3 direction. Due to condition (18) both E_{13} and E_{23} repel the interior orbits. Thus, the boundary equilibria of (2) have no stable manifold intersecting the interior of the positive octant. From the above analysis of the boundary flow the phase portrait for each two-dimensional subsystem reveals the fact that no equilibrium is chained to itself and no subsets of M form a cycle; see Fig. 1A. If repelling

boundary limit cycles exist the situation is similar. Thus, M is acyclic; that is, the boundary flow of (1) is acyclic and the proof of permanence follows from the theorem of Butler and Waltman (1986).

(b) In this case, the set of feasible boundary equilibria is

$$M = \{E_0, E_1, E_2, E_{12}, E_{13}\}.$$

The behavior of trajectories in the neighborhood of boundary equilibria is the same as that in case (a) with the exception that E_2 is locally stable along the x_3 direction; see Fig. 1B. So the proof follows from Part (a).

(c) This case is similar to (b) if we replace E_{13} by E_{23} and E_2 by E_1 ; see Fig. 1C.

(d) In this case $M = \{E_0, E_1, E_2, E_{12}\}$, and the proof is the same as in the previous case; see Fig. 1D.

APPENDIX B: PERMANENCE OF (3)

PROPOSITION 2. *Assume that if a boundary limit cycle of (3) exists then it repels interior trajectories. Let*

$$m < \frac{e_1 K_1 \lambda_1}{1 + h_1 \lambda_1 K_1} \quad (20)$$

Then system (3) is permanent.

Proof. Under the given conditions, E_{13} is feasible and globally asymptotically stable in the plane Π_2 . Since

$$\left. \frac{x'_2}{x_2} \right|_{E_{13}} = a_2,$$

it follows that E_{13} repels the interior orbits. Moreover,

$$\left. \frac{x'_3}{x_3} \right|_{E_{12}} = \frac{e_1 \lambda_1 K_1}{1 + h_1 \lambda_1 K_1} - m;$$

i.e., the feasibility of E_{13} implies that E_{12} repels interior trajectories. The remaining part of the proof is the same as that of part (b) of Proposition 1.

APPENDIX C: PERMANENCE OF (1)

PROPOSITION 3. *Assume that if a boundary limit cycle of (1) exists then it repels interior trajectories.*

A. Let $K_1 > x_1^*$. Then system (1) governed by optimal foraging strategy is permanent if one of the following conditions holds:

(Aa)

$$m < \frac{e_2 K_2 \lambda_2}{1 + h_2 K_2 \lambda_2},$$

and

$$\begin{aligned} -\frac{ma_1 \lambda_2}{(e_1 - mh_1) K_1 \lambda_1} &< a_2 \lambda_1 - a_1 \lambda_2 \\ &< \frac{ma_2 \lambda_1}{(e_2 - mh_2) K_2 \lambda_2}. \end{aligned} \quad (21)$$

(Ab)

$$\frac{e_2 K_2 \lambda_2}{1 + h_2 K_2 \lambda_2} < m < \frac{e_2}{h_2},$$

and

$$-\frac{ma_1 \lambda_2}{(e_1 - mh_1) K_1 \lambda_1} < a_2 \lambda_1 - a_1 \lambda_2.$$

(Ac)

$$\frac{e_2}{h_2} < m < \frac{e_1 K_1 \lambda_1}{1 + h_1 K_1 \lambda_1}.$$

B. Let $K_1 < x_1^*$. Then system (1) governed by optimal foraging strategy is permanent if one of the conditions of Proposition 1 holds.

Proof. Since the theorem of Butler and Waltman (1986), which we want to use, is for continuous dynamical systems we have to prove first that trajectories of (1) driven by optimal foraging strategy depend continuously on the initial condition. This follows from the fact that solutions of (1) driven by optimal foraging strategy are uniquely defined on any forward time interval (Křivan 1996) and from the corollary on p. 93 in Filippov (1988). Moreover, we note that in the boundary plane Π_2 the right-hand sides of (2) and (3) coincide; i.e., (1) driven by optimal foraging strategy is described in Π_2 by a differential equation with a smooth right-hand side.

(A) Note that if $K_1 > x_1^*$ then (16) holds. In this case E_{12} lies in G^2 and it is a repeller with respect to the interior flow because in all three cases the assumptions of

Proposition 3 together with (16) imply that $m < e_1 K_1 \lambda_1 / (1 + h_1 K_1 \lambda_1)$. In what follows we will show that in all cases the boundary equilibria are repelling interior trajectories. The proof of acyclicity and isolatedness follows the same lines as in the proof of Proposition 1 and it is clear from Fig. 4. To prove permanence we have to show that planar feasible equilibria are repelling interior orbits.

(Aa) In this case (16) implies that E_{13} and E_{23} are feasible and E_{13} is in G^1 ; see Fig. 4A. Condition (21) implies that E_{13} and E_{23} repel interior orbits.

(Ab) In this case assumptions of proposition and (16) imply that only E_{13} is feasible, it lies in G^1 , and it repels interior trajectories (due to (8)); see Fig. 4B.

(Ac) In this case assumptions of proposition and (16) imply that only E_{13} is feasible and it lies in G^2 ; see Fig. 4C. In this case E_{13} is always repelling interior trajectories.

(B) If $K_1 < x_1^*$ then E_{12} and E_{13} , if feasible, belong to G^1 where system (1) driven by optimal foraging strategy is described by (2). Therefore Proposition 1 applies.

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