MATHEMATICAL MODELS OF
PREDATOR MUTUALISTS

H.I. FREEDMAN, R. KUMAR, A.K. EASTON AND M. SINGH

ABSTRACT. Systems of differential equations are proposed as models of predator mutualists which cooperate in hunting for prey. In the case that the mutualism is facultative on at least one of the predators, it is shown that both predators may persist on only one prey population. In the case of obligate mutualism, it is shown that if the mutualism is sufficiently strong, then a reversal of outcome is possible in the sense that there may exist a positive stable invariant set.

1. Introduction. The occurrence of mutualism in nature is not so rare as many individuals believe and can arise in a great variety of ways [1, 2]. Many of these occurrences are because of interactions with a third population in a competitive or predator-prey situation. Although most such mutualisms involving predator-prey systems usually occur with the prey, there are instances when the mutualism is with the predator, and mathematical models have been developed to describe some of these mutualisms [7, 9, 17].

In the above-mentioned papers, the population mutualist to the predator population is able to survive in the absence of the mutualism, i.e., the mutualism is obligate on, at most, one of the two mutualist populations. However, it may be that both of the mutualists predate on the same prey so that obligate mutualism, if it occurs, would be obligate on both mutualist populations. This would be the first time, to the best of our knowledge, that a model of a two predator-one prey system is used to model mutualism rather than competition [6, 11] between predators.

An example of the type of mutualism described above occurs in the Red Sea [19], where the effect of mutualism is to increase the predator functional response. There, Yellowsaddle goatfish, *P. cyclostomus*, and

bird wrasse, *Gomphosus caeruleus*, tackle coral reefs from both sides so that the prey may be driven toward each other and thereby caught and eaten. Without the cooperation between these two fish species, such prey would be available only minimally and with great difficulty. Hence, the effect of each predator population on the other is to increase hunting efficiency.

A second example of such mutualism occurs in streams [**21, 22**], where the mortality of the mayfly (Eshemerella) was greater than expected in the presence of both fish (Comis) and stoneflies (Agnetina), because the stoneflies under the rocks caused the mayflies to come into the open with greater exposure to the fish, and the presence of the fish drove the mayflies to the rocks with greater exposure to the stoneflies.

It is the main purpose of this paper to develop and analyze a model of such a mutualistic system.

This paper is organized as follows. In the next section we develop our model. In Section 3 we discuss the question of persistence or extinction of populations and apply our criteria in later sections. Section 4 is devoted to the facultative mutualism case, and Section 5 to the semi obligate case. Section 6 deals with the full obligatory case. Sections 4–6 contain some numerical examples to show that the theory is not vacuous. The final section contains a brief discussion of our results.

2. The model. We consider the following system of ODEs as a model of two mutualist predators and a single prey:

$$\dot{x} = xg(x) - y_1 p_1(x, y_2) - y_2 p_2(x, y_1)$$
$$\dot{y}_1 = y_1\{-s_1(y_1) + c_1 p_1(x, y_2)\}$$
(1)
$$\dot{y}_2 = y_2\{-s_2(y_2) + c_2 p_2(x, y_1)\},$$
$$x(0) = x_0 \geq 0, \quad y_i(0) = y_{i0} \geq 0, \quad i = 1, 2 \text{ and ``·''} = \frac{d}{dt}.$$

We assume the following standard hypotheses on the given functions [**6**]:

(H0) All functions are sufficiently smooth so that existence, uniqueness and continuability for all positive time of initial value problems are satisfied.

(H1) $g(x) : R_+ \rightarrow R$; $g(0) > 0$; $g'(x) < 0$; there exists $K > 0$ such that $g(K) = 0$.

Note that $g(x)$ is the specific growth rate of the prey and K is the carrying capacity of the environment.

(H2) $p_i(x, y_j) : R_+^2 \rightarrow R_+$; $p_i(0, y_j) = 0$; $(\partial p_i)/(\partial x) > 0$, $i, j = 1, 2$, $i \neq j$.

$p_i(x, y_j)$ is the predator functional response of the prey to the ith predator.

(H3) $(\partial p_i(x, y_j))/(\partial y_j) > 0$, $i, j = 1, 2$, $i \neq j$.

Hypothesis (H3) describes how the mutualism between the predators occurs, namely, by each increasing the hunting ability of the other.

(H4) $s_i(y_i) : R_+ \rightarrow R_+$; $s_i(0) > 0$; $s_i'(y_i) \geq 0$; $c_i > 0$; $i = 1, 2$.

The function $s_i(y_i)$ represents a density-dependent death rate for the ith predator population when food is scarce while c_i is the conversion rate of prey biomass to predator biomass for the ith predator population.

It is straightforward to show that all solutions of (1) are bounded. In fact, similar to [**10**], one can prove the following theorem.

Theorem 2.1. *Let* $\tilde{s} = \min(c_1 s_1(0), c_2 s_2(0))$ *and* $\tilde{G} = \sup_{0 \leq x \leq K}(\tilde{s} + g(x))x$. *Let* $\mathcal{A} = \{(x, y_1, y_2) : 0 \leq x \leq K, 0 \leq x + (y_1/c_1) + (y_2/c_2) \leq (\tilde{G}/\tilde{S})\}$. *Then*

(i) $\mathcal{A}$ *is positively invariant.*

(ii) $(x(t), y_1(t), y_2(t)) \rightarrow \mathcal{A}$ *as* $t \rightarrow \infty$.

3. Persistence and extinction. Persistence theory is an attempt to describe mathematically what is intuitively meant in biology by survival or continuous existence of populations as opposed to local extinction. The definitions we employ here may be found in [**8**] or [**11**]. For a general background on persistence, see [**15**].

A population $N(t)$ is said to exhibit *weak persistence* if $N(0) > 0$, $N(t) > 0$ and $\lim\sup_{t \rightarrow \infty} N(t) > 0$. $N(t)$ is said to exhibit (*strong*) *persistence* if, in addition, $\lim\inf_{t \rightarrow \infty} N(t) > 0$. Further, $N(t)$ is said to exhibit *uniform persistence* if also there exists $\delta > 0$ independent of

$N(0)$ such that $\liminf_{t\to\infty} N(t) \geq \delta$.

A system of populations exhibits weak, strong or uniform persistence if each component population does. Finally, a system exhibits *non-persistence* if any component does not persist, corresponding to local extinction of that component population.

The general technique for proving persistence in other than Lotka-Volterra systems was developed in [**11**]. It requires each closed invariant boundary set to be isolated, hyperbolic and unstable locally in the directions interior to R^n_+ for Euclidean space. The Butler-McGehee lemma is instrumental in showing that solutions initiating in the interior of R^n cannot have ω-limit points on the boundary, which is equivalent to persistence. Since in this paper all boundaries are at most two-dimensional, the closed invariant sets are either equilibria, periodic solutions, or equilibria connected by saddle connectors. In our models here the last of these cannot occur.

In [**3**] it was shown that under additional hypotheses of diffusivity of the system and acyclicity of the boundary closed invariant sets, the persistence will be uniform and there will exist an interior equilibrium.

Persistence theory may be extended to abstract sets with interior and boundary in Banach spaces and to semi-dynamical systems including partial differential systems, time delay systems and discrete maps. See [**15**] for references.

4. The facultative case. In this section we consider the case where the mutualism is facultative, i.e., where both predator populations can survive on their own but are able to sustain higher population numbers due to the mutualism. In order for this to occur in model (1), there must exist $\tilde{x}_i$, $i = 1, 2$, such that

$$(2) \qquad -s_i(0) + c_i p_i(\tilde{x}_i, 0) = 0, \quad \tilde{x}_i < K,$$

[**6**].

In the case that (2) is satisfied, then the following equilibria exist in $x - y_1 - y_2$ space: $E_0(0, 0, 0)$, $E_K(K, 0, 0)$, $\widehat{E}_1(\widehat{x}_1, \widehat{y}_1, 0)$ and $\widehat{E}_2(\widehat{x}_2, 0, \widehat{y}_2)$, where $(\widehat{x}_i, \widehat{y}_i)$ satisfy

$$(3) \qquad \begin{aligned} \widehat{x}_i g_i(\widehat{x}_i) - \widehat{y}_i p_i(\widehat{x}_i, 0) &= 0 \\ -s_i(\widehat{y}_i) + c_i p_i(\widehat{x}_i, 0) &= 0. \end{aligned}$$

Note that $\tilde{x}_i \leq \hat{x}_i < K$. In addition, there may be an interior equilibrium of the form $E^*(x^*, y_1^*, y_2^*)$, which may not be unique.

In order to check that this is a reasonable model of mutualism, one must ensure that neither predator population will become extinct due to the presence of the other. To this end we first consider $\hat{E}_1$. Computing the variational matrix about $\hat{E}_1$, we obtain

$$\widehat{M}_1 = \begin{bmatrix} \hat{x}_1 g'(\hat{x}_1) + g(\hat{x}_1) - \hat{y}_1 \frac{\partial p_1}{\partial x}(\hat{x}_1, 0) & -p_1(\hat{x}_1, 0) & -p_2(\hat{x}_1, \hat{y}_1) \\ c_1 \hat{y}_1 \frac{\partial p_1}{\partial x}(\hat{x}_1, 0) & -\hat{y}_1 s_1'(\hat{y}_1) & c_1 \hat{y}_1 \frac{\partial p_1}{\partial y_2}(\hat{x}_1, 0) \\ 0 & 0 & -s_2(0) + c_2 p_2(\hat{x}_1, \hat{y}_1) \end{bmatrix}.$$

From $\widehat{M}_1$, one can see that the eigenvalue governing the stability locally in the y_2 direction is $\hat{\lambda}_2 = -s_2(0) + c_2 p_2(\hat{x}_1, \hat{y}_1)$. If $\hat{\lambda}_2 < 0$, then the strong stable manifold of $\hat{E}_1$ intersects the interior of the positive octant, and extinction will occur for at least some positive initial conditions. This is contrary to our notion of mutualism. Similar considerations would apply at $\hat{E}_2$. Hence, we make the assumptions

$$(4) \qquad -s_i(0) + c_i p_i(\hat{x}_j, \hat{y}_j) > 0, \quad i, j = 1, 2; \quad j \neq i.$$

If the $\hat{E}_i$ are globally stable with respect to positive solutions in their respective planes (see [**5, 14, 18**] for criteria for this to be true), then using arguments similar to those in [**17**], we would obtain that system (1) is uniformly persistent, and all populations survive. In this case it also follows that E^* exists. However, if there are limit cycles in the $x-y_i$ plane (which must be the case if $\hat{E}_i$ is unstable in this plane), then one also must require that the characteristic exponent corresponding to the y_j direction for each such limit cycle is positive, i.e.,

$$(5) \qquad \int_0^\omega [-s_i(0) + c_i p_i(\hat{\varphi}_j(t), \hat{\psi}_j(t))]\, dt > 0,$$

where ω is the period and $(\hat{\varphi}_j, \hat{\psi}_j)$ parameterizes the limit cycle in the $x - y_j$ plane (see [**16**] for criteria for unique limit cycles). If there are more than a finite number of limit cycles, then persistence cannot be proved.

We illustrate the above results with an example. As in all our examples, the parameters are chosen to represent feasibility and are not necessarily related to any actual biological interactions.

Consider the system

$$\dot{x} = x(2 - x) - xy_1\left(1 + \frac{3}{2}y_2\right) - xy_2\left(1 + \frac{3}{2}y_1\right)$$

$$\dot{y}_1 = y_1\left(-\frac{3}{2} + x\left(1 + \frac{3}{2}y_2\right)\right)$$

$$\dot{y}_2 = y_2\left(-\frac{3}{2} + x\left(1 + \frac{3}{2}y_1\right)\right)$$

$$x(0) \geq 0, \quad y_i(0) \geq 0, \quad i = 1, 2.$$

The nonnegative equilibria can be found as $E_0(0,0,0)$, $E_k(2,0,0)$, $E_1(3/2, 1/2, 0)$, $E_2(3/2, 0, 1/2)$ and $E^*(1, 1/3, 1/3)$. Computing the inequality in (4), we get $-s_i(0) + c_i p_i(\hat{x}_j, \hat{y}_j) = -3/2 + (3/2)(5/4) > 0$, $i = 1, 2$, so that the system persists.

The variational matrix about E^* is given by

$$M^* = \begin{bmatrix} -1 & -2 & -2 \\ \frac{1}{2} & 0 & \frac{1}{2} \\ \frac{1}{2} & \frac{1}{2} & 0 \end{bmatrix},$$

leading to the characteristic equation for the eigenvalues,

$$\lambda^3 + \lambda^2 + \frac{7}{4}\lambda + \frac{3}{4} = 0,$$

which by Routh-Hurwitz criteria has all eigenvalues with negative real parts.

Here we see that the effect of the mutualism is to preserve the existence of both predators.

5.   The facultative-obligate case.   We now suppose that the mutualism is obligate for one of the predators and facultative for the other. The mutualism will be obligate for y_1, if

(6a)
$$\lim_{x \to \infty} p_1(x, 0) \leq \frac{s_1(0)}{c_1},$$

or

(6b) $$p_1(\tilde{x}_1, 0) = \frac{s_1(0)}{c_1} \quad \text{and} \quad K \leq \tilde{x}_1.$$

It will be obligate for y_2 if

(7a) $$\lim_{x \to \infty} p_2(x_2, 0) \leq \frac{s_2(0)}{c_2}$$

or

(7b) $$p_2(\tilde{x}_2, 0) = \frac{s_2(0)}{c_2} \quad \text{and} \quad K \leq \tilde{x}_2.$$

We will analyze the case where the mutualism is obligate for y_1, i.e., (6) holds but (7) fails. The other case is analyzed similarly.

In this case there will be no equilibrium in the interior of the nonnegative $x - y_1$ quadrant, i.e., $\widehat{E}_1$ fails to exist. Thus, the only boundary equilibria will be E_0, E_K and $\widehat{E}_2$.

E_0 is stable locally in the y_1 and y_2 directions and unstable locally in the x direction. E_K is stable locally in the x and y_1 directions and unstable locally in the y_2 direction. Either $\widehat{E}_2$ is globally stable in the $x - y_2$ plane with respect to initial conditions in the interior of the positive quadrant in this plane, or there is an outermost limit cycle lying in this quadrant, asymptotically stable from the outside. If $\widehat{E}_2$ is asymptotically stable in the $x - y_2$ plane, then we require (4) to be satisfied with $i = 1$, $j = 2$. If $\widehat{E}_2$ is unstable in the $x - y_2$ plane, there must exist a stable limit cycle. For each stable limit cycle, we assume (5) is satisfied with $i = 1$, $j = 2$. Hence, any equilibrium or limit cycle which is asymptotically stable in the $x - y_2$ plane will be unstable locally in the y_1 direction.

Since E_K is asymptotically stable locally in the y_1 direction, in the $x - y_1$ plane, y_1 goes to extinction. However, the following result provides conditions for the reversal of outcome, i.e., persistence, due to the mutualism between y_1 and y_2.

Theorem 5.1. *Let all the assumptions of this section hold, in particular those just enunciated on $\widehat{E}_2$ and any limit cycles surrounding it. Then system (1) is persistent, i.e., $\liminf_{t \geq \infty} x(t) > 0$, $\liminf_{t \to \infty} y_i(t) > 0$, $i = 1, 2$, provided $x_0, y_{i0} > 0$, $i = 1, 2$.*

The proof is similar to proofs of persistence as mentioned in Section 3 and will not be given in detail. By the results in [**3**], in the case of persistence, E^* must exist.

To illustrate the above results, we consider the system

$$\dot{x} = x(2 - x) - xy_1\left(1 + \frac{5}{2}y_2\right) - xy_2\left(1 + \frac{5}{2}y_1\right)$$

$$\dot{y}_1 = y_1\left(-2 + x\left(1 + \frac{5}{2}y_2\right)\right)$$

$$\dot{y}_2 = y_2\left(-\frac{3}{2} + x\left(1 + \frac{5}{2}y_1\right)\right) \quad x(0) \geq 0, \quad y_i(0) \geq 0.$$

The nonnegative equilibria are $E_0(0,0,0)$, $E_K(2,0,0)$, $\widehat{E}_2(3/2,0,1/2)$ and $E^*(1,1/5,2/5)$. $\widehat{E}_1$ does not exist. Inequalities (4) become $-s_1(0) + c_1p_1(\widehat{x}_2, \widehat{y}_2) = -2 + (3/2)(1 + (5/2) \cdot (1/2)) = (11/8) > 0$, and so persistence occurs.

The variational matrix about E^* is

$$M^* = \begin{bmatrix} -1 & -3 & -2 \\ \frac{2}{5} & 0 & \frac{1}{2} \\ \frac{3}{5} & 1 & 0 \end{bmatrix},$$

leading to the characteristic equation $\lambda^3 + \lambda^2 + (19/10)\lambda + (6/5) = 0$, which again by the Routh-Hurwitz criteria, has all the roots (i.e., eigenvalues) with negative real parts.

Here we see that, due to the mutualism, y_1 now persists instead of going extinct.

6. The obligate case. In this section we assume that neither $\widehat{E}_1$ nor $\widehat{E}_2$ exists. Then since E_K is now asymptotically stable, persistence with respect to the coordinate axes and planes is impossible. Notwithstanding, we will derive criteria for there to exist either an asymptotically stable interior equilibrium or a stable limit cycle. Of course, this reversal of outcome of extinction of the predators to positive coexistence is due to the mutualism.

First of all, $E^*(x^*, y_1^*, y_2^*)$ exists if and only if the algebraic system

(8a) $$xg(x) - y_1 p_1(x, y_2) - y_2 p_2(x, y_1) = 0$$

(8b) $$-s_1(y_1) + c_1 p_1(x, y_2) = 0$$

(8c) $$-s_2(y_2) + c_2 p_2(x, y_1) = 0$$

has a positive solution (x^*, y_1^*, y_2^*). Note that in the case that s_1 and s_2 are constant, since $p_i(x, y_j)$ are increasing functions of both variables, if $\lim_{\substack{x \to \infty \\ y_j \to \infty}} p_i(x, y_j) > (s_i/c_i)$, $i = 1, 2$, $j \neq i$, then y_j, $j = 1, 2$, can be solved from equations (8b), (8c) as functions of x, i.e., there exists $\overline{X}$, $0 \leq \overline{X} < \infty$, such that for each $x > \overline{X}$, there exists $\overline{Y}_j$, $0 < \overline{Y}_j < \infty$, such that $-s_i + c_i p_i(x, y_j) = 0$ for some $y_j > \overline{Y}_j$.

In general we suppose that equations (8b), (8c) can be solved for y_1 and y_2 as positive functions of x, say $y_1 = \varphi_1(x)$, $y_2 = \varphi_2(x)$ valid on $x \geq \overline{X}$. Then, upon substitution into equation (8a), we obtain

(9) $$xg(x) - \varphi_1(x)p_1(x, \varphi_2(x)) - \varphi_2(x)p_2(x, \varphi_1(x)) = 0.$$

Equation (9) has $x = 0$ as a solution. If there is a positive solution x^*, $0 < x^* < K$, then E^* exists, where $y_i^* = \varphi_i(x^*)$, $i = 1, 2$. E^* may not be unique.

If E^* is unstable, it may be the case that all predators go extinct, or that there is a positive stable limit cycle surrounding it. If, however, E^* is asymptotically stable, then there is a coexistence region enclosing E^*.

To test the stability of E^*, we compute the variational matrix of system (1) about E^*, which is

$$M^* = \begin{bmatrix} H^* & -L_i^* & -L_2^* \\ c_1 y_1^* p_x^* & -y_1^* s_1'^* & c_1 y_1^* p_{1y_2}^* \\ c_2 y_2^* p_{2x}^* & c_2 y_2^* p_{2y_1}^* & -y_2^* s_2'^* \end{bmatrix},$$

where

$$H^* = g^* + x^* g'^* - y_1^* p_{1x}^* - y_2^* p_{2x}^*$$

$$L_1^* = \frac{s_1^*}{c_1} + y_2^* p_{2y_2}^*$$

$$L_2^* = \frac{s_2^*}{c_2} + y_1^* p_{1y_1}^*,$$

and

$$p_{ix}^* = \frac{\partial p_i}{\partial x}(x^*, y_j^*), \quad \text{etc.}$$

We now need to compute the eigenvalues of M^*, which are given as solutions to the equation $\det(\lambda I - M^*) = 0$.

Expanding this determinant we get $\det(\lambda I - M^*) = P(\lambda)$, where $P(\lambda) = \lambda^3 + a_1\lambda^2 + a_2\lambda + a_3$, where

$$
\begin{aligned}
a_1 &= y_1^* s_1'^* + y_2^* s_2'^* - H^* \\
a_2 &= y_1^* y_2^* (s_1'^* s_2'^* - c_1 c_2 p_{1y_1}^* p_{2y_2}^*) + y_1^* (c_1 p_{1x}^* L_1^* - s_1'^* H^*) \\
&\quad + y_2^* (c_2 p_{2x}^* L_2^* - s_2'^* H^*) \\
a_3 &= y_1^* y_2^* [c_1 p_{1x}^* s_2'^* L_1^* + c_2 p_{2x}^* s_1'^* L_2^* - s_1'^* s_2'^* H^* \\
&\quad + c_1 c_2 (p_{1x}^* p_{2y_1}^* L_2^* + p_{1y_2}^* p_{2x}^* L_1^* + p_{1y_2}^* p_{2y_1}^* H^*)].
\end{aligned}
$$

Then the Routh-Hurwitz criteria for all roots of $P(\lambda)$ to have negative real parts are $a_1 > 0$, $a_2 > 0$, $a_3 > 0$, $a_1 a_2 > a_3$.

Note that in the special case that s_1 and s_2 are constants, we get

$$
\begin{aligned}
a_1 &= -H^* \\
a_2 &= c_1 p_{1x}^* L_1^* + c_2 P_{2x}^* L_2^* - c_1 c_2 y_1^* y_2^* p_{1y_2}^* p_{2y_1}^* \\
a_3 &= c_1 c_2 y_1^* y_2^* (p_{1x}^* p_{2y_1}^* L_2^* + p_{1y_2}^* p_{2x}^* L_1^* + p_{1y_2}^* p_{2y_1}^* H^*).
\end{aligned}
$$

From this, we see that a necessary condition for asymptotic stability of E^* is that $H^* < 0$.

Even in the simpler case, the criteria for asymptotic stability of E^*, representing a reversal of outcome, are complicated.

If $a_1 > 0$, $a_2 > 0$, $a_3 > 0$, then the stability of E^* rests with $a_1 a_2 - a_3$. If $a_1 a_2 - a_3 > 0$, then E^* is stable, whereas if $a_1 a_2 - a_3 < 0$, then E^* is unstable.

We now show that a Hopf bifurcation is possible. Let

$$\varepsilon = a_1 a_2 - a_3.$$

As ε passes through $\varepsilon = 0$ from positive to negative, the stability changes from stable to unstable with $\text{Re}(\text{eigenvalues})|_{\varepsilon=0} = 0$. If

$(d\mathrm{Re}\,(\lambda)/d\varepsilon)|_{\varepsilon=0} \neq 0$, a Hopf bifurcation occurs (otherwise a more general bifurcation may occur). This is demonstrated in the following example.

We consider the system with a parameter μ

$$\dot{x} = x(2-x) - xy_1(1+4y_2) - xy_2(1+4y_1)$$
$$\dot{y}_1 = \mu y_1(-2 + x(1+4y_2))$$
$$\dot{y}_2 = \mu y_2(-2 + x(1+4y_1)).$$

The nonnegative equilibria are $E_0(0,0,0)$, $E_K(2,0,0)$ and $E^*(1,1/4,1/4)$. The variational matrix about E^* is

$$M^* = \begin{bmatrix} -1 & -3 & -3 \\ \frac{\mu}{2} & 0 & \mu \\ \frac{\mu}{2} & \mu & 0 \end{bmatrix},$$

giving the characteristic equation $\lambda^3 + \lambda^2 + (3\mu - \mu^2)\lambda + 2\mu^2 = 0$. Hence $\varepsilon = a_1 a_2 - a_3 = 3\mu - \mu^2 - 2\mu^2 = 3\mu(1-\mu)$. Note that if $\mu \lesseqgtr 1$, then $\varepsilon \lesseqgtr 0$. Hence we may take μ as the bifurcation parameter and the critical value for bifurcation to be $\mu = 1$. Note, however, that the condition for obligate mutualism is satisfied since (7) is satisfied.

A straightforward calculation shows that, if $\lambda(\mu) = \alpha(\mu) + i\beta(\mu)$, then $(d\alpha(1)/d\mu) = 1/2 \neq 0$, and so a Hopf bifurcation occurs at $\mu = 1$. Hence, for $\mu > 1$, but close to 1, the system is obligate, and there is a stable limit cycle surrounding E^*, showing a reversal of outcome.

7. Discussion. In this paper we were concerned about persistence and extinction of predator populations. There are many factors which could contribute to the survival of such populations, without which they may go extinct. Such factors may be environmental change, diffusion, or cooperation, for example. Here we have focused on the cooperation aspect.

The fact that there are examples in nature of populations of two different species cooperating in hunting the same prey is of great interest in itself, since most predator populations would compete rather than hunt (wolves and Canada lynx on snowshoe hares, e.g., in Newfoundland).

In the first example cited in the introduction, the prey normally hid deep within the coral reefs where they are inaccessible to the predatory fish. Without the cooperation, there would be a significant reduction in the food available to the predators.

Here we have modeled such a system. The most interesting case is the case where a reversal of outcome is possible: extinction of one or both predator populations in the absence of mutualism and survival (at least locally) with mutualism present in sufficient strength.

One flaw in the coral reef model is that the environment is "lumped" into a single uniform patch. Whereas this is true for the predators, it is not true for the prey. Hence, in future work, we intend to introduce diffusion in the prey equation and analyze the modified system.

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SCHOOL OF MATHEMATICAL SCIENCES, SWINBURNE UNIVERSITY OF TECHNOLOGY, HAWTHORNE, VICTORIA, AUSTRALIA 3122
and
APPLIED MATHEMATICS INSTITUTE, DEPARTMENT OF MATHEMATICAL SCIENCES, UNIVERSITY OF ALBERTA, EDMONTON, ALBERTA, CANADA T6G 2G1
E-mail address: `hfreedman@math.ualberta.ca`

DEPARTMENT OF MATHEMATICS, DYALBAGH EDUCATIONAL INSTITUTE, DYALBAGH, AGRA 282005, U.P. INDIA
E-mail address: `drravinderkumar@yahoo.com`

SCHOOL OF MATHEMATICAL SCIENCES, SWINBURNE UNIVERSITY OF TECHNOLOGY, HAWTHORNE, VICTORIA, AUSTRALIA 3122

SCHOOL OF MATHEMATICAL SCIENCES, SWINBURNE UNIVERSITY OF TECHNOLOGY, HAWTHORNE, VICTORIA, AUSTRALIA 3122