

INTERACTIONS LEADING TO PERSISTENCE IN PREDATOR–PREY SYSTEMS WITH GROUP DEFENCE

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In previous work (Freedman and Wolkowicz, 1986; *Bull. math. Biol.* **48**, 493–508) it was shown that in a predator–prey system where the prey population exhibits group defence, it is possible that enrichment of the environment could lead to extinction of the predator population.

In this paper a third population is introduced and criteria are derived under which persistence of all populations will occur. In particular, criteria for a superpredator and for a competitor to stabilize the system in the sense of persistence are analyzed.

1. Introduction. In a previous paper, Freedman and Wolkowicz (1986) considered a predator–prey system in which the prey population exhibited group defence. Specific examples to illustrate group defence were musk ox (Tener, 1965) for which lone oxen or pairs are often successfully attacked by wolves, but groups of six or more are rarely if ever successfully attacked; prey identification by predators which cannot identify their prey as such when they swarm as opposed to flying individually (Holmes and Bethel, 1972); microbial toxicity by some species of microbes competing with others in a chemostat so that if the amount of toxicity is sufficient due to the size of the population, competitive outcome may be reversed (Yang and Humphrey, 1975). Group defence by yellow-hooded blackbirds against parasitism by cowbirds has been indicated by May and Robinson (1985). Further to this work Wolkowicz (1988) has looked at bifurcation problems in models with group defence and Mischaikow and Wolkowicz (1986) have indicated how connection matrices can be utilized in analyzing predator–prey models with group defence.

A consequence of the analysis in Freedman and Wolkowicz (1986) is that in the case of no mutual interference, if the carrying capacity of the prey population is sufficiently large, the predator population is almost always

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driven to extinction. Biologically, this is intuitive, since the environment is such that the prey population can increase to the point where group defence prevents the predator population from increasing at any level. This is also related to the paradox of enrichment as described in Rosenzweig (1971).

The overriding theme of that part of the above-mentioned paper is that group defence can lead to extinction. Yet in nature the predators of prey exhibiting group defence do not seem to go extinct. There could be many reasons why this is so. One of these was considered in Freedman and Wolkowicz (1986), namely mutual interference among predators.

In the present paper, we consider another way in which the predator is prevented from heading to extinction, namely, through interactions of the predator-prey system with a third population. This is a reasonable situation to consider since rarely will a predator-prey system exist in nature in isolation.

The techniques for examining the three-species interaction models will be similar to those utilized in Freedman and Waltman (1984, 1985) and Freedman and So (1985). We will define persistence in dynamical systems and derive criteria for such persistence to hold in our models. The definition of persistence (and uniform persistence) defined in the text will intuitively agree with a biological interpretation of persistence, namely the survival of all populations in an interacting community.

A third population could interact with the predator-prey system in many ways. After a general discussion, we will consider two specific ways, namely by forming a food chain, and by competition with the prey. Both of these are discussed in Freedman and Waltman (1984), but without group defence and with restricting all boundary invariant sets to be equilibria.

The organization of the remainder of this paper is as follows. In the next section we will present the model and the definition of persistence. In Section 3 we present our main results followed by specific applications to "food chain" and "one predator-two competing prey" systems in Section 4. We finish with a discussion in Section 5. The proof of our main theorem is deferred to the Appendix.

2. The Model. We take as a model of our three interacting populations the system of autonomous Kolmogorov-type differential equations

$$\begin{aligned} \dot{x} &= xF(x, y, z) \\ \dot{y} &= yG(x, y, z) \\ \dot{z} &= zH(x, y, z) \\ x(0) = x_0 \geq 0, y(0) = y_0 \geq 0, z(0) = z_0 \geq 0 \\ \cdot &= \frac{d}{dt}, x, y, z \geq 0. \end{aligned} \tag{2.1}$$

Simultaneously, we will consider the submodel

$$\begin{aligned} \dot{u} &= uf(u, v) \\ \dot{v} &= vg(u, v), \\ u(0) &= u_0 \geq 0, v(0) = v_0 \geq 0, \end{aligned} \tag{2.2}$$

where

$$f(u, v) = F(u, v, 0), g(u, v) = G(u, v, 0). \tag{2.3}$$

We think of $x(t)$ as a prey population, and $y(t)$ as its predator population. $z(t)$ represents a third population which interacts with one or both of x and y . Simultaneously, system (2.2) represents the predator–prey subsystem by setting $z(t) \equiv 0$ in (2.1).

2.1. Hypotheses. We impose hypotheses which simulate our requirements. The first hypothesis is a motherhood hypothesis for ODE models.

(H1): F, G, H are sufficiently smooth so that solutions to initial value problems of (2.1) exist uniquely, and are continuable for all positive t .

(H2): $F(0, 0, 0) > 0$; there exists a unique $K > 0$ such that $F(K, 0, 0) = 0$; there exists a unique $C > 0$ such that $F(0, C, 0) = 0$.

The above hypothesis may be interpreted as stating that for small populations, in the absence of other interactions, the prey population grows in time. However, there is a carrying capacity of the environment beyond which the prey population will decline. Further, for small values of x , but large values of y , the x population will decline.

(H3): $F_y(x, y, z) \leq 0$. Since y is a predator of x , the larger the y population, the smaller the specific growth rate of x .

(H4): $G(0, y, 0) < 0$; there exists $B(y) \geq A(y) > 0$ such that $B(0) > A(0) > 0$ and $G(A(y), y, 0) = 0, G(B(y), y, 0) = 0, 0 \leq y \leq y_M \leq \infty$.

For small values of x , the predator population declines. For fixed positive predator values, possibly not too large, there is a range of prey values for which the predator population will increase. However, if the population is too large, the predator population will once more decrease (group defence effect). $A(y)$ and $B(y)$ are the predator isoclines. If there were no group defence effects, $B(y)$ would not exist at all. $A(y)$ is the isocline corresponding to $dy/dt = 0$ when $p(x)$ is increasing and $B(y)$ to $dy/dt = 0$ when $p(x)$ is decreasing.

(H5): There exists $D > 0$ such that $A(0) \leq D \leq B(0)$, and

$$\begin{aligned} G_x(x, 0, 0) &> 0, \quad 0 \leq x < D \\ &< 0, \quad D < x. \end{aligned}$$

This once more shows the group defence effect.

(H6): $G_y(x, y, 0) \leq 0$.

A larger predator population will decrease its specific growth rate due to intraspecific competition for its food.

The hypotheses relating to F_z , G_z and H are deferred to later on in the text, since they are related to boundedness and persistence criteria, as well as to the type of interactions between z and x, y .

Note that if $G_y(x, y, 0) = 0$, then $A(y) \equiv A(0)$, $B(y) \equiv B(0)$, $y_M = +\infty$ and $A(0) < D < B(0)$. If $G_y(x, y, 0) < 0$ on $\{(x, y): A(y) \leq x \leq B(y), 0 \leq y \leq y_M\}$, then $A(0) = B(0) = 0$.

2.2. Dissipativeness. In order to have a biologically realistic model, we will require system (2.1) to be dissipative. Dissipativeness may be interpreted as saying that in time all populations are uniformly limited by their environments. Hence we assume,

(H7): There exists $\alpha, \beta, \gamma > 0$ such that $\Omega(x_0, y_0, z_0) \subset \mathcal{A} = \{(x, y, z): 0 \leq x \leq \alpha, 0 \leq y \leq \beta, 0 \leq z \leq \gamma\}$ for all $x_0, y_0, z_0 \geq 0$, where $\Omega(x_0, y_0, z_0)$ is the omega limit set of the orbit initiating at (x_0, y_0, z_0) .

In specific cases (H7) may follow from other hypotheses.

2.3. Persistence. Let $N(t) > 0$ for $t \geq 0$. We say that $N(t)$ is *persistent* provided $\liminf_{t \rightarrow \infty} N(t) > 0$. A differential equation *exhibits persistence* provided all solutions with positive initial conditions are persistent.

A differential equation *exhibits uniform persistence* provided there exists $\delta > 0$ such that each solution $N(t)$ for which $N(0) > 0$ satisfies $N(t) > 0$ for $t > 0$ and $\liminf_{t \rightarrow \infty} N(t) \geq \delta$.

A system of differential equations in R^n exhibits (uniform) persistence provided each component of the solution is (uniformly) persistent.

These definitions agree with those used in Freedman and So (1985), Freedman and Waltman (1985) and Freedman and Wolkowicz (1986). Biologically, if the interactions between populations can be represented by a system of differential equations, then persistence of this system corresponds to the survival of all interacting populations.

2.4. The predator-prey submodel. For submodel (2.2), hypotheses (H1)–(H7) become as follows:

(h1): Existence, uniqueness and continuability of solutions of initial value problems for (2.2).

(h2): $f(0, 0) > 0$; there exists a unique $K > 0$ such that $f(K, 0) = 0$; there exists a unique $C > 0$ such that $f(0, C) = 0$.

(h3): $f_y(x, y) \leq 0$.

(h4): $g(0, y) < 0$; there exists $B(y) \geq A(y) > 0$ such that $B(0) > A(0)$ and $g(A(y), y) = 0, g(B(y), y) = 0, 0 \leq y \leq y_M \leq \infty$.

(h5): There exists $D > 0$ such that $A(0) \leq D \leq B(0)$ and

$$g_x(x, 0) > 0, \quad 0 \leq x < D$$

$$< 0, \quad D < x$$

(h6): $g_y(x, y) \leq 0$.

(h7): There exists $\alpha, \beta > 0$ such that $\Omega(x_0, y_0) \subset \mathcal{A}_0 = \{(x, y) : 0 \leq x \leq \alpha, 0 \leq y \leq \beta\}$ for all $x_0, y_0 \geq 0$. This follows automatically from hypotheses (h2)–(h6).

Using similar techniques of analysis as those used for the class of models in Freedman and Wolkowicz (a subset of the class of models considered here), under the above hypotheses it can be shown that there are two positive equilibria, (\bar{x}_1, \bar{y}_1) and (\bar{x}_2, \bar{y}_2) with $\bar{x}_1 < \bar{x}_2$. The first of these may be stable or unstable and there may be one or more limit cycles surrounding it. The second of them is always a saddle point. Now we state our next hypothesis, which is equivalent to the extinction case in group defence.

$$(H8) = (h8) \quad \bar{x}_2 < K.$$

Under assumption (h8) there is a set of positive measure of positive initial values of system (2.2) for which $\lim_{t \rightarrow \infty} (x(t), y(t)) = (K, 0)$, representing extinction of the predator population.

3. Persistence Results. In this section we analyze system (2.1), and obtain criteria for persistence. These criteria follow lines established in Freedman and Waltman (1984, 1985) and involve invariant sets located in the coordinate axes and planes.

3.1. Equilibria. In system (2.1) under hypotheses (H1)–(H7), certain equilibria always exist, while others may or may not exist. We consider all of these.

$E_0(0, 0, 0)$ and $E_K(K, 0, 0)$ always exist. There are no equilibria on the positive y -axis. However, there may or may not be an equilibrium of the form $E_L(0, 0, L)$ for some $L > 0$.

We have already established the existence of two equilibria in the interior of the positive x - y plane, $\bar{E}_1(\bar{x}_1, \bar{y}_1, 0)$ and $\bar{E}_2(\bar{x}_2, \bar{y}_2, 0)$. There may or may not be one or more equilibria in the interior of the positive x - z plane of the form $\hat{E}(\hat{x}, 0, \hat{y})$ and similarly for the y - z plane of the form $\tilde{E}(0, \tilde{y}, \tilde{z})$.

Finally there may or may not be one or more equilibria in the interior of the positive octant of the form $E^*(x^*, y^*, z^*)$. In Corollary 2 we establish criteria for such an equilibrium to exist.

3.2. *Stability of equilibria.* In order to discuss the local stability properties of the equilibria mentioned in the above subsection, we need to compute the variational matrix about all of these equilibria. If $E^0(x^0, y^0, z^0)$ is an equilibrium, then the equations

$$x^0 F(x^0, y^0, z^0) = y^0 G(x^0, y^0, z^0) = z^0 H(x^0, y^0, z^0) = 0 \tag{3.1}$$

holds. The variational matrix about E^0 is given by

$$M^0 = \begin{bmatrix} x^0 F_x + F & x^0 F_y & x^0 F_z \\ y^0 G_x & y^0 G_y + G & y^0 G_z \\ z^0 H_x & z^0 H_y & z^0 H_z + H \end{bmatrix}, \tag{3.2}$$

where all functions are evaluated at (x^0, y^0, z^0) .

Taking the equilibria in order and utilizing appropriate corresponding notations for M^0 , we get

$$M_0 = \begin{bmatrix} F(0, 0, 0) & 0 & 0 \\ 0 & G(0, 0, 0) & 0 \\ 0 & 0 & H(0, 0, 0) \end{bmatrix}$$

$$M_K = \begin{bmatrix} KF_x(K, 0, 0) & KF_y(K, 0, 0) & KF_z(K, 0, 0) \\ 0 & G(K, 0, 0) & 0 \\ 0 & 0 & H(K, 0, 0) \end{bmatrix}$$

$$M_L = \begin{bmatrix} F(0, 0, L) & 0 & 0 \\ 0 & G(0, 0, L) & 0 \\ LH_x(0, 0, L) & LH_y(0, 0, L) & LH_z(0, 0, L) \end{bmatrix}$$

$$\bar{M}_i = \begin{bmatrix} \bar{x}_i F_x(\bar{x}_i, \bar{y}_i, 0) & \bar{x}_i F_y(\bar{x}_i, \bar{y}_i, 0) & \bar{x}_i F_z(\bar{x}_i, \bar{y}_i, 0) \\ \bar{y}_i G_x(\bar{x}_i, \bar{y}_i, 0) & \bar{y}_i G_y(\bar{x}_i, \bar{y}_i, 0) & \bar{y}_i G_z(\bar{x}_i, \bar{y}_i, 0) \\ 0 & 0 & H(\bar{x}_i, \bar{y}_i, 0) \end{bmatrix}, i = 1, 2$$

$$\begin{aligned}
 \hat{M} &= \begin{bmatrix} \hat{x}F_x(\hat{x}, 0, \hat{z}) & \hat{x}F_y(\hat{x}, 0, \hat{z}) & \hat{x}F_z(\hat{x}, 0, \hat{z}) \\ 0 & G(\hat{x}, 0, \hat{z}) & 0 \\ \hat{z}H_x(\hat{x}, 0, \hat{z}) & \hat{z}H_y(\hat{x}, 0, \hat{z}) & \hat{z}H_z(\hat{x}, 0, \hat{z}) \end{bmatrix} \\
 \tilde{M} &= \begin{bmatrix} F(0, \tilde{y}, \tilde{z}) & 0 & 0 \\ \tilde{y}G_x(0, \tilde{y}, \tilde{z}) & \tilde{y}G_y(0, \tilde{y}, \tilde{z}) & \tilde{y}G_z(0, \tilde{y}, \tilde{z}) \\ \tilde{z}H_x(0, \tilde{y}, \tilde{z}) & \tilde{z}H_y(0, \tilde{y}, \tilde{z}) & \tilde{z}H_z(0, \tilde{y}, \tilde{z}) \end{bmatrix}. \tag{3.3}
 \end{aligned}$$

To obtain M^* , simply substitute (x^*, y^*, z^*) for (x^0, y^0, z^0) in M^0 .

From the hypotheses of our model, we can say the following. E_0 is a saddle point since $F(0, 0, 0) > 0$ and $G(0, 0, 0) < 0$. The dimensions of its stable and unstable manifolds depend on $H(0, 0, 0)$.

From (H2) and (H8), $F_x(K, 0, 0) < 0$, $G(K, 0, 0) < 0$, and hence E_K is asymptotically stable in the plane, corresponding to extinction of the predator population in model (2.2) for a large set of initial values. Further, E_K will be stable or unstable in the z direction as $H(K, 0, 0)$ is negative or positive, respectively.

Nothing can be said about the stability of E_L if it exists until further hypotheses are imposed in specific cases.

As previously mentioned, \bar{E}_1 can be stable or unstable in the x - y plane. However, \bar{E}_2 is a saddle point in this plane. $\bar{E}_i, i = 1, 2$, is stable or unstable in the z direction depending on whether $H(\bar{x}_i, \bar{y}_i, 0)$ is negative or positive, respectively.

At this time nothing can be said about the stability characteristics of \hat{E} , if it exists in the x - y plane. However, clearly \hat{E} is stable or unstable in the y direction according to whether $G(\hat{x}, 0, \hat{z})$ is negative or positive, respectively.

Similarly \tilde{E} if it exists is stable or unstable in the x direction according to whether $F(0, \tilde{y}, \tilde{z})$ is negative or positive, respectively.

Nothing can be said for this general model about the stability of E^* , should it exist.

3.3. Periodic orbits. There may be one or more periodic orbits in any of the coordinate planes. Consider first the x - y plane. As already mentioned, if there is a periodic orbit in this plane, it must surround \bar{E}_1 . Let $x = \varphi(t), y = \psi(t), z = 0$ be a parametrization of such periodic orbit if it exists. Then except in critical cases, the stability of this periodic orbit is given by Floquet multipliers of the variational system.

$$\Phi(t) = P(t)\Phi(0), \quad \Phi(0) = I, \tag{3.4}$$

where $P(t)$ is the matrix $(p_{ij}(t))_{3 \times 3}$, I is the identity matrix, and

$$\begin{aligned}
 p_{11}(t) &= \varphi(t)F_x(\varphi(t), \psi(t), 0) + F(\varphi(t), \psi(t), 0) \\
 p_{12}(t) &= \varphi(t)F_y(\varphi(t), \psi(t), 0) \\
 p_{13}(t) &= \varphi(t)F_z(\varphi(t), \psi(t), 0) \\
 p_{21}(t) &= \psi(t)G_x(\varphi(t), \psi(t), 0) \\
 p_{22}(t) &= \psi(t)G_y(\varphi(t), \psi(t), 0) + G(\varphi(t), \psi(t), 0) \\
 p_{23}(t) &= \psi(t)G_z(\varphi(t), \psi(t), 0) \\
 p_{31}(t) &= p_{32}(t) = 0 \\
 p_{33}(t) &= H(\varphi(t), \varphi(t), 0).
 \end{aligned} \tag{3.5}$$

Let ω be the period of the periodic solution. Then, clearly, the Floquet multiplier corresponding to the z direction is given by $\exp\{\omega^{-1} \int_0^\omega H(\varphi(t), \psi(t), 0) dt\}$. Hence the periodic solution is stable or unstable in the z direction according to whether $\int_0^\omega H(\varphi(t), \psi(t), 0) dt$ is negative or positive, respectively.

Similarly, if \hat{E} exists and there are one or more periodic solutions in the x - z plane surrounding it with parametrization $x = \hat{\varphi}(t)$, $y = 0$, $z = \hat{\zeta}(t)$ and period $\hat{\omega}$, then this periodic solution is stable or unstable in the y directions according to whether $\int_0^{\hat{\omega}} G(\hat{\varphi}(t), 0, \hat{\zeta}(t)) dt$ is negative or positive, respectively.

Finally, if \tilde{E} exists and there are one or more periodic solutions surrounding it in the y - z plane with parametrization $x = 0$, $y = \tilde{\psi}(t)$, $z = \tilde{\zeta}(t)$ and with period $\tilde{\omega}$, then the periodic solution is attracting or repelling in the x direction in accordance with $\int_0^{\tilde{\omega}} F(0, \tilde{\psi}(t), \tilde{\zeta}(t)) dt$ being negative or positive, respectively.

3.4. Acyclicity and isolatedness of invariant sets. In addition to equilibria and periodic orbits, there could occur other closed paths on the boundary of R_+^3 , namely homoclinic (Freedman and Wolkowicz, 1986) or heteroclinic (Freedman and Waltman, 1985) orbits. These are special cases of cyclic sets of invariant manifolds as defined in Butler *et al.* (1986) or Butler and Waltman (1986).

A closed invariant set \mathcal{M}_1 is said to be chained to a closed invariant set \mathcal{M}_2 if there exists a point u such that if $\mathcal{O}(u)$ is the orbit through u and $A(u)$, $\Omega(u)$ are the α - and ω limit sets of $\mathcal{O}(u)$ respectively, then $A(u) \cap \mathcal{M}_1 \neq \emptyset$ and $\Omega(u) \cap \mathcal{M}_2 \neq \emptyset$. In this case we say $\mathcal{M}_1 \rightarrow \mathcal{M}_2$. If $\mathcal{M}_1 \rightarrow \mathcal{M}_2 \rightarrow \dots \rightarrow \mathcal{M}_k$, we say that $\{\mathcal{M}_1, \dots, \mathcal{M}_k\}$ forms a chain. If $\mathcal{M}_k = \mathcal{M}_1$, then the chain forms a cycle. If no cycle exists in some set contained in our space, we say the set is acyclic.

In the case that there are closed invariant sets on the boundary which are connected to each other in a closed chain (see Butler *et al.*, 1986; or Butler and Waltman, 1986), persistence may or may not occur, and in any case if it occurs,

is extremely difficult to prove. In Butler and Waltman (1986) and Freedman and Waltman (1985) and the references therein, examples are given of nonpersistence in the case of such cyclicity. Hence we assume

(H9)=(h9): For system (2.1) (and hence (2.2)), the boundary of R_+^3 is acyclic.

Note that the above hypothesis precludes those cases from consideration where there is a homoclinic orbit in model (2.2).

It is possible that closed invariant sets on the boundary of R_+^3 are not isolated (as in certain Lotka-Volterra equations). If this occurs, it also presents a major problem in proving persistence by our techniques, and indeed is essential in the proof of the Butler-McGehee Lemma (Freedman and Waltman, 1984). Hence we further assume

(H10)=(h10): All closed invariant sets on the boundary of R_+^3 for system (2.1) (and hence for system (2.2)) are isolated on that boundary.

3.5. *Persistence criteria.* The main results of this paper are given in Theorem 1 and Corollary 2 which appear below.

THEOREM 1. *Let hypotheses (H1)–(H10) hold. Let E_L , if it exists, have a nontrivial strong unstable manifold. In addition let the following hold*

$$H(K, 0, 0) > 0 \tag{3.6a}$$

$$H(\bar{x}_i, \bar{y}_i, 0) > 0, \quad i = 1, 2 \tag{3.6b}$$

$$G(\hat{x}, 0, \hat{z}) > 0 \quad \text{for each } \hat{E} \text{ that exists} \tag{3.6c}$$

$$F(0, \tilde{y}, \tilde{z}) > 0 \quad \text{for each } \tilde{E} \text{ that exists.} \tag{3.6d}$$

Further, let

$$\int_0^\omega H(\varphi(t), \psi(t), 0) \, dt > 0 \tag{3.7a}$$

$$\int_0^{\hat{\omega}} G(\hat{\varphi}(t), 0, \hat{\zeta}(t)) \, dt > 0 \tag{3.7b}$$

$$\int_0^{\tilde{\omega}} F(0, \tilde{\psi}(t), \tilde{\zeta}(t)) \, dt > 0 \tag{3.7c}$$

provided that the appropriate corresponding planar periodic solution exists. Then system (2.1) exhibits persistence.

COROLLARY 2. *In addition to the hypotheses of Theorem 1, let all closed invariant sets in the boundary of R_+^3 be isolated with respect to the interior of R_+^3 . Then system (2.1) exhibits uniform persistence and E^* exists.*

The proofs of these are deferred to the Appendix.

Basically, Theorem 1 describes how the z population can aid the y (predator) population so that it survives. z must interact with x and y in such a way that no closed invariant set on the boundary can be an attractor with respect to any orbits initiating in the interior of R_+^3 , i.e. these closed invariant sets repel in the direction of the interior.

4. Examples. In this section we give two examples to illustrate how our theorem may be applied. The first example we consider will be the situation where $z(t)$ represents a population competing with $x(t)$. In the second example, $z(t)$ will form a food chain by predating on $y(t)$.

4.1. Persistence as a consequence of competition. In this example we think of $z(t)$ as representing a population which competes with $x(t)$. This will be represented through the following additional hypotheses on system (2.1) (also see Hutson, 1984).

(J1): $F_z(x, y, z) < 0$ when $x, z > 0$.

The larger the z population, the greater the competition effect on x .

(J2): $G_z(x, y, z) \geq 0$.

If $G_z(x, y, z) > 0$, then z is also a prey of y . If $G_z(x, y, z) \equiv 0$, then z and y do not interact directly.

(J3): $H(0, 0, 0) > 0$; there exists a unique $L > 0$ such that $H(0, 0, L) = 0$. $H_x(x, y, z) < 0$, $H_y(x, y, z) \leq 0$, $H_z(x, 0, z) < 0$ for $x, z > 0$.

In the absence of predation and competition, z is capable of growing to carrying capacity L . If $H_y > 0$ then z is a prey of y , and if $H_y \equiv 0$, then it is not.

For this model, since both $x(t)$ and $z(t)$ are self limiting through their carrying capacities, and since $y(t)$ is limited by $x(t)$ and possibly $z(t)$, hypothesis (H7) will be automatically satisfied.

We note that in the competitive x - z plane, there cannot be any nontrivial periodic solutions, so that (3.7b) is meaningless.

The requirement in Theorem 1 that $H(K, 0, 0) > 0$ holds implies that in the competitive x - y plane solutions initiating near $(K, 0, 0)$ are repelled into the interior of the plane, i.e. x cannot always outcompete z .

The condition that E_L be a saddle point requires that at least one of $F(0, 0, L) > 0$, $G(0, 0, L) > 0$ hold. If z is a prey of y , $G(0, 0, L) > 0$ may or may not hold. If z is not a prey of y , then $G(0, 0, L) = G(0, 0, 0) < 0$. If $F(0, 0, L) > 0$, then solutions initiating near $(0, 0, L)$ are repelled into the interior. Combining with the previous statements, we see that in this case there must exist an equilibrium of the type \hat{E} , which is asymptotically stable in the x - y plane. There may exist other equilibria of the type \hat{E} as well. At least one of these must then be a saddle point in the x - y plane.

4.2. *A food chain.* We consider the example where $z(t)$ is a predator of $y(t)$. In this case $z(t)$ must also predate on $x(t)$, for otherwise persistence would be impossible. The hypotheses, in addition to (H1)–(H10), are as follows (also see Rescigno and Jones, 1972).

(Q1): $F_z(x, y, z) < 0$ for $z > 0$.

$z(t)$ is a predator of $x(t)$.

(Q2): $G_z(x, y, z) < 0$ for $z > 0$.

$z(t)$ is a predator of $y(t)$.

(Q3): $H(0, y, z) < 0$, $H_x(x, y, z) > 0$, $H_y(x, y, z) > 0$, $H_z(x, y, z) \leq 0$.

Without the x population, neither y nor z can survive. However, increasing either x or y increases the growth rate of z . For fixed x and y , increasing z may increase its intraspecific competition for food which in turn may lead to a decrease in its growth rate.

Note that under hypotheses (Q1)–(Q3), E_L and \tilde{E} do not exist.

The requirement in Theorem 1 that $H(K, 0, 0) > 0$ implies that the z population can survive on the x population in the absence of the y population. This also implies that a unique (because of (Q1)–(Q3)) equilibrium of the type \hat{E} also exists. In other words, the x population exhibits effective group defence against the y -population, but not against the z population.

5. *Discussion.* In this paper we have considered a predator-prey system, where the prey population exhibits group defence against the predator population, and where the predator-prey system interacts with a third population in such a way that extinction of any population is prevented.

We have modelled our interacting populations by a system of autonomous ordinary differential equations. The hypotheses on this system simulate predator-prey behaviours with group defence (Freedman and Wolkowicz, 1986), where the predator cannot survive on the prey due to group defence effects in the absence of additional interactions.

The main theorem in subsection 3.5 gives additional conditions for persistence of all three populations. Most of these conditions state that invariant sets in the planes repel orbits initiating near them in the interior of R_+^3 . Biologically, this may be interpreted as saying that the third population can successfully invade a system where the other two are interacting in a closed environment.

Some of the conditions, such as acyclicity and isolatedness of closed invariant sets are for technical mathematical reasons, since without these conditions our techniques for proving persistence do not seem to work. No biological interpretations for these are available at this time.

However, the condition that $H(K, 0, 0) > 0$ is readily interpreted in terms of the interactions between the x population and the z population in the absence

of the y population. This condition implies that at carrying capacity, the prey can be successfully invaded by the z population.

One can easily see the role of z in its relation to the predator y . The predator cannot survive on the prey, not because there are too few prey, but rather because there are too many. It is then the role of the z population to bring the prey population down to a level where the group defence mechanism no longer is in effect.

This was illustrated by the two examples. In the first example the z population is a competitor with the prey for certain resources. The z population may itself be a prey of y and supply sufficient food for y to survive. If not, then z must outcompete x to the point where the x population level is lowered, but not so low that x goes extinct. In other words, as competitors, x and z must be capable of coexisting in the absence of y . This, of course, can occur even in Lotka–Volterra models of coexistence.

In the second example, the z population is a predator of both the x and y populations. The y population is in the anomalous situation of requiring z for its own survival, but at the same time must pay the cost by having z predate on it as well. Hence z is at the same time a predator and obligate mutualist of y .

These two examples indicate only two interpretations of the z population. There are many other possible interpretations. z could be a pure mutualist of y , or z could predate on x and not interact directly with y , for instance.

This paper deals with survival of the predator population as a consequence of the predator–prey system interacting with a third population. Another mechanism leading to survival of the predator population was discussed in Freedman and Wolkowicz (1986), namely mutual interference among predators.

There could be other mechanisms leading to predator survival. It may be that the predator–prey system will interact with several other populations, leading to predator survival. Possible dispersal among patches in a heterogeneous environment or the introduction of time delays will lead to predator survival. We leave investigations of these other possibilities to future work.

APPENDIX

In this appendix we prove Theorem 1 and Corollary 2. First we require a lemma.

LEMMA (BUTLER–MCGEREE). *Let $P_0 \in \mathcal{R}^n$, $\mathcal{O}(P_0)$ be the orbit through P_0 , $\Omega(P_0)$ be the omega limit set of $\mathcal{O}(P_0)$. Let \mathcal{M} be a compact, isolated invariant set in \mathcal{R}^n , and let $W^+(\mathcal{M})$ ($W^-(\mathcal{M})$) be the strong stable (unstable) manifold of \mathcal{M} and $W_w^+(\mathcal{M})$ ($W_w^-(\mathcal{M})$) be the weak stable (unstable) manifold of \mathcal{M} . Suppose that $W_w^+(\mathcal{M}) \setminus W^+(\mathcal{M}) \cap \Omega(P_0) \neq \emptyset$ ($W_w^-(\mathcal{M}) \setminus W^-(\mathcal{M}) \cap \Omega(P_0) \neq \emptyset$) then $W^+(\mathcal{M}) \setminus \mathcal{M} \cap \Omega(P_0) \neq \emptyset$ and $W^-(\mathcal{M}) \setminus \mathcal{M} \cap \Omega(P_0) \neq \emptyset$.*

The proof may be found in Butler and Waltman (1986).

Proof of Theorem 1. We first note that the dissipativeness of system (2.1) implies that if $P_0 \in R_+^3$, the nonnegative orthant, then $\Omega(P_0)$ is contained in a compact set. In addition, we note that the coordinate planes are invariant, and by isolatedness, there are at most a finite number of closed, finite invariant sets in the coordinate planes.

Now let \mathcal{M}_1 be a compact invariant set in the coordinate planes. Further, suppose $\mathcal{M}_1 \cap \Omega(P_0) \neq \emptyset$ for some $P_0 \in \text{int } R_+^3$. By hypotheses (3.6) and (3.7), $\mathcal{O}(P_0)$ cannot approach \mathcal{M}_1 monotonically, and hence $W_w^+(\mathcal{M}_1) \setminus W^+(\mathcal{M}_1) \cap \Omega(P_0) \neq \emptyset$. Now by the Lemma, $W^+(\mathcal{M}_1) \setminus \mathcal{M}_1 \cap \Omega(P_0) \neq \emptyset$.

Hence there is a point P_1 such that $P_1 \in W^+(\mathcal{M}_1) \setminus \mathcal{M}_1$ and $P_1 \in \Omega(P_0)$. By the properties of omega limit sets of dynamical systems, $\text{cl } \mathcal{O}(P_1) \subset \Omega(P_0)$. If $\text{cl } \mathcal{O}(P_1)$ is unbounded, we have a contradiction. If not there must exist an invariant set in the coordinate planes, \mathcal{M}_2 such that $\mathcal{M}_2 \rightarrow \mathcal{M}_1$ and $\mathcal{M}_2 \cap \Omega(P_0) \neq \emptyset$. Repeating the arguments for \mathcal{M}_1 , we conclude the existence of $\mathcal{M}_3, \mathcal{M}_4, \dots$. But this must terminate after a finite number of times, since there are only a finite number of such invariant sets in the coordinate planes and they are acyclic. Hence there is a k such that $P_k \in W^+(\mathcal{M}_k) \setminus \mathcal{M}_k \cap \Omega(P_0)$ and $\text{cl } \mathcal{O}(P_k)$ is unbounded, contradicting the statement that $\mathcal{M}_1 \cap \Omega(P_0) \neq \emptyset$.

Since $\Omega(Q)$ is an invariant set when $Q \in \partial R_+^3$, then $\Omega(P_0) \cap \partial R_+^3 = \emptyset$ and system (2.1) is persistent.

Proof of Corollary 2. By assumption of this Corollary, system (2.1) now satisfies all the assumptions of Theorem of Butler *et al.* (1986), from which the Corollary follows.

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