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PERMANENCE IN SOME DIFFUSIVE LOTKA-VOLTERRA MODELS FOR THREE INTERACTING SPECIES.

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ABSTRACT: We obtain conditions for permanence (i.e. uniform persistence) in some diffusive Lotka-Volterra systems modeling three interacting species. Some of the results are based on the Hale-Waltman acyclicity theorem, others on average Lyapunov functions. All the results on permanence use hypotheses involving the signs of the principal eigenvalues of associated linear elliptic operators.

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1. INTRODUCTION.

A fundamental problem in biology is to determine conditions under which all species in a system of interacting species survive in the long term. The classical approach has often been to consider the global or asymptotic stability of an interior equilibrium. However, this places inappropriately strong restrictions on the asymptotic behavior of orbits, and fairly recently there has been a considerable amount of discussion of an alternative criterion, that of permanence (or uniform persistence), which allows arbitrary asymptotic behavior so long as all species densities are in a certain uniform sense eventually bounded away from zero; for background information see [22], [27], and [42]. The terms permanence and uniform persistence are both used to describe this concept, with permanence more often used by Europeans and uniform persistence more often used by North Americans. We have used the term permanence here to be consistent with earlier work we have done on the subject [8,23-27]. Some authors use uniform persistence to mean that densities are eventually bounded away from zero in a uniform sense and use permanence to mean uniform persistence together with dissipativity, so that densities are also eventually bounded above. In cases where different notations and terminology are currently in use we have generally followed the usage in [27]. The conditions for permanence can be expressed as the requirement that the boundary of the phase space (corresponding to zero density of at least one species) should be a repeller, and this raises some mathematical problems with a somewhat different flavor from that of global or asymptotic stability. When species dispersal is taken into account, a common model is a reaction-diffusion system, and a direct stability analysis is effectively ruled out except in the very simplest of cases. Indeed it is often difficult even to establish the existence of an interior equilibrium. Our aim

The triple $(Y, \pi, \mathbb{R}_+)$ is said to be a *semiflow* if $\pi : Y \times \mathbb{R}_+ \to Y$ is continuous and satisfies

(i) $\pi(u, 0) = u$ va

(ii) $\pi(\pi(u,t), s) = \pi(u, t+s) \qquad (s, t \in \mathbb{R}_+)$

for all $u \in Y$. For convenience we often write $\pi(u,t) = u.t$.

A *solution* ϕ through u is a continuous map $\phi : \mathbb{R} \to Y$ such that $\phi(0) = u$ and $\pi(\phi(\tau), t) = \phi(t + \tau)$ for $t \in \mathbb{R}_+$, $\tau \in \mathbb{R}$. The range of ϕ is denoted by $\gamma(u)$ and is called an *orbit* through u. We assume that the backward continuation when it exists is unique. The forward orbit $\{u.t : t \geq 0\}$ through u is denoted by $\gamma^+(u)$ and the corresponding backward orbit (when it exists) by $\gamma^-(u)$. Define $\gamma^+(U) = \bigcup_{u \in U} \gamma^+(u)$ and $\gamma(U)$ analogously. Note that the existence of a backward continuation is not assured, so an assertion as to its existence (for example implicitly contained in Theorem (2.1) below) is a strong restriction on the semiflow with wide ranging consequences.

A set U is said to be *forward invariant* if $\gamma^+(U) \subset U$and invariant if $\gamma(U) \subset U$. The omega-limit set of u is denoted by $\omega(u)$, and when there is an orbit through u, its alpha-limit set is denoted by $\alpha(u)$. Also $\omega(U)$ is defined by taking unions. This notation differs from that used in [19] but is more convenient in the present context; see [27]. The stable and unstable sets of a compact invariant set A are defined as follows (with the obvious restriction on the existence of an orbit for the second):

$$W^s(A) = \{u : u \in Y,\ \omega(u) \neq \emptyset,\ \omega(u) \subset A\},$$
$$W^u(A) = \{u : u \in Y,\ \alpha(u) \neq \emptyset,\ \alpha(u) \subset A\}.$$

The semiflow is said to be *dissipative* if there is a bounded set U such that $\lim_{t\to\infty} d(u.t, U) = 0$ for all $u \in Y$. The set U is said to be a *global attractor* if it is compact invariant and $\lim_{t\to\infty} \overline{d}(V.t, U) = 0$ for all bounded V.

Theorem 2.1. (Billoti and LaSalle [2]) Let Y be complete and suppose that the semiflow is dissipative. Assume that there is a $t_0 \geq 0$ such that $\pi(\cdot, t)$ is compact for $t > t_0$. Then there is a non-empty global attractor, $\mathcal{A}$ say.

The concept of permanence in a semiflow context is next considered. It will be assumed that $Y = Y_0 \cup \partial Y_0$ where Y_0 is open, and that Y_0, ∂Y_0 are forward invariant. In relation to the remarks in the introduction, ∂Y_0 will consist of the states with at least one species absent.

Definition 2.2. The semiflow is said to be *permanent* if there exists a bounded set U with $\underline{d}(U, \partial Y_0) > 0$ such that $\lim_{t\to\infty} d(v.t, U) = 0$ for all $v \in Y_0$.

If the requirement that U is bounded is removed then the semiflow is said to be uniformly persistent. The results we shall use to establish permanence/uniform persistence all require dissipativity and thus yield the stronger conclusion of permanence rather than merely uniform persistence, so we shall use permanence as the basic concept here.

The following definitions and theorem are taken from [19]. A set $U \subset Y_0$ is said to be *strongly bounded* if it is bounded and $\underline{d}(U, \partial Y_0) > 0$. $\mathcal{A}_0$ is said to be a *global attractor relative to strongly bounded sets* if it is a compact invariant subset of Y_0 and $\lim_{t\to\infty} \overline{d}(U.t, \mathcal{A}_0) = 0$ for all strongly bounded U.

Theorem 2.3. Assume that the conditions of Theorem 2.1 hold, and let Y_0 and ∂Y_0 be defined as above. Then if permanence holds, there are global attractors $\mathcal{A}$, $\mathcal{A}_\partial$ for π_∂ (that is π restricted to ∂Y_0), and a global attractor $\mathcal{A}_0$ relative to strongly bounded sets.

We come now to the first abstract permanence theorem which is based on the idea of using a weakened version of a Liapunov function P called here an 'average' Liapunov function. Take an ε-neighborhood $B(\mathcal{A},\varepsilon)$ of the global attractor $\mathcal{A}$ of Theorem 2.1, set $X = cl\pi(B(\mathcal{A},\varepsilon),[1,\infty))$ and let $S = X \cap \partial Y_0$. In the reaction-diffusion context S, X are compact, and this is assumed in the following result. In this form it is given in [23]; see also the review article [27] for further background.

Theorem 2.4. Assume that the conditions of Theorem 2.1 hold, and let X, S be as defined above. Suppose that $P : X\backslash S \to I\!R_+$ is continuous, strictly positive and bounded, and for $u \in S$ define

$$\alpha(t,u) = \liminf_{\substack{v \to u \\ v \in X\backslash S}} P(v.t)/P(v).$$

Then the semiflow is permanent if

$$\sup_{t>0} \alpha(t,u) > \begin{cases} 1 & (u \in \omega(S)) \\ 0 & (u \in S) \end{cases}$$

The second abstract permanence theorem exploits a knowledge of the geometry of the flow in ∂Y_0. The discussion below follows [19], and we again refer the reader to [27] for the background. Y will henceforth be assumed complete. We need to recall some further terminology.

Let M be a non-empty invariant set. It is said to be an *isolated invariant set* if it has a neighborhood U, called an *isolating neighborhood*, such that M is the maximal invariant subset of U. The set $\omega(\partial Y_0)$ is said to be *isolated* if it has a finite covering $M = \bigcup_{n=1}^{k} M_n$ by pairwise disjoint compact isolated invariant sets M_n which are isolated both for π_∂ and π. M is then called an *isolated covering.*

Let M, N be not necessarily distinct isolated invariant sets. Then M is said to be *chained* to N, written $M \to N$, if there exists $u \notin M \cup N$ with $u \in W^u(M) \cap W^s(N)$. A finite sequence of isolated invariant sets $M_1, ..., M_k$ is called a *chain* if $M_1 \to M_2 \to ... \to M_k (M_1 \to M_1$ if $k = 1)$. The chain is a *cycle* if $M_k = M_1$. The set $\omega(\partial Y_0)$ is said to be *acyclic* if there exists an isolated covering $\bigcup_{n=1}^{k} M_n$ such that no subset of the M_n form a cycle.

Theorem 2.5. (Hale and Waltman [19]) Assume that the conditions of Theorem 2.1 hold. Suppose that:

(i) $\omega(\partial Y_0)$ is isolated and acyclic;

(ii) $W^s(M_n) \cap Y_0 = \emptyset$ for all n.

Then the semiflow is permanent.

One could view Theorems 2.4 and 2.5 as establishing uniform persistence under the previous assumption of dissipativity in Theorem 2.1. However, dissipativity is itself a hypothesis of the original formulations of these theorems, so the stronger conclusion of permanence is automatic. Thus it is appropriate to state the theorems in terms of permanence rather than to weaken their conclusions just to preserve the use of the terminology of uniform persistence.

Finally we discuss how the reaction-diffusion system (1.1) fits into the above abstract setting. The first step is to notice that (1.1) induces a semiflow on certain C^k spaces; a convenient reference here is [38]. The general background on semiflows generated by reaction-diffusion equations is treated in [20]. Backward uniqueness of orbits in reaction-diffusion systems is shown in [14]. More background material with a specific focus on permanence is given in [27], [8].

As usual C^k will denote sets of k-times differentiable functions (from $\overline{\Omega}$ into $\mathbb{R}^n$). We shall also use the Banach spaces $C^k(\overline{\Omega})$, where the sup norm on functions and the appropriate derivatives is imposed. The norms will be denoted by $\| \cdot \|_k$, and the closed subspaces of functions vanishing on $\partial\Omega$ by $C_0^k(\overline{\Omega})$. $C_+^k(\overline{\Omega})$ will denote the positive cones with respect to the usual ordering; note that these sets are invariant (in view of the form of the equations (1.1)) on the maximal interval of existence of orbits. The following conditions will be imposed on the system (1.1).

(H1) (a) $\mu_i > 0$ for $i = 1, .., n$.

(b) $\Omega \subset \mathbb{R}^m$ is bounded and open, with $\partial\Omega$ uniformly $C^{3+\alpha}$ for some $\alpha > 0$.

(c) $f_i \in C^2(\mathbb{R}_+^n, \mathbb{R}^n)$.

(H2) *Uniformly boundedness* in $C_{0+}^0(\overline{\Omega})$. Given $\beta > 0$, there exists $B(\beta)$ such that $\| u(0) \|_0 \leq \beta \to \| u(t) \|_0 \leq B(\beta)$ for $t \geq 0$.

(H3) *Dissipativity in* $C_{0+}^0(\overline{\Omega})$. There exists γ such that; given $u_0 \in C_{0+}^0(\overline{\Omega})$, there is a $t(u_0)$ such that $\| u(t) \|_0 \leq \gamma$ for $t \geq t(u_0)$.

Theorem 2.6. Let (H1)-(H3) hold. Then the reaction-diffusion system (1.1) generates a semiflow on $C_{0+}^0(\Omega)$, and its restriction to $C_{0+}^1(\overline{\Omega})$ is also a semiflow. Dissipativity in $C_{0+}^1(\overline{\Omega})$ holds. Also, $\pi(\cdot, t)$ is a compact operator on $C_{0+}^1(\overline{\Omega})$ for every $t > 0$. There is a bounded set U_2 in $C_+^2(\overline{\Omega})$ such that if $U \subset C_{0+}^1(\overline{\Omega})$ is bounded, then $U.t \subset U_2$ for $t \geq 1$.

We note that it follows from this theorem together with Theorem 2.1 that there is a global attractor $\mathcal{A}$ in $C_{0+}^1(\overline{\Omega})$, and that as previously asserted $X = cl\pi(B(\mathcal{A}, \varepsilon), [1, \infty))$ is compact in $C_{0+}^1(\overline{\Omega})$ and forward invariant.

In the sequel we shall take $Y = C_{0+}^1(\overline{\Omega})$, so that Theorem 2.6 yields an appropriate metric space for the application of Theorems 2.4 and 2.5. As they stand these theorems do not quite yield permanence in the sense of Definition 1.1. However, the existence of the global attractor $\mathcal{A}_0$ relative to strongly bounded sets assured by Theorem 2.3 enables us to strengthen the result in a fairly simple manner:

Theorem 2.7. Suppose the conclusion of Theorem 2.4 or 2.5 hold. Then the system (1.1) is permanent in the sense of Definition 1.1.

In outline the proof is based on the following ideas. Since we can work in $C_{0+}^1(\overline{\Omega})$ and since solutions of parabolic equations of the form $w_t = \mu\Delta w + c(x,t)w$ satisfy a version of the strong maximum principle, permanence implies that for each component

$u_i(x,t)$ of an orbit $u(t)$ starting in the interior of the positive cone, $u_i(x,t) \geq e_i(x)$ for t sufficiently large, where $e_i(x) > 0$ on Ω and $\partial e_i/\partial n < 0$ on $\partial\Omega$; see [8] for a proof and more discussion of this point.

3. DISSIPATIVITY AND THE DYNAMICS OF SUBSYSTEMS.

In this section we discuss some results on dissipativity and on the dynamics of two-species subsystems which are required for the application of the abstract results of the preceding section. We begin with a lemma on diffusive logistic equations which follows from results in [6]:

Lemma 3.1. Suppose that $f \in C^2(\overline{\Omega} \times \mathbb{R}_+, \mathbb{R})$ with

$$f(x_0, 0) > 0 \qquad \text{for some } x_0 \in \Omega,$$

$$\frac{\partial f}{\partial w}(x,w) < 0 \qquad \text{for } (x,w) \in \overline{\Omega} \times \mathbb{R}_+, \text{ and}$$

$$\text{for some } M > 0, \quad f(x,M) \leq 0 \text{ for } x \in \overline{\Omega}.$$

Let λ_1 be the positive principal eigenvalue for

$$\begin{aligned} -\mu\Delta\psi &= \lambda f(x,0)\psi \quad \text{in } \Omega \\ \psi &= 0 \qquad\qquad\quad \text{on } \partial\Omega. \end{aligned} \tag{3.1}$$

If $\lambda_1 > 1$ the problem

$$\begin{aligned} w_t &= \mu\Delta w + f(x,w)w \qquad \text{in } \Omega \times \mathbb{R}_+ \\ w &= 0 \qquad\qquad\qquad\qquad \text{on } \partial\Omega \times \mathbb{R}_+ \end{aligned} \tag{3.2}$$

has no positive equilibria and all nonnegative solutions decay to zero as $t \to \infty$. If $\lambda_1 < 1$ then (3.2) has a unique positive equilibrium $\overline{w}$ which is a global attractor for nontrivial nonnegative solutions to (3.2). We have $0 < \overline{w} < M$ on Ω and $\partial w/\partial n < 0$ on $\partial\Omega$.

The systems we consider can all be rescaled into the form

$$\begin{aligned} u_{it} &= \mu_i\Delta u_i + (a_i - u_i + \sum_{j\neq i}\delta_{ij}u_j)u_i \qquad \text{on } \Omega \times \mathbb{R}_+,\ i = 1,2,3 \\ u &= 0 \qquad\qquad\qquad\qquad\qquad\qquad\qquad \text{on } \partial\Omega \times \mathbb{R}_+ \end{aligned} \tag{3.3}$$

where either $\delta_{ij} \leq 0$ for all i,j, corresponding to the case of three competitors, or $\delta_{ij} \leq 0$ for $i = 1,2$ but $\delta_{3j} \geq 0$, corresponding to two competing prey and one predator. By the smoothing properties of the semiflow it suffices to show dissipativity for (3.3) in $C^0_{0+}(\overline{\Omega})$ (Theorem 2.6). We have

Lemma 3.2. If $\delta_{ij} \leq 0$ for $i = 1,2$ and $j \neq i$ then the system (3.3) is dissipative in $C^0_{0+}(\overline{\Omega})$. Uniform boundedness then follows from semigroup theory via the variation of parameters formula, and those properties extend to $C^1_{0+}(\overline{\Omega})$ by the smoothing properties of the semigroup.

Discussion: This result follows from the simplest arguments used in [8] to obtain the corresponding results for two species. Specifically, for $i = 1,2$ the solution component u_i of (3.3) is a subsolution of the scalar problem $w_{it} = \mu_i\Delta w_i + (a_i - w_i)w_i$ subject to the same initial and boundary conditions, so $u_i \leq w_i$. By Lemma 3.1, $w_i < a_i$ for t sufficiently large. If $\delta_{3j} \leq 0$ we may apply the same argument to u_3. If not, we observe that sufficiently large t, u_3 is a subsolution of $w_{3t} = \mu_3 \Delta w_3 + (a_3 + \delta_{31} a_1 + \delta_{32} a_2 - w_3) w_3$, so eventually $u_3 \leq w_3 < a_3 + \delta_{31} a_1 + \delta_{32} a_2$. (These arguments generalize immediately to more general systems whose nonlinearities satisfy the corresponding monotonicity conditions.) Once dissipativity is established in $C^0_{0+}(\overline{\Omega})$, the remaining properties follow as in [8].

We now turn to the problem of characterizing the dynamics of two species subsystems. We shall consider first the case of two competitors since that system generates a monotone semiflow. Specifically, if (u_1, u_2) and (v_1, v_2) satisfy

$$\begin{aligned} u_{1t} - \mu_1 \Delta u_1 - (a_1 - u_1 - \varepsilon_{12} u_2) u_1 &\geq v_{1t} - \mu_1 \Delta v_1 - (a_1 - v_1 - \varepsilon_{12} v_2) v_2 \\ u_{2t} - \mu_2 \Delta u_2 - (a_2 - u_2 - \varepsilon_{21} u_1) u_2 &\leq v_{2t} - \mu_2 \Delta v_2 - (a_2 - v_2 - \varepsilon_{21} v_1) v_2 \end{aligned} \tag{3.4}$$

in $\Omega \times I\!R_+$ with $0 \leq v_1 \leq u_1$ and $0 \leq u_2 \leq v_2$ on $\Omega \times \{0\}$ and $\partial\Omega \times I\!R^+$ then $u_1 \geq v_1$ and $u_2 \leq v_2$ on $\Omega \times I\!R_+$ with either strict inequality or $v_i \equiv u_i$. The monotonicity properties of the Lotka-Volterra competition model for two species are well known and have been widely exploited; see for example [9,31,37] among many others. If $\underline{w}_1(x)$, $\overline{w}_2(x)$ satisfy

$$\begin{aligned} \mu_1 \Delta \underline{w}_1 + (a_1 - \underline{w}_1 - \varepsilon_{12} \overline{w}_2) \underline{w}_1 &\geq 0 \\ \mu_2 \Delta \overline{w}_2 + (a_2 - \overline{w}_2 - \varepsilon_{21} \underline{w}_1) \overline{w}_2 &\leq 0 \end{aligned} \tag{3.5}$$

and v_1, v_2 satisfy the competition system

$$\begin{aligned} v_{it} &= \mu_i \Delta v_i + (a_i - v_i - \varepsilon_{ij} v_j) v_i, \quad j \neq i;\ i = 1,2 \quad \text{in } \Omega \times I\!R_+ \\ v &= 0 \quad \text{on } \partial\Omega \times I\!R_+ \end{aligned} \tag{3.6}$$

with $v_1(x,0) = \underline{w}_1(x)$, $v_2(x,0) = \overline{w}_2(x)$ then $v_1, v_2, \underline{w}_1, \overline{w}_2$ satisfy (3.4) (with the v's on the left) so that $v_1(x,t) \geq \underline{w}_1(x) = v_1(x,0)$ and $v_2(x,t) \leq \overline{w}_2(x) \leq v_2(x,0)$ for any $t > 0$. For any $h > 0$, the pairs $(v_1(x,t), v_2(x,t))$ and $(v_1(x,t+h), v_2(x,t+h))$ satisfy (3.6) with $v_1(x,h) \geq v_1(x,0)$ and $v_2(x,h) \leq v_2(x,0)$ so that we may use (3.4) with $v_i = v_i(x,t)$, $u_i = v_i(x,t+h)$ to conclude that for $t > 0$, $v_1(x,t+h) \geq v_1(x,t)$ and $v_2(x,t+h) \leq v_2(x,t)$ with equality only if v_1, v_2 depend only on x. Hence, v_1 is increasing in t and v_2 is decreasing. If we also can find $\overline{w}_1, \underline{w}_2$ satisfying (3.5) with the inequalities reversed and $\underline{w}_i \leq \overline{w}_i$ then $v_1 \leq \overline{w}_1$ and $v_2 \geq \underline{w}_2$ so $v_1 \uparrow v_1^*(x)$ and $v_2 \downarrow v_2^*(x)$ pointwise. Parabolic regularity then implies that the convergence is actually in $C^{2,\alpha}(\Omega)$ so that (v_1^*, v_2^*) is an equilibrium of (3.6). This sort of argument is discussed in more detail in the case of a scalar equation in [18], specifically Theorems 4.2 and 4.8; see also [7] and [9] for related ideas and results. We have now set the stage for the proof of the following:

Lemma 3.3. Suppose that $a_i > \mu_i \rho_1$ for $i = 1,2$ where ρ_1 is the principal eigenvalue for $-\Delta\phi = \rho\phi$ on Ω, $\phi = 0$ on $\partial\Omega$, so that by Lemma 3.1 each of the problems $u_{it} = \mu_i \Delta u_i + (a_i - u_i) u_i$, $i = 1,2$, has a positive equilibrium $\overline{u}_i$ which is a global attractor for nonnegative nontrivial solutions. Suppose further that the principal eigenvalue σ_1 of the problem $\mu_1 \Delta\phi + (a_1 - \varepsilon_{12} \overline{u}_2)\phi = \sigma\phi$ in Ω, $\phi = 0$ on $\partial\Omega$, is positive and that (3.6) has no equilibria (u_1^*, u_2^*) with both components positive. Under these hypotheses any solution (u_1, u_2) of (3.6) with $u_1(x,0) \geq 0$, $u_1(x,0) \not\equiv 0$ must approach $(\overline{u}_1, 0)$ as $t \to \infty$.

Proof: If (u_1, u_2) satisfies (3.6) and $u_1 \geq 0$, $u_1 \not\equiv 0$ at $t = 0$ then $u_1 > 0$ in Ω and $\partial u_1/\partial n < 0$ on $\partial\Omega$ for any $t > 0$ by the strong maximum principle. Also,

u_2 is a subsolution to $u_t = \mu_2\Delta u + (a_2 - u)u$ so for any $\varepsilon > 0$ and t sufficiently large we have $u_2 \leq (1+\varepsilon)\overline{u}_2$. Choose $\varepsilon > 0$ sufficiently small that the principal eigenvalue σ_1' of $\mu_1\Delta\phi + (a_1 - \varepsilon_{12}(1+\varepsilon)\overline{u}_2)\phi = \sigma\phi$ is still positive and t_0 large enough that $u_2 < (1+\varepsilon)\overline{u}_2$ for $t \geq t_0$. Let $\underline{w}_1 = \delta\phi_1$ where $\phi_1 > 0$ is the eigenfunction corresponding to σ_1' and $\delta > 0$ will be chosen later and let $\overline{w}_2 = (1+\varepsilon)\overline{u}_2$. It is easy to verify that $\mu_2\Delta\overline{w}_2 + (a_2 - \overline{w}_2 - \varepsilon_{21}\underline{w}_1)\overline{w}_2 \leq 0$ and for $\delta > 0$ sufficiently small $\mu_1\Delta\underline{w}_1 + (a_1 - \underline{w}_1 - \varepsilon_{12}\overline{w}_2)\underline{w}_1 \geq 0$. Also, we have $u_2(x,t_0) \leq \overline{w}_2$ and for δ small enough $u_1(x,t_0) \geq \underline{w}_1$. Finally, we may take $\underline{w}_2 = 0$ and $\overline{w}_1 = (1+\varepsilon)\overline{u}_1$. We have $\underline{w}_1 \leq u_1 \leq \overline{w}_1$ and $\underline{w}_2 \leq u_2 \leq \overline{w}_2$ for $t = t_0$. Let v_1, v_2 be the solution of (3.6) with $v_1(x,t_0) = \underline{w}_1(x)$ and $v_2(x,t_0) = \overline{w}_2(x)$. Then $v_1 \leq u_1 \leq \overline{w}_1$ and $v_2 \geq u_2 \geq \underline{w}_2 \equiv 0$ and $v_1 \uparrow v_1^*$, $v_2 \downarrow v_2^*$ where (v_1^*, v_2^*) is an equilibrium of (3.6). But by hypothesis (3.6) has no equilibria with both components positive, so we must have $v_2^* = 0$ and $v_1^* = \overline{u}_1$. It follows that $u_1 \to \overline{u}_1$ and $u_2 \to 0$ as $t \to \infty$.

Corollary 3.4. The hypotheses of Lemma 3.3 are satisfied if

$$a_1/\mu_1 \geq a_2/u_2 \geq \rho_1 \quad \text{and} \quad \varepsilon_{12}\mu_2/\mu_1 \leq 1 < \varepsilon_{21}\mu_1/\mu_2 \tag{3.7}$$

Discussion: Any equilibrium of (3.6) must satisfy $\mu_i\Delta u_i + (a_i - u_i - \varepsilon_{ij}u_j)u_i = 0$, $j \neq i$, $i = 1,2$ which can be rewritten as $\Delta u_i + (a_i/\mu_i - u_i/\mu_i - \varepsilon_{ij}u_j/\mu_i)u_i = 0$, or by taking $w_i = u_i/\mu_i$ as $\Delta w_i + (a_i/\mu_i - w_i - (\varepsilon_{ij}\mu_j/\mu_i)w_j)w_i = 0$, which is the form treated in [4]. By Theorem 2.1 of [4] hypothesis (3.7) excludes equilibria positive in both components. The eigenvalue problem $\mu_1\Delta\phi + (a_1 - \varepsilon_{12}\overline{u}_2)\phi = \sigma\phi$ transforms into $\Delta\phi + (a_1/\mu_1 - (\varepsilon_{12}\mu_2/\mu_1)\overline{w}_2)\phi = (\sigma/\mu_1)\phi$ where $\overline{w}_2 = \overline{u}_2/\mu_1$, and the positivity σ_1/μ_1 and hence of σ_1 follows from Theorem 2.2 of [4].

Remark: Other conditions are also possible; see [4,7,9-11,15,30,31,33,35,37] for related results.

We now consider the case of a predator-prey system. The analysis is more delicate than in the case of two competitors because monotonicity is lost. We shall proceed in two steps. First, we shall establish some estimates that will completely characterize the dynamics of the system in a special case and which give some information about the location of possible equilibria in general. We shall then give a condition in terms of those estimates which is sufficient for the existence of a coexistence state that is a global attractor for positive solutions. We shall need some notation. Suppose that $m(x) \in C^2(\overline{\Omega})$ and $m(x_0) > 0$ for some $x_0 \in \overline{\Omega}$. Let $\lambda_1(m(x))$ be the principal positive eigenvalue of

$$\begin{aligned} -\Delta\psi &= \lambda m(x)\psi && \text{in } \Omega \\ \psi &= 0 && \text{on } \partial\Omega. \end{aligned} \tag{3.8}$$

If $\lambda_1(m(x)) < 1$ let $\theta[m]$ denote the unique positive solution of

$$\begin{aligned} \Delta\theta + (m(x) - \theta)\theta &= 0 && \text{in } \Omega \\ \theta &= 0 && \text{on } \partial\Omega. \end{aligned}$$

It follows from Theorem 2.2 of [6] that θ is monotone increasing in m and the map $m \mapsto \theta(m)$ from $L^\infty(\Omega)$ to $C^1(\Omega)$ is continuous. It is easy to see that the positive solution of $\mu\Delta u + (m(x) - u)u = 0$ is $\mu\theta[m/\mu]$ provided $\mu\lambda_1(m) < 1$ and that the positive solution of $\mu\Delta u + (m(x) - c\theta[m/\mu] - u)u = 0$ is $(\mu - c)\theta[m/\mu]$ if $c < \mu$.

We shall consider systems of the form

$$\begin{aligned} u_{1t} &= \mu_1 \Delta u_1 + (a_1 - u_1 - \alpha_1 u_3) u_1 && \text{in } \Omega \times \mathbb{R}_+ \\ u_{3t} &= \mu_3 \Delta u_3 + (a_3 - u_3 + \beta_1 u_1) u_3 && \\ u_1 &= u_3 = 0 && \text{on } \partial\Omega \times \mathbb{R}_+. \end{aligned} \tag{3.9}$$

Lemma 3.5. Suppose that (u_1^*, u_3^*) is any coexistence state for (3.8). Assume that

$$\begin{aligned} &\mu_1 a_1 > \rho_1 \text{ and } \mu_3 \lambda_1 (a_3 + (\beta_1 \mu_1 - \alpha_1 \beta_1 \mu_3 - \alpha_1 \beta_1^2 \mu_1) \theta[a_1/\mu_1]) < 1, \\ \text{and} \quad &a_1/\mu_1 \geq a_3/\mu_3, \\ &\mu_1 - \alpha_1 \mu_3 - \alpha_1 \beta_1 \mu_1 > 0. \end{aligned} \tag{3.10}$$

Then any coexistence equilibrium (u_1^*, u_3^*) satisfies

$$\begin{aligned} (\mu_1 - \alpha_1 \mu_3 - \alpha_1 \beta_1 \mu_1) \theta[a_1/\mu_1] &\leq u_1^* \leq \mu_1 \theta[a_1/\mu_1] \\ \mu_3 \theta[(a_3 + (\beta_1 \mu_1 - \alpha_1 \beta_1 \mu_3 - \alpha_1 \beta_1^2 \mu_1) \theta[a_1/\mu_1])/\mu_3] &\leq u_3^* \leq (\mu_3 + \beta_1 \mu_1) \theta[a_1/\mu_1] \end{aligned} \tag{3.11}$$

and the set of pairs (u_1, u_3) satisfying (3.11) contains a global attractor for nontrivial nonnegative solutions.

Remark: Hypothesis (3.10) implies that $\mu_3 \lambda_1 (a_3 + \beta_1 \mu_1 \theta[a_1/\mu_1]) < 1$; the hypothesis is needed for the existence of the equilibrium solutions $\theta[\cdot] > 0$ of scalar equations used in (3.11). The second inequality in (3.11) may be simplified with some loss of precision by noting that since $\beta_1 \mu_1 - \alpha_1 \beta_1 \mu_3 - \alpha_1 \beta_1^2 \mu_1 > 0$,

$$\theta[a_3/\mu_3] \leq \theta[(a_3 + (\beta_1 \mu_1 - \alpha_1 \beta_1 \mu_3 - \alpha_1 \beta_1^2 \mu_1) \theta[a_1/\mu_1])/\mu_3).$$

The lower bound on u_3^* in (3.11) could be used to obtain a stronger upper bound on u_1^*, namely

$$\begin{aligned} u_1^* &\leq \mu_1 \theta[a_1 - \alpha_1 \mu_3 \theta[a_3 + (\beta_1 \mu_1 - \alpha_1 \beta_1 \mu_3 - \alpha_1 \beta_1^2 \mu_1) \theta[a_1/\mu_1]/\mu_3]/\mu_1] \\ &< \mu_1 \theta[a_1/\mu_1]. \end{aligned}$$

In principle the estimation process could be further refined but the estimates become very complicated.

Proof. Recall that $\mu\theta[m/\mu]$ is a global attractor for nonnegative nontrivial solutions of $v_t = \mu \Delta v + (m(x) - v) v$ under Dirichlet boundary conditions so if v is any solution and $u \leq v$ then for any $\varepsilon > 0$ we have $u \leq (1+\varepsilon)\mu\theta[m/\mu]$ for t sufficiently large. It will be convenient to write $u \to\leq \mu\theta[m/\mu]$ to denote this, and similarly $u \to\geq \mu\theta[m/\mu]$ if for any $\varepsilon > 0$ and t sufficiently large we have $u \geq (1-\varepsilon)\mu\theta[m/\mu]$. If v satisfies $v_t = \mu\Delta v + (m(x) - v) v$ with $u \geq v$ and $v(x,0) \geq 0$, $v(x,0) \not\equiv 0$ then $u \to\geq \mu\theta[m/\mu]$.

Any solution of $u_{1t} = \mu_1 \Delta u_1 + (a_1 - u_1 - \alpha_1 u_3) u_1$ is a subsolution of $u_t = \mu_1 \Delta u + (a_1 - u) u$, so $u_1 \to\leq \mu_1 \theta[a_1/\mu_1]$. Thus, for any $\varepsilon > 0$ and t large, u_3 is a subsolution of $u_t = \mu_3 \Delta u + (a_3 + (1+\varepsilon)\beta_1 \mu_1 \theta[a_1/\mu_1] - u) u$ so if $\mu_3 \lambda_1 (a_3 + \beta_1 \mu_1 \theta[a_1/\mu_1]) < 1$, which follows from (3.9), then $u_3 \to\leq \mu_3 \theta[(a_3 + (1+\varepsilon)\beta_1 \mu_1 \theta[a_1/\mu_1])/\mu_3]$ for any $\varepsilon > 0$. It then follows from the monotonicity and continuity properties of $\theta[m]$ with respect to m that $u_3 \to\leq \mu_3 \theta[a_3/\mu_3 + (\beta_1 \mu_1/\mu_3) \theta[a_1/\mu_1]]$. Since $a_3/\mu_3 \leq a_1/\mu_1$ we have

$$u_3 \to\leq \mu_3\theta[a_1/\mu_1 + (\beta_1\mu_1/\mu_3)\theta[a_1/\mu_1]] =$$
$$= \mu_3(1 + \beta_1\mu_1/\mu_3)\theta[a_1/\mu_1] \tag{3.12}$$
$$= (\mu_3 + \beta_1\mu_1)\theta[a_1/\mu_1].$$

Hence, u_1 is eventually a supersolution to

$$u_t = \mu_1\Delta u + (a_1 - (1-\varepsilon)\alpha_1(\mu_3 + \beta_1\mu_1)\theta[a_1/\mu_1] - u)u$$

for any $\varepsilon > 0$ so

$$u_1 \to \geq \mu_1(1 - (\alpha_1(\mu_3 + \beta_1\mu_1)/\mu_1))\theta[a_1/\mu_1]$$
$$= (\mu_1 - \alpha_1\mu_3 - \alpha_1\beta_1\mu_1)\theta[a_1/\mu_1].$$

Finally, u_3 is a supersolution for any $\varepsilon > 0$ to

$$u_t = \mu_3\Delta u + (a_3 + (1-\varepsilon)\beta_1(\mu_1 - \alpha_1\mu_3 - \alpha_1\beta_1\mu_1)\theta[a_1/\mu_1] - u)u$$

so

$$u_3 \to\geq \mu_3\theta[(a_3 + (\beta_1\mu_1 - \alpha_1\beta_1\mu_3 - \alpha_1\beta_1^2\mu_1)\theta[a_1/\mu_1])/\mu_3]. \tag{3.13}$$

If $u_i \to\geq v_i$ for any nonnegative nontrivial solution (u_1, u_2) to (3.9) then the set $\{(u_1, u_2) : u_i \geq v_i\}$ contains a global attractor for such solutions and hence for any coexistence state (u_1^*, u_2^*) we have $u_i^* \geq v_i$. Together with the corresponding result for the opposite inequality this yields the conclusions of the lemma.

In principle it is possible to continue the iteration of estimates of the forms (3.12), (3.13), and so on; but in practice the estimates become very complicated in the general case. The reason is that for $A \leq B$ it is possible to get explicit estimates $\theta[A+g(x)] \leq \theta[B + g(x)]$ of the type used in (3.12) but there seems to be no correspondingly simple explicit estimate for the constant K such that $K\theta[A + g(x)] \geq \theta[B + g(x)]$, which is what would be needed to put the estimate in (3.13) into terms of $\theta[a_1/\mu_1]$. There will always exist such a constant K by the strong maximum principle, and K can be estimated in certain special cases, as in [1,9], but in general the dependence of K on Ω and the coefficients of (3.9) will be complicated. In the special case $a_1/\mu_1 = a_3/\mu_3$ the estimate in (3.13) converts to an estimate in terms of $\theta[a_1/\mu_1]$ and we may continue the iteration. It turns out that for this special case the method used in Lemma 3.5 can completely characterize the dynamics of (3.9), while the general case requires some other ideas as well. For simplicity we shall state the next lemma for the case $\mu_1 = \mu_3 = 1$, $a_1 = a_3 = a > \rho_1$, although the results can be extended to $a_1/\mu_1 = a_3/\mu_3$.

Lemma 3.6. Suppose that $\mu_1 = \mu_3 = 1$, that $a_1 = a_3 = a > \rho_1$, and that $1 - \alpha_1 - \alpha_1\beta_1 > 0$. Then the coexistence state $(u_1^*, u_3^*) = (\{(1-\alpha_1)/(1+\alpha_1\beta_1)\}\theta[a], \{(1 + \beta_1)/(1+\alpha_1\beta_1\}\theta[a])$ is a global attractor for nontrivial nonnegative solutions of (3.9).

Remark: The conditions on the coefficients imply that the hypotheses of Lemma 3.5 are satisfied.

Proof: We follow the proof of Lemma 3.5 up to (3.13) so that for any nontrivial solution (u_1, u_3) we have

$$u_1 \to\leq \theta[a]$$
$$u_3 \to\leq (1 + \beta_1)\theta[a]$$
$$u_1 \to\geq (1 - \alpha_1 - \alpha_1\beta_1)\theta[a]$$

and from (3.13)

$$\begin{aligned} u_3 \to &\geq \theta[a + (\beta_1 - \alpha_1\beta_1 - \alpha_1\beta_1^2)\theta[a]] \\ &= (1 + \beta_1 - \alpha_1\beta_1 - \alpha_1\beta_1^2)\theta[a]. \end{aligned}$$

We may continue the iterated estimates based on Lemma 3.1 and the theory of sub- and supersolutions as in the proof of Lemma 3.5 to obtain

$$\begin{aligned} u_1 \to &\leq \theta[a - \alpha_1(1 + \beta_1 - \alpha_1\beta_1 - \alpha_1\beta_1^2)\theta[a]] \\ &= 1 - \alpha_1(1 + \beta_1 - \alpha_1\beta_1 - \alpha_1\beta_1^2)\theta[a] \\ &= (1 - \alpha_1 - \alpha_1\beta_1 + \alpha_1^2\beta_1 + \alpha_1^2\beta_1^2)\theta[a] \end{aligned}$$

so that

$$\begin{aligned} u_3 \to &\leq \theta[a + \beta_1(1 - \alpha_1 - \alpha_1\beta_1 + \alpha_1^2\beta_1 + \alpha_1^2\beta_1^2)\theta[a] \\ &= (1 + \beta_1(1 - \alpha_1 - \alpha_1\beta_1 + \alpha_1^2\beta_1 + \alpha_1^2\beta_1^2))\theta[a] \\ &= (1 + \beta_1 - \alpha_1\beta_1 - \alpha_1\beta_1^2 + \alpha_1^2\beta_1^2 + \alpha_1^2\beta_1^3)\theta[a], \end{aligned}$$

and so on. After n iterations the estimates for u_1 be written for n even as

$$\begin{aligned} u_1 \to &\leq \{(1 - \alpha_1) - \alpha_1\beta_1(1 - \alpha_1) + \alpha_1^2\beta_1^2(1 - \alpha_1) - \ldots + \\ &-\alpha_1^{n-1}\beta_1^{n-1}(1 - \alpha_1) + \alpha_1^n\beta_1^n\}\theta[a] \\ &= \{(1 - \alpha_1)\sum_{k=0}^{n-1}(-1)^k(\alpha_1\beta_1)^k + \alpha_1^n\beta_1^n\}\theta[a] \end{aligned} \tag{3.14}$$

and for n odd as

$$u_1 \to \geq \{(1 - \alpha_1)\sum_{k=0}^{n-1}(-1)^k(\alpha_1\beta_1)^k - \alpha_1^n\beta_1^n\}\theta[a]$$

while those for u_3 may be written for $n = 2m$ as

$$\begin{aligned} u_3 &\to \leq \{(1 + \beta_1)\sum_{k=0}^{n}(-1)^k(\alpha_1\beta_1)^k\}\theta[a] \\ u_3 &\to \geq \{(1 + \beta_1)\sum_{k=0}^{n+1}(-1)^k(\alpha_1\beta_1)^k\}\theta[a]. \end{aligned} \tag{3.15}$$

Since $\alpha_1\beta_1 < 1$ by hypothesis the summations in (3.14) and (3.15) all converge as $n \to \infty$, and we obtain

$$\begin{aligned} u_1 &\to \leq \{(1 - \alpha_1)/(1 + \alpha_1\beta_1)\}[a], \\ u_1 &\to \geq \{(1 - \alpha_1)/(1 + \alpha_1\beta_1)\}\theta[a] \end{aligned}$$

so that $u_1 \to \{(1 - \alpha_1)/(1 + \alpha_1\beta_1)\}\theta[a]$ and similarly $u_3 \to \{(1 + \beta_1)/(1 + \alpha_1\beta_1)\}\theta[a]$, so that $u_1^* = \{(1 - \alpha_1)/(1 + \alpha_1\beta_1)\}\theta[a]$, $u_3^* = \{(1 + \beta_1)/(1 + \alpha_1\beta_1)\}\theta[a]$ is a global attractor for nontrivial nonnegative solutions.

Remarks. Similar sorts of iterations have been used to estimate coexistence states in competition models [4,31,37] or to study uniqueness of coexistence states in some predator prey models as in [31] and in some of the references therein. We need the additional information that the coexistence state is a global attractor to rule out periodic solutions or other more complicated dynamics.

Our results for the general case use the estimates of Lemma 3.5 in a crucial way. We shall need to estimate the ratio u_1/u_3 for large t. By the strong maximum principle $0 < \inf(u_1/u_3)$ and $\sup(u_1/u_3) < \infty$ over Ω for any fixed $t > 0$. Similarly, the supremum and infimum of $\theta[A(x)]/\theta[B(x)]$ are both positive numbers if $\theta[A(x)], \theta[B(x)] > 0$ exist. For A and B constant, $\sup\theta[A]/\theta[B]$ can be estimated in terms of A, B, ρ_1, and (for the case of more than one space dimension) other geometric quantities associated with Ω; see for example [1] or [9]. To state the next lemma we define the following quantities arising from ratios of the $\theta[\cdot]$'s occuring in (3.11):

$$\begin{aligned} &K_1(a_1,a_3,\mu_1,\mu_3,\alpha_1,\beta_1) = (\mu_1 - \alpha_1\mu_3 - \alpha_1\beta_1\mu_1)/(\mu_3+\beta_1\mu_1) \\ &K_2(a_1,a_3,\mu_1,\mu_3,\alpha_1,\beta_1,\Omega) = \\ &\quad(\mu_1/\mu_3)\sup(\theta[a_1/\mu_1]\ /\theta[(a_3+(\beta_1\mu_1-\alpha_1\beta_1\mu_3-\alpha_1\beta_1^2\mu_1)\theta[a_1/\mu_1]/\mu_3]). \end{aligned} \tag{3.16}$$

We have

Lemma 3.7. Suppose that the hypotheses of Lemma 3.5 are satisfied and that

$$\begin{aligned} K_1 &< \frac{2+\alpha_1\beta_1+2\sqrt{1+\alpha_1\beta_1}}{2\alpha_1^2} \\ K_2 &> \frac{2+\alpha_1\beta_1-2\sqrt{1+\alpha_1\beta_1}}{2\alpha_1^2} \end{aligned} \tag{3.17}$$

where K_1, K_2 are defined in (3.16). Then the system (3.9) has a unique coexistence state (u_1^*, u_3^*) which is a global attractor for nontrivial nonnegative solutions.

Remarks: For our purposes uniqueness of the coexistence state is not sufficient, since we need to characterize the ω-limit set of (3.9) and to do that we must also consider the possibility of periodic orbits. Arguments similar to those used here are also discussed in [1,9,30]. A criterion for uniqueness of the coexistence state given in [30] that is similar in spirit to (3.17) but different in form is also sufficient for the stronger conclusions of this lemma.

Proof. Lemma 3.5 implies permanence for (3.9) so by [8] there must be a coexistence state (u_1^*, u_3^*) satisfying (3.11). Suppose that (u_1, u_3) is any positive solution of (3.8) and let $p_1 = u_1 - u_1^*$, $p_3 = u_3 - u_3^*$. We have

$$\begin{aligned} p_{1t} &= \mu_1\Delta p_1 + (a_1 - u_1^* - \alpha_1 u_3^*)p_1 - u_1p_1 - \alpha_1u_1p_3 \\ p_{3t} &= \mu_3\Delta p_3 + (a_3 - u_3^* + \beta_1u_1^*)p_3 + \beta_1u_3p_1 - u_3p_3 \end{aligned} \tag{3.18}$$

in $\Omega \times I\!R_+$, $p_1 = p_3 = 0$ on $\partial\Omega \times I\!R_+$. Since $u_1^* > 0$ is a solution of the eigenvalue problem

$$\mu_1\Delta\psi + (a_1 - u_1^* - \alpha_1u_3^*)\psi = \sigma\psi$$

with $\sigma = 0$, the principal eigenvalue must be $\sigma_1 = 0$ and hence by the variational characterization of eigenvalues we have

$$\int[-\mu_1 \mid \nabla\psi\mid^2 + (a_1 - u_1^* - \alpha_1u_3^*)\psi^2]dx \le 0 \tag{3.19}$$

for any $\psi \in W_0^{1,2}(\Omega)$, and similarly

$$\int[-\mu_3 \mid \nabla\psi\mid^2 + (a_3 - u_3^* + \beta_1u_1^*)\psi^2]dx \le 0. \tag{3.20}$$

Multiplying the ith equation in (3.18) by p_i, integrating by parts, and using (3.19), (3.20) yields

$$\frac{d}{dt}\left(\frac{1}{2}\int_\Omega (p_1^2+p_3^2)dx\right) \le -\int_\Omega (u_1p_1^2+(\alpha_1u_1-\beta_1u_3)p_1p_3+u_3p_3^2)dx. \quad (3.21)$$

If the expression inside the integral on the right in (3.21) is positive definite then the conclusion of the lemma must hold. (If $(p_1,p_2)\to 0$ in $[L^2(\Omega)]^2$ then since the system (3.18) is parabolic with smooth bounded coefficients we must also have $(p_1,p_2)\to 0$ in $C_0^0(\overline{\Omega})$ by parabolic regularity.) The quadratic form in (3.21) is positive definite if $(\beta_1u_3-\alpha_1u_1)^2-4u_1u_3<0$, or equivalently

$$\alpha_1^2(u_1/u_3)^2-(2\alpha_1\beta_1+4)(u_1/u_3)+\beta_1^2<0$$

which will be true provided u_1/u_3 lies between the roots of the quadratic $\alpha_1^2x^2-(2\alpha_1\beta_1+4)x+\beta_1^2=0$. Thus, the quadratic form in (3.21) is positive definite provided

$$\frac{2+\alpha_1\beta_1-2\sqrt{1+\alpha_1\beta_1}}{2\alpha_1^2}<u_1/u_3<\frac{2+\alpha_1\beta_1+2\sqrt{1+\alpha_1\beta_1}}{2\alpha_1^2}; \quad (3.22)$$

but by Lemma (3.5) we have $K_2-\varepsilon<u_1/u_3<K_1+\varepsilon$ for any $\varepsilon>0$ if t is sufficiently large, so that (3.17) implies (3.22) for large t and the result follows.

Remark: The alternative estimates in the remarks following the statement of Lemma 3.5 could be used to give simpler or sharper but more complicated expressions for K_1 and K_2.

For the analysis of the full semiflow with all three species present we shall need some information about the linearizations of the system about certain equilibria in the boundary of the positive cone. In the case of two competitors the hypotheses of Lemma 3.3 already impose conditions on the linearized problem at $(\overline{u}_1,0,0)$. Lemmas 3.6 and 3.7 also have consequences for the linearized problems at $(\overline{u}_1,0,0)$ and at $(0,0,\overline{u}_3)$ (if the system has a predator equilibrium $\overline{u}_3>0$ in the absence of prey), but they are not stated explicitly in terms of the relevant eigenvalues of linearized problems. We remedy that omission with the following:

Lemma 3.8. Suppose that (u_1^*,u_3^*) is a global attractor for nonnegative solutions of (3.9) which are not identically zero in either component. The principal eigenvalue σ_0 of the linearized problem

$$\begin{aligned}\mu_3\Delta\phi+[a_3+\beta_1\overline{u}_1]\phi &= \sigma\phi \quad \text{in } \Omega\\ \phi &= 0 \quad \text{in } \partial\Omega\end{aligned} \quad (3.23)$$

satisfies $\sigma_0>0$. If the system admits a positive equilibrium $\overline{u}_3$ satisfying $\mu_3\Delta u_3+(a_3-\overline{u}_3)\overline{u}_3=0$ then the principal eigenvalue σ_1 of

$$\begin{aligned}\mu_1\Delta\phi+[a_1-\alpha_1\overline{u}_3]\phi &= \sigma\phi \quad \text{in } \Omega,\\ \phi &= 0 \quad \text{on } \partial\Omega\end{aligned} \quad (3.24)$$

satisfies $\sigma_1>0$.

Remarks: If (3.9) admits an equilibrium (u_1^*,u_3^*) then necessarily there is an equilibrium $(\overline{u}_1,0)$ but there may or may not be an equilibrium $(0,\overline{u}_3)$. The eigenvalue $\mu_1\lambda_1(a_1)$ satisfies $\mu_1\lambda_1(a_1)<\mu_1\lambda_1(a_1-\alpha_1u_3^*)$, but since u_1^* is a positive solution of

$\mu_1\Delta u + [a_1 - \alpha_1 u_3^* - u]u = 0$ we must have $\mu_1\lambda_1(a_1 - \alpha_1 u_3^*) < 1$, so $\mu_1\lambda_1(a_1) < 1$, so $\overline{u}_1 > 0$ exists. The presence or absence of $\overline{u}_3$ depends on the size of a_3.

Proof. Observe that $\overline{u}_1$ is a strict supersolution to $\mu_1\Delta u_1 + (a_1 - \alpha_1 u_3^* - u_1)u_1 = 0$, which has the solution $u = u_1^*$; (alternatively u_1^* is a strict subsolution to $\mu_1\Delta u + (a_1 - u)u = 0$ which has a solution $\overline{u}_1$) so it follows from the usual theory of sub- and supersolutions together with the strong maximum principle that $\overline{u}_1 > u_1^*$ in Ω and $\partial\overline{u}_1/\partial n < \partial u_1^*/\partial n$ on $\partial\Omega$. Since (u_1^*, u_3^*) is a global attractor for nontrivial nonnegative solutions, we must have $u_1 \leq \overline{u}_1$ for large t for any solution (u_1, u_2) of (3.9) that is nonnegative and nonzero in both components. (Recall that we can consider the semiflow on $C^1_{0+}(\overline{\Omega})$.) Suppose that $\sigma_0 \leq 0$ in (3.22). Let $\phi_0 > 0$ be an eigenfunction corresponding to σ_0, and let (u_1, u_3) be any nontrivial, nonnegative solution of (3.9), so that $u_i \to u_i^*$ as $t \to \infty$ for $i = 1, 3$. We have

$$\begin{aligned}\frac{d}{dt}\int_\Omega \phi_0 u_3 &= \int_\Omega \phi_0[\mu_3\Delta u_3 + (a_3 + \beta_1 u_1 - u_3)u_3] \\ &= \int_\Omega [\mu_3\Delta\phi_0 + (a_3 + \beta_1\overline{u}_1)\phi_0]u_3 \\ &\quad + \int_\Omega [\beta_1(u_1 - \overline{u}_1) - u_3]\phi_0 u_3 \\ &= \int_\Omega \sigma_0\phi_0 u_3 + \beta_1(u_1 - \overline{u}_1)\phi_0 u_3 - \phi_0 u_3^2.\end{aligned}$$

We have $\sigma_0\phi_0 u_3 \leq 0$ and for some $T_0 > 0$ we have $u_1 - \overline{u}_1 \leq 0$ and $u_3 \geq (1/2)u_3^*$ for $t > T_0$ since $u_i \to u_i^*$ as $t \to \infty$ and $u_1^* < \overline{u}_1$ on Ω, $\partial u_1^*/\partial n > \partial\overline{u}_1/\partial n$ on $\partial\Omega$. Thus, for $t > T_0$ we have

$$\frac{d}{dt}\int_\Omega \phi_0 u_3 \leq -\frac{1}{4}\int_\Omega \phi_0 (u_3^*)^2 \equiv -\delta_0 < 0,$$

so

$$\int_\Omega \phi_0 u_3 \Big|_t \leq \int_\Omega \phi_0 u_3 \Big|_{T_0} - \delta_0(t - T_0). \tag{3.25}$$

Inequality (3.24) implies $\int_\Omega \phi_0 u_3 < 0$ for large t, which is impossible since $u_3 \geq 0$, $\phi_0 > 0$. To avoid the contradiction we must have $\sigma_0 > 0$.

If $\overline{u}_3 > 0$ exists then we may observe that u_3^* is a strict supersolution to $\mu_3\Delta u + (a_3 - u)u = 0$ so $u_3^* > \overline{u}_3$. Hence, $a_1 - \alpha_1 u_3^* < a_1 - \alpha_1\overline{u}_3$, so $\lambda_1(a_1 - \alpha_1\overline{u}_3) < \lambda_1(a_1 - \alpha_1 u_3^*)$. Since the problem $\mu_1\Delta u + (a_1 - \alpha_1 u_3^* - u)u = 0$ has a positive solution u_1^*, we have $\mu_1\lambda_1(a_1 - \alpha_1 u_3^*) < 1$ so $\mu_1\lambda_1(a_1 - \alpha_1\overline{u}_3) < 1$. That implies $\sigma_1 > 0$, because $\lambda_1(q/\mu_1) \equiv \mu_1\lambda_1(q) < 1$ if and only if the principal eigenvalue σ^* of $\mu_1\Delta\phi + q\phi = \sigma^*\phi$ is positive. The last observation is based on positivity considerations: if $\mu_1\lambda_1(q) < 1$ but $\sigma^* \leq 0$, let $\phi^* > 0$ be an eigenfunction for σ^*; then $-\mu_1\Delta w = \alpha q w + h$ has the positive solution $w = \phi^*$ with $h = -\sigma^*\phi^* \geq 0$ and $\alpha > \mu_1\lambda_1(q)$, which violates Proposition 3 of [21]. Thus if $\mu_1\lambda_1(q) < 1$ we must have $\sigma^* > 0$. (A similar argument yields the other direction of the equivalence, but we do not need that here.)

4. PERMANENCE FOR 2-PREY 1-PREDATOR SYSTEMS.

We consider the question of permanence for a reaction-diffusion system modelling two-prey one-predator interactions, the reaction terms being of Lotka-Volterra type. As was mentioned in the introduction the case of zero Neumann conditions, corresponding to no migration across $\partial\Omega$, was considered in [14] and [26]. The interest here is in investigating the much more difficult case when zero Dirichlet conditions are assumed. Biologically this corresponds to the assumption that species may diffuse across the boundary, but die out in the surrounding area. The main difficulty (which was tackled in section 3) is to find reasonable conditions under which the ω-limit set of the boundary of the phase space (corresponding to the absence of at least one species) is sufficiently simple to allow the conditions of the theorem to be checked - essentially it must consist of equilibria only. Then we shall show that it is enough if the obviously necessary conditions, that these boundary equilibria repel into the interior, hold. There are various possible combinations of equilibria which may yield permanence. However, we do not attempt here to be exhaustive and give the argument only in some typical cases. Other cases may be treated similarly. Some further discussion is given in section 6. The case we treat in this section corresponds to a situation where there are two prey and one predator species, one prey species would drive the other to extinction in the absence of the predator, but with the predator present all three species coexist. This phenomenon is called predator mediated coexistence.

Let Ω be a domain restricted as in section 2, and consider the following reaction-diffusion system on $\Omega \times I\!R_+$:

$$\frac{\partial u_1}{\partial t} = \mu_1 \Delta u_1 + u_1(a_1 - u_1 - c_{12}u_2 - c_{13}u_3), \tag{4.1a}$$

$$\frac{\partial u_2}{\partial t} = \mu_2 \Delta u_2 + u_2(a_2 - c_{21}u_1 - u_2 - c_{23}u_3), \tag{4.1b}$$

$$\frac{\partial u_3}{\partial t} = \mu_3 \Delta u_3 + u_3(a_3 + c_{31}u_1 + c_{32}u_2 - u_3), \tag{4.1c}$$

with zero Dirichlet conditions imposed on each component u_i on $\partial\Omega$. We shall in fact assume throughout this section, without further comment that the boundary conditions are *always* of zero Dirichlet type. We remark that so long as intraspecific competition holds for each species, the coefficient of u_i in the ith equation may be taken to be unity without loss of generality since this may be achieved by a rescaling.

A number of conditions will be imposed on the system in order first to ensure that the first two species behave like prey and the third like a predator, and second to achieve permanence. In order to assist the reader some informal comments referring to Fig.1 will be made, this being intended to give a hint as to the direction of the (infinite dimensional) vector field near the equilibria. The most difficult part of the analysis is contained in section 3. There conditions are given which first ensure the existence of a unique interior equilibrium P_1 (i.e. a coexistence state) in the $u_1 - u_3$ face, and second its global attractivity (for orbits with u_1, u_3 initially non-trivial); similar conditions are obviously sufficient for the equilibrium P_2 in the $u_2 - u_3$ face. Second, in section 3, Lemma 3.3 and Corollary 3.4, conditions are given ensuring that there is no interior equilibrium in the $u_1 - u_2$ (competing species) face and that A_1 is globally attracting (in a similar sense). There may or may not be an equilibrium Q on the u_3-axis. The arrow at P_1 indicates that orbits starting near P_1 with $u_2 > 0$

are pushed into the interior, and so are not attracted to P_1; this is obviously a necessary condition for permanence. The other arrows indicate the situation at the other equilibria. The actual technical conditions yielding the directions of the vector fields near equilibria involve the sign of the eigenvalues for certain Dirichlet problems; for the corresponding Neumann problems these conditions reduce to assumptions on the signs of coefficients in (4.1). Consider then the following conditions.

(C1) *All the μ_i, a_i, c_{ij} are constants and*

(a) $\mu_i > 0 \quad (i = 1,2,3)$
(b) $c_{ij} > 0 \quad (i,j = 1,2,3,\ i \neq j)$.

(C2) *Let ρ_1, ϕ_1 be the principal eigenvalue and eigenfunction respectively of $-\Delta$ on Ω, and assume that*

(a) $a_1 > \mu_1\rho_1$;
(b) $a_2 > \mu_2\rho_1$.

It is clearly equivalent to assume that $\sigma_1, \sigma_2 > 0$ where σ_i the largest eigenvalue of

$$\mu_i\Delta\phi_1 + a_i\phi_1 = \sigma_i\phi_1. \tag{4.2}$$

From Lemma 3.1 these conditions ensure that there are unique equilibria $(\overline{u}_1, 0, 0)$ and $(0, \overline{u}_2, 0)$ on each of the u_1, u_2 axes respectively and that these attract all orbits except 0 in these axes.

We do not yet impose any restriction on the u_3-axis, but note that if $a_3 > \mu_3\rho_1$ there will be an equilibrium Q in this axis whereas if $a_3 < \mu_3\rho_1$ there will be no such equilibrium.

(C3) *The conditions of Lemma* 3.3 or *Corollary* 3.4 *hold, which implies inter alia that the largest eigenvalue σ_3 of*

$$\mu_1\Delta\phi_3 + (a_1 - c_{12}\overline{u}_2)\phi_3 = \sigma_3\phi_3 \tag{4.3}$$

is greater than zero.

Recall that it follows that $(\overline{u}_1, 0, 0)$ is globally attracting in the $u_1 - u_2$ face if $u_1 \neq 0$ initially.

(C4) *There are unique globally attracting equilibria $P_1(\hat{u}_1, 0, \hat{u}_3)$ in the interior of the $u_1 - u_3$ face and $P_2(0, u_2^*, u_3^*)$ in the interior of the $u_2 - u_3$* face. Sufficient conditions are given by Lemmas 3.6 and 3.7. It follows from Lemma 3.8 that $\sigma_4 > 0$ and $\sigma_5 > 0$ where σ_4 and σ_5 are the largest eigenvalues of the following problems:

$$\mu_3\Delta\phi_4 + (a_3 + c_{31}\overline{u}_1)\phi_4 = \sigma_4\phi_4; \tag{4.4}$$

$$\mu_3\Delta\phi_5 + (a_3 + c_{32}\overline{u}_2)\phi_5 = \sigma_5\phi_5. \tag{4.5}$$

If $a_3 > \mu_3\rho_1$ so that $Q = (0, 0, \overline{u}_3)$ with $\overline{u}_3 > 0$ exists then Lemma 3.8 also implies that $\sigma_6 > 0$ and $\sigma_7 > 0$ where σ_6 and σ_7 are the largest eigenvalues of the following problems:

$$\mu_1\Delta\phi_6 + (a_1 - c_{13}\overline{u}_3)\phi = \sigma_6\phi_6; \tag{4.6}$$

$$\mu_2\Delta\phi_7 + (a_2 - c_{23}\overline{u}_3)\phi_7 = \sigma_7\phi_7. \tag{4.7}$$

Hypotheses C3 and C4 are really just conditions on the dynamics of the pairwise interactions between species. By C3, the first competitor excludes the second in the absence of the predator. By C4, the predator can coexist (at a stable equilibrium) with either of the prey species.

(C5) *Let σ_8 and σ_9 be the largest eigenvalues of*

$$\mu_1\Delta\phi_8 + (a_1 - c_{12}u_2^* - c_{13}u_3^*)\phi_8 = \sigma_8\phi_8; \tag{4.8}$$

$$\mu_2\Delta\phi_9 + (a_2 - c_{21}\hat{u}_1 - c_{23}\hat{u}_3)\phi_9 = \sigma_9\phi_9, \tag{4.9}$$

and assume $\sigma_8 > 0$ and $\sigma_9 > 0$.

Condition (C5) ensures that near P_2 when $u_1 > 0$ the vector field points inward toward the interior of the positive cone, and that an analogous condition holds near P_1. The biological interpretation of (C5) is that each equilibrium with the predator and one prey species present is unstable relative to the other prey species; i.e. if the predator and one prey are at equilibrium and a small number of the second prey are introduced then the second prey species increase in numbers. This is known in the biological literature as "invasibility," as it means that each prey species can invade a region in which the predator and the other prey are at equiblibrium.

Theorem 4.1. Under conditions (C1)-(C5) permanence holds for the system (4.1) in the sense of Definition 1.1.

Proof. Dissipativity follows easily from Lemma 3.2, so we can apply Theorem 2.5 directly. Observe next that the assumed conditions imply that the ω-limit set of the boundary consists exactly of the equilibria $0, A_1, A_2, P_1, P_2$ and Q (if this exists). Thus the plan is to take the isolated covering $\bigcup M_n$ (described in section 2) to be these points themselves. We must show

(i) that this covering is isolated,

(ii) $W^s(M_n) \cap Y_0 = \emptyset$, and (iii) that the covering is acyclic. To establish (i) and (ii) it is convenient to write down a simple preliminary lemma.

Lemma 4.2. Suppose $f \in C^2(\overline{\Omega}, I\!R)$ and $\mu > 0$. Let λ be the largest eigenvalue (with corresponding eigenfunction ϕ) of the problem

$$\mu\Delta\phi + f(x)\phi = \lambda\phi, \tag{4.10}$$

and assume that $\lambda > 0$. Suppose that for some $k > 0$ and $\varepsilon \in (0, \lambda)$, u satisfies the following in a neighborhood U of 0 in $C^1_{0+}(\overline{\Omega})$:

$$\begin{aligned} \frac{\partial u}{\partial t} &\geq \mu\Delta u + [f(x) - \varepsilon]u, \\ u(x,0) &\geq k\phi(x) \qquad\qquad (x \in \overline{\Omega}). \end{aligned} \tag{4.11}$$

Then for $u \in U$,

$$u(x,t) \geq ke^{(\lambda-\varepsilon)t}\phi(x).$$

Proof. With $v(x,t) = ke^{(\lambda-\varepsilon)t}\phi(x)$,

$$\left\{\frac{\partial u}{\partial t} - \mu\Delta u - [f(x) - \varepsilon]u\right\} - \left\{\frac{\partial v}{\partial t} - \mu\Delta v - [f(x) - \varepsilon]v\right\}$$

$$= \left\{\frac{\partial u}{\partial t} - \mu\Delta u - [f(x) - \varepsilon]u\right\} - ke^{(\lambda-\varepsilon)t}\{-\mu\Delta\phi - [f(x) - \lambda]\phi\}$$

$$\geq 0,$$

by (4.10) and (4.11). The result follows from a standard comparison principle. (We are working in C^1_{0+} but the result is still valid in $C^0_{0+}(\overline{\Omega})$.)

We need to prove (i) and (ii) for each equilibrium. The proofs are essentially the same with only minor differences so it will be enough to illustrate by considering a typical calculation, and we choose the point A_1 for this purpose. To prove that A_1 is isolated we must show that there is a neighborhood of A_1 which does not contain a full orbit (other than A_1 itself). We shall argue by contradiction and assume that every neighborhood of A_1 contains a full orbit.

Suppose first that such an orbit lies in the u_1-axis in a small neighborhood of A_1, and note that by (C2) A_1 is a global attractor for all orbits in the axis except 0. Then by compactness its α-limit set is non-empty and disjoint from A_1 (since this is attracting.) But the existence of the α-limit set contradicts the attractivity of A_1. Assumption (C3) shows by a similar argument that such an orbit cannot lie in the $u_1 - u_2$ face. Thus if such an orbit exists, for any point of the orbit $u_3 > 0$ ($x \in \Omega$). We shall show that such an orbit exits from every sufficiently small neighborhood U of A_1. For by the strong maximum principle, for any full orbit with $u_3 \geq 0$ and $u_3 \not\equiv 0$ we must have $u_3(x,t) \geq k(t)\phi_4(x)$ for some $k(t) > 0$; in particular there exists a $k > 0$ so that on $u_3(x,0) \geq k\phi_4(x)$ for $x \in \overline{\Omega}$. (Here ϕ_4 is the eigenfunction defined in (4.4)). It is clear from (4.1c) that for any given value of $\varepsilon > 0$ we can choose a neighborhood U of $A_1 = (\overline{u}_1, 0, 0)$ so that in U, $\dfrac{\partial u_3}{\partial t} - \mu_3\Delta u_3 - u_3(a_3 + c_{31}\overline{u}_1 - \varepsilon) \geq 0$. Choose $\varepsilon \in (0, \sigma_4)$, then choose such a neighborhood U. It follows from Lemma 4.2 that u_3 must increase until (u_1, u_2, u_3) exits U, so that U cannot in fact contain a full orbit. Therefore A_1 is isolated. A similar argument shows that $W^s(A_1) \cap Y_0 = \emptyset$, since at any point of Y_0 sufficiently close to A_1 the component u_3 must increase so (u_1, u_2, u_3) cannot approach A_1 along $W^s(A_1)$.

The final step in the proof is to rule out the existence of a cycle in the boundary as defined in section 2. We shall give the proof for the slightly more difficult case when there is an equilibrium Q in the u_3-axis. We first note that by (C4), P_1 and P_2 are attracting and so clearly cannot form a part of a cycle. Also by (C2) and (C4) the origin 0 is repelling and so also cannot form part of a cycle. Thus only A_1, A_2 and Q need be considered. However, any orbit in the $u_1 - u_3$ face (apart from the axes) is attracted to P_1, which as remarked above cannot be a part of a cycle. Thus A_1 cannot be chained to itself, Q to itself, nor can A_1 and Q be chained by an orbit in the $u_1 - u_3$ face. Similar remarks apply to the $u_2 - u_3$ face. The only other possibility is that A_1 and A_2 are cyclic. But this is obviously impossible as by (C3) A_1 is globally attracting in the $u_1 - u_2$ plane. This rules out the existence of a cycle and completes the proof of permanence. The same sort of argument applies when there is no predator equilibrium Q; that case is actually slightly simpler since there is one less equilibrium to consider.

In general conditions (C3)-(C5) may be difficult to check analytically. However, in the special cases treated in Corollary 3.4 and Lemma 3.6 we can find sufficient conditions for permanence in terms of the coefficients of the system. We collect the hypotheses as follows:

$$\text{(C6)} \qquad \mu_i = 1, \quad a_i = a > \rho_1, \quad i = 1,2,3$$
$$c_{12} < 1 < c_{21}$$
$$c_{i3} < 1, \quad c_{i3}c_{3i} < 1, \quad i = 1,2$$
$$c_{12}(1 - c_{23}) + c_{13}(1 + c_{32}) < 1 + c_{23}c_{32}$$
$$c_{21}(1 - c_{13}) + c_{23}(1 + c_{31}) < 1 + c_{13}c_{31}$$

(Recall that ρ_1 is the principal eigenvalue for $-\Delta\phi = \rho\phi$.)

The first condition is imposed to facilitate computation. Under that condition, the next two conditions in (C6) are the hypotheses of Corollary 3.4 and Lemma 3.6, and they imply (C2), (C3), and (C4). The second condition implies that u_1 will force u_2 to extinction in the absence of u_3 by virtue of superior competitive ability. The third condition implies that either u_1 or u_2 alone could coexist at a unique equilibrium with the predator u_3. The last two conditions imply that each equilibrium with only one competitor and the predator present is unstable with respect to the other competitor, that is, that (C5) holds. Under the hypotheses of Lemma 3.6 we find that $u_2^* = [(1 - c_{23})/(1 + c_{23}c_{32})]\theta[a]$, $u_3^* = [(1 + c_{32})/(1 + c_{23}c_{32})]\theta[a]$ (recall the definition of $\theta[m(x)]$ immediately following formula (3.8)), so that (4.8) becomes under (C6)

$$\Delta\phi_8 + (a - [(c_{12}(1 - c_{23}) + c_{13}(1 + c_{32}))/(1 + c_{23}c_{32})]\theta[a])\phi_8 = \sigma_8\phi_8. \qquad (4.12)$$

We note that the largest eigenvalue of $\Delta\phi + (a - \theta[a])\phi = \sigma\phi$ is $\sigma = 0$ since for $\sigma = 0$, $\theta[a] > 0$ is an eigenfunction. It follows from monotonicity of eigenvalues that the largest eigenvalue of $\Delta\phi + (a - \delta\theta[a])\phi = \sigma\phi$ is positive if $\delta < 1$ and negative if $\delta > 1$. Using $\delta = (c_{12}(1-c_{23})+c_{13}(1+c_{32}))/(1+c_{23}c_{32})$ we see that $\delta < 1$ is equivalent to the fourth inequality of (C6), so that (C6) implies $\sigma_8 > 0$ in (4.8). Similarly, the last inequality in (C6) implies $\sigma_9 > 0$ in (4.9), so (C5) holds and thus Theorem 4.1 yields the following:

Corollary 4.3. Under condition (C6) permanence holds for the system (4.1) in the sense of Definition 1.1.

Remark: It is not too difficult to verify that the algebraic conditions of (C6) are satisfied for values of a, c_{ij} lying in some nonempty open subset of $\mathbb{R}_+^7$.

5. PERMANENCE FOR THREE COMPETING SPECIES.

In the previous section an application of Theorem 2.5 was given. We now turn to a situation where this theorem does not appear to be applicable since it does not seem to be possible to find an acyclic cover of $\omega(\partial Y_0)$. The model was originally studied in an ordinary differential equation context, see [36], [40] and [25], and it is then possible to give a sharp condition for permanence. This is also the case for a reaction-diffusion model when homogeneous Neumann conditions are imposed; a proof may be given by an amendment of the argument in [26], see also the remarks in [27, Chapter 4].

The problem is a great deal more difficult under homogeneous Dirichlet conditions. Here we shall consider a rather special case and present the best result we are able to obtain. Some general remarks concerning the status of this problem are made at the end of this section.

Consider the system

$$\frac{\partial u_1}{\partial t} = \mu\Delta u_1 + u_1(1 - u_1 - \alpha u_2 - \beta u_3), \tag{5.1}$$

$$\frac{\partial u_2}{\partial t} = \mu\Delta u_2 + u_2(1 - u_2 - \alpha u_3 - \beta u_1), \tag{5.2}$$

$$\frac{\partial u_3}{\partial t} = \mu\Delta u_3 + u_3(1 - u_3 - \alpha u_1 - \beta u_2), \tag{5.3}$$

with $u = 0$ on $\partial\Omega$. Assume that $\mu > 0$ and $0 < \alpha < 1 < \beta$. The structure of the nonlinearity is admittedly rather special; however, special cases of this type have played a major role in the development of our understanding of Lotka-Volterra models as in [3,9] and even appear in the biological literature as in [36,41]. In order to construct an appropriate average Liapunov function, certain eigenvalue problems must be introduced.

Let ρ_1 be the principal eigenvalue for the problem

$$-\Delta\phi = \rho\phi \tag{5.4}$$

with $\phi = 0$ on $\partial\Omega$. Then by Lemma 3.1 the assumption $\mu < \rho_1^{-1}$ insures that there exists a unique steady state $(\overline{u}, 0, 0)$ with $\overline{u} > 0$ on the semi-axis $u_1 > 0$, $u_2 = u_3 = 0$ which is a global attractor for all initial values on this semi-axis. Thus $\overline{u}$ satisfies

$$\mu\Delta\overline{u} + \overline{u}(1 - \overline{u}) = 0 \tag{5.5}$$

with $\overline{u} = 0$ on $\partial\Omega$. Now let σ, ψ be the largest eigenvalue and corresponding eigenvector respectively for the problem

$$\mu\Delta\psi + (1 - \alpha\overline{u})\psi = \sigma\psi \tag{5.6}$$

with $\psi = 0$ on $\partial\Omega$, and assume that $\sigma > 0$.

The application of Theorem 2.4 to give a sufficient condition for permanence is next considered. Recall that the set S defined in section 2 consists essentially of a part of the three 'faces' obtained by setting $u_1 = 0$, $u_2 = 0$ and $u_3 = 0$ in turn. As average Liapunov function take

$$\begin{aligned} P(v) &= \prod_{i=1}^{3} \int_\Omega \psi v_i dx \\ &= \exp\left\{\sum_{i=1}^{3} \log \int_\Omega \psi v_i dx\right\}, \end{aligned} \tag{5.7}$$

where ψ satisfies (5.6). From (5.7) computation yields

$$\frac{P(v.t)}{P(v)} = \exp\left\{\int_0^t dt \left[\sum_{i=1}^{3} \int_\Omega \psi v_{it} dx \Big/ \int_\Omega \psi v_i dx\right]\right\}. \tag{5.8}$$

It is necessary to take certain limits as v tends to points in $\omega(S)$. Here only the formal stages in the argument are presented; in view of the smoothness of solutions of reaction-diffusion systems proofs are not difficult to supply, and they are given in detail in [8]. Note that from Lemma 3.3 and Corollary 3.4, $\omega(S)$ consists of four equilibria, the origin and the equilibria $(\overline{u},0,0)$, $(0,\overline{u},0)$ and $(0,0,\overline{u})$ on the axes.

For $(\overline{u},0,0)$ we have from (5.1)

$$\begin{cases} \liminf_{(v_1,v_2,v_3)\to(\overline{u},0,0)} \int_\Omega \psi v_{1t} dx / \int \psi v_1 dx \\ = \liminf_{(v_1,v_2,v_3)\to(\overline{u},0,0)} \int_\Omega \psi[\mu\Delta v_1 + v_1(1 - v_1 - \alpha v_2 - \beta v_3)]dx / \int_\Omega \psi v_1 dx \\ = 0 \end{cases}$$

from (5.5). Also, using first (5.2) and Green's Theorem,

$$\begin{aligned} &\liminf_{(v_1,v_2,v_3)\to(\overline{u},0+,0+)} \int_\Omega \psi v_{2t} dx / \int_\Omega \psi v_2 dx \\ &= \liminf_{(v_1,v_2,v_3)\to(\overline{u},0+,0+)} \int_\Omega \psi[\mu\Delta v_2 + v_2(1 - v_2 - \alpha v_3 - \beta v_2)]dx / \int_\Omega \psi v_2 dx \\ &= \liminf_{(v_1,v_2,v_3)\to(\overline{u},0+,0+)} \int_\Omega v_2[\mu\Delta\psi + \psi(1 - v_2 - \alpha v_3 - \beta v_1]dx / \int_\Omega \psi v_2 dx \\ &= \liminf_{v_2\to 0+} \int_\Omega v_2[\mu\Delta\psi + \psi(1 - \beta\overline{u})]dx / \int_\Omega \psi v_2 dx \\ &= \sigma + \liminf_{v_2\to 0+}(\alpha - \beta) \int_\Omega \psi v_2 \overline{u} dx / \int_\Omega \psi v_2 dx, \end{aligned} \tag{5.9}$$

where the last step follows from a rearrangement of the term in the square bracket and use of (5.6). The second term in the last equation is evidently

$$(\alpha - \beta) \limsup_{v_2\to 0+} \int_\Omega \psi v_2 \overline{u} dx / \int_\Omega \psi v_2 dx.$$

The lim sup term is clearly not greater than $\| \overline{u} \|_0$. On the other hand this maximum value is certainly attained, for v_2 could tend to 0+ through a sequence of smooth functions with successively smaller supports in a neighborhood of a point where $\overline{u}$ has its maximum. Thus the contribution of this term is $(\alpha - \beta) \| \overline{u} \|_0$, and the right hand side of (5.9) is $\sigma - (\beta - \alpha) \| \overline{u} \|_0$. A similar calculation for the last term in the sum in (5.8) shows that its contribution is σ. Thus

$$\liminf_{(v_1,v_2,v_3)\to(\overline{u},0,0)} \sum_{i=1}^{3} \int_\Omega \psi v_{it} dx / \int_\Omega \psi v_i dx = 2\sigma - (\beta - \alpha) \| \overline{u} \|_0 .$$

From the symmetry of the system (5.1)-(5.3) the calculation is analogous for the other equilibria on the axes. The origin $(0,0,0)$ also lies in $\omega(S)$, but an easy calculation shows that its contribution to the square bracketed term is always positive. Also a simple argument using super solutions shows that (H2) and (H3) hold. Finally applying Theorems 2.4 and 2.7 we obtain the following result.

Theorem 5.1. Suppose that (H1)(b) holds, and assume that $0 < \mu < \rho_1^{-1}$ and $0 < \alpha < 1 < \beta$. Then the system (5.1)-(5.3) under zero Dirichlet conditions is permanent if

$$2\sigma - (\beta - \alpha) \parallel \overline{u} \parallel_0 > 0, \tag{5.10}$$

where $\overline{u}$ is defined by (5.5) and σ by (5.6).

For the reaction analogue of (5.1)-(5.3) the condition $\alpha + \beta < 2$ is known to be necessary and sufficient for permanence, see [40], and it is possible to prove that this is also the case for the reaction-diffusion system (5.1)-(5.3) under zero Neumann conditions. It is therefore of interest to enquire how near (5.10) is to being a necessary condition. If $\mu \to 0$, clearly $\overline{u} \to 1$ (in L_1), and the condition $\alpha + \beta < 2$ is recovered from (5.10), which is thus near to sharp for small μ. However, if μ is not small it is unlikely that (5.10) is sharp. It seems likely that to obtain a sharp condition a much more clever choice of average Liapunov function is necessary, and we have been unable to make any progress in obtaining such a function.

From a different point of view, if μ is not small but $\mu = (1-\varepsilon)/\rho_1$ where ε is small ($\rho_1; \phi$ being defined by (5.4)), a simpler form of (5.10) may be obtained. A formal calculation shows that (5.10) becomes to first order in ε,

$$2(1 - \alpha) - (\beta - \alpha)k > 0, \tag{5.11}$$

where

$$k = \parallel \phi \parallel_0 / \int_\Omega \phi^3.$$

It would probably not be hard to justify this rigorously, but (5.11) is perhaps of rather limited interest, so we shall not pursue this point further here. Some related results in a different context are obtained by local bifurcation theory in [4]; see also [15].

Finally, one might consider taking a more general system than (5.1)-(5.3), for example by considering unequal diffusion rates. Although some progress may be made along the above lines, the resulting conditions are rather complicated, and it is not easy to determine whether they would hold for a range of interest of the parameter values.

6. GENERAL CONCLUSIONS.

The results of sections 4 and 5 demonstrate how the idea of permanence may be used to study models for three interacting species with diffusion. An approach using permanence or some related idea is probably necessary since even models for three species without diffusion may have periodic orbits or perhaps even more complicated dynamics; see [25,36,40]. As noted in [8], permanence implies the presence of a coexistence equilibrium, but in general the converse is false. Our results could be extended or refined in several ways. We have not attempted a systematic treatment of Lotka-Volterra type models for three species, and have not even considered more complicated models. In principle it would be possible to treat very general reaction terms as is done for two species in [8]; however, the analysis of section 3 and verification of hypotheses analogous to (C3)-(C5) of section 4 become more complicated and less illuminating in very general situations. Many forms of Lotka-Volterra systems could be treated by the methods of sections 4 and 5. In particular, systems with three competitors in which some pairs of competitors have globally stable coexistence states could be treated as in section 4. Conditions under which diffusive Lotka-Volterra models for two competitors have stable coexistence states are discussed for example in [1,5,9]. It would be fairly easy to treat models with spatially varying coefficients. The main difference would be in the conditions involving eigenvalues, which would in some cases become more complicated. We have chosen the specific examples we have treated because they are mathematically representative and at least historically of biological interest. The example of section 4 displays the biologically important but somewhat counterintuitive phenomenon of predator mediated coexistence (see [25]) in which two competitors can coexist only in the presence of a predator which controls the population of the superior competitor. The example of section 5 is a diffusive version of the model used in [36] to show that three competing species may have periodic cycles.

The hypotheses involving eigenvalues lead to elliptic problems that could be further analyzed in several ways. For specific cases, numerical methods such as those discussed in [43] could be used. Various estimates of eigenvalues in terms of parameters could be given as in [4-8,15,29,35,37]. Specific applications of that approach to some ecological questions are discussed in [7]. Only in fairly special cases can eigenvalue conditions be verified by simple algebraic computation. One such case is characterized by hypothesis (C6).

There remain many open questions about the dynamics of reaction-diffusion models for three interacting species, and about the techniques we have used to study them. The examples we have treated show that approaches based on the idea of permanence can be effective in translating dynamic questions into static ones, specifically elliptic eigenvalue problems. Since eigenvalue problems have been widely studied and since eigenvalues typically depend strongly on domain geometry, such a translation is useful in analyzing spatial effects; see [5] for more discussion. We hope that our work will stimulate others to investigate other models or to study further some of the problems we have considered here.

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