ROCKY MOUNTAIN
JOURNAL OF MATHEMATICS
Volume 26, Number 1, Winter 1996

ECOLOGICAL MODELS, PERMANENCE AND SPATIAL HETEROGENEITY

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ABSTRACT. We model the interactions of two theoretical populations which are allowed to move at random throughout a bounded habitat via systems of two weakly coupled reaction-diffusion equations. The reaction terms in these systems involve parameters which are subject to biological interpretation and which are assumed to be spatially dependent. We examine the effect of spatial heterogeneity on the long-term viability of each of the populations, with the aim of quantifying the effect in terms of the biological parameters in the models. To this end, we employ the dynamic concept of permanence of the interacting populations, conditions for which lead directly to the spectral theory for linear elliptic boundary value problems, so that the long-term viability of the populations can be expressed in terms of eigenvalues depending on the biological parameters of the models in directly quantifiable ways. We give a number of examples and demonstrate for the first time via reaction-diffusion equations that spatial heterogeneity can lead to coexistence in situations wherein extinction would result, were the habitat spatially homogeneous.

1. Introduction. In this article we continue the examination of the long-term dynamics of two interacting species which was begun in [**14**]. We assume that the species are free to move at random throughout some bounded habitat. Under this assumption, we model the interaction of the species via a system of partial differential equations of the form

$$(1.1) \qquad \begin{cases} u_{i_t} = \mu_i \Delta u_i + f_i(x, u_1, u_2)u_i & \text{in } \Omega \times (0,\infty), \\ B_i u_i = 0 & \text{on } \partial\Omega \times (0,\infty), \\ u_i(x,0) = u_i^0(x) \geq 0 & \text{in } \Omega, \end{cases}$$

$i = 1, 2$, where u_i denotes the *population density* of the ith interacting species, $\Omega \subseteq \mathbf{R}^N$ (usually $N = 2$ or 3) is the habitat in question and

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Received by the editors on August 25, 1993, and in revised form on July 1, 1994.
AMS (MOS) *Subject Classifications.* 92D40, 35K57.
Research of the first and second authors supported in part by NSF grants DMS 8802346 and DMS 9002943.

the homogeneous boundary condition B_i represents (usually) either a barrier (i.e., $B_i u_i = \partial u_i/\partial \nu$, the outer normal derivative) or a completely hostile exterior (i.e., $B_i u_i = u_i$). Here u_{i_t} denotes $\partial u_i/\partial t$ and, as usual, $\Delta = \partial^2/\partial x_1^2 + \cdots + \partial^2/\partial x_N^2$ is the Laplace operator (accounting for the freedom of motion for each species), $\mu_i > 0$ is the diffusion rate for the ith species, and $f_i(x, u_1, u_2)$ is the local per capita growth law for the ith species (accounting for possible spatial heterogeneity in the habitat and for the effects of interspecies interactions).

There are two fundamental, related questions of biological interest concerning the model. First, is the effect of interspecies interaction the long-term survival of both of the species, i.e., coexistence? Second, how is the answer to the first question affected by the spatial variation in the problem? (Here the spatial variation is due to the random motion of the species and the possible spatial heterogeneity in the habitat.) In order to address the first question, it is necessary to give a precise notion of what is meant by long-term coexistence. If (1.1) admits a globally attracting componentwise-positive equilibrium, we would certainly say that we have long-term coexistence for the species modeled by (1.1). However, a globally attracting componentwise positive equilibrium is far too restrictive a notion to use for long-term coexistence since, for example, a globally attracting componentwise positive periodic orbit (representing a stable fluctuation in the population densities) should surely also be a guarantee of long-term coexistence. Consequently, we employ the more inclusive notions of long-term coexistence in $[C(\overline{\Omega})]^2$ in (1.1) of *uniform persistence* and *permanence*. We say that (1.1) is *uniformly persistent* if there are continuous functions on $\overline{\Omega}$, say v_1 and v_2, with $v_i(x) > 0$ for $x \in \Omega$ and $i = 1, 2$, so that the solution to (1.1) corresponding to $u_1^0(x) \not\equiv 0$ and $u_2^0(x) \not\equiv 0$ has the property that there is a t_0 depending only on u_1^0 and $u_2^0 (t_0 = t_0(u_1^0, u_2^0))$ so that

$$u_i(x,t) \geq v_i(x)$$

for $x \in \overline{\Omega}$ and $i = 1, 2$, provided $t \geq t_0$. If, in addition, there are constants V_1 and V_2 so that

$$u_i(x,t) \leq V_i$$

for $x \in \overline{\Omega}$, $i = 1, 2$, $t \geq t_0$, we say that (1.1) is *permanent.*

In [**14**], we established conditions which guarantee permanence in (1.1). We favored permanence as a notion of long-term survival of both species over the slightly less restrictive uniform persistence since it is biologically quite reasonable to expect whatever conditions we impose on (1.1) to prohibit unbounded growth in the densities u_1 and u_2 as $t \to \infty$. The criterion for permanence in the context of (1.1) in [**14**] was expressed in terms of the signs of eigenvalues to linear elliptic differential equations whose coefficients are closely related to the coefficients in (1.1). As a consequence, in determining conditions for permanence, we were also implicitly measuring the effect of the geometry of the habitat and the spatial variation therein on the question of the long-term survival of both species. In this present article we use the criterion established in [**14**] as a starting point to explore the effect of spatial heterogeneity on the predictions for coexistence of the species modeled by (1.1). Our approach is to analyze several specific but representative examples. In particular, we focus on Lotka-Volterra systems wherein growth rates and/or interaction rates are allowed to vary with location. Such models not only provide good examples for illustrating our techniques but also have biological implications of independent interest. For example, one of the biological conclusions that we draw is that spatial heterogeneity permits coexistence in situations when it would not be possible in a spatially homogeneous environment. This phenomenon has been observed elsewhere, though not deduced from a reaction-diffusion model.

The remainder of the article is structured as follows. In Section 2 we reinterpret the conditions $\sigma_1 > 0$ and $\sigma_2 > 0$ from Theorem 1.1 so as to highlight the interrelations among the biological parameters of the system that permit the assertion of permanence in (1.1). We then use the results to explore the interplay among diffusion, spatial heterogeneity, species interaction and habitat geometry that will guarantee permanence. In Section 3 we consider some examples with nontrivial spatial variation that nevertheless permit exactly computable conditions for permanence, sometimes involving well-known classical special functions. In Section 4 we discuss the role of spatial heterogeneity in maintaining biodiversity. Specifically, we give in Theorem 4.2 conditions under which spatial heterogeneity may permit coexistence of competitors in situations when it would not be possible in a spatially homogeneous environment. Finally, our analysis requires some new results on a single diffusive logistic equation subject to homogeneous Neumann boundary data, and these are presented in the Appendix.

Before recalling the criterion for permanence in (1.1) that will serve as the point of departure for our present analysis, we briefly describe its development. A full, detailed presentation of the development is available to the interested reader in [**14**], and we make no attempt to duplicate that effort here. However, we believe that it is particularly important that this article be reasonably self-contained, since we hope the paper will be read by mathematical and biological scientists, and we believe a brief summary of the development of our criterion for permanence in (1.1) is necessary to achieve the goal of self-containment.

To begin, we use the theory of reaction-diffusion equations as presented in [**26**] to formulate (1.1) as a semi-dynamical system in an appropriate Banach space, where we employ the theory of semi-dynamical systems as in [**18, 21**] to obtain permanence in the context of semiflows. We then show that this notion of permanence implies permanence of (1.1) in the sense previously described in this paper. The choice of Banach space is contingent upon the boundary data imposed in (1.1). The reason for this is that the *dynamical systems machinery we use requires a cone with nonempty interior upon which the semiflow in question is forward invariant*. In the case of (1.1), this cone corresponds to ordered pairs of nonnegative functions. In case both u_1 and u_2 in (1.1) are subject to a homogeneous Neumann boundary condition, it suffices to consider the Cartesian product $[C(\overline{\Omega})]^2$ of continuous functions on $\overline{\Omega}$. In this case the interior of the cone of ordered pairs of nonnegative functions consists of ordered pairs of functions which are positive on $\overline{\Omega}$, and the parabolic maximum principle guarantees $u_i(x,t) > 0$ on $\overline{\Omega}$ for $i = 1, 2$, and $t > 0$ (so long as $u_i(x,0) \not\equiv 0$). However, the cone of ordered pairs of nonnegative functions fails to have interior in the closed subspace $[C_0(\overline{\Omega})]^2$ of $[C(\overline{\Omega})]^2$ determined by the additional requirement that the functions vanish in $\partial\Omega$. Consequently, in the case of zero Dirichlet boundary data on u_1 and u_2 in (1.1), we use the Banach space $[C_0^1(\overline{\Omega})]^2$ of ordered pairs of continuously differentiable functions which vanish on $\partial\Omega$, for the cone of pairs of nonnegative functions in this case has interior

$$\left\{(v_1, v_2) : v_i(x) > 0 \text{ on } \Omega \text{ and } \frac{\partial v_i}{\partial \nu} < 0 \text{ on } \partial\Omega,\ i = 1, 2\right\}.$$

The first step in showing that the semiflow π arising from (1.1) is permanent is demonstrating the existence of a compact global attractor, say $\mathcal{A}$, relative to the cone Y of ordered pairs of nonnegative functions. By a result of Bilotti and LaSalle [**5**] (see also [**18**]), a compact global attractor is assured if we know that π is point dissipative (i.e., there is a bounded subset U of Y so that $\pi((u_1^0(x), u_2^0(x)), t) \in U$ for all $t \geq t_0$, where t_0 is a fixed time dependent only on (u_1^0, u_2^0) and U) and that $\pi(\cdot, t) : Y \to Y$ is compact for $t > 0$. We meet these requirements on π by the assumptions we make upon the local per capita growth laws f_1 and f_2 in (1.1). These assumptions are biologically reasonable and allow us to conclude point dissipativity for π in the $[C(\overline{\Omega})]^2$ topology on Y as detailed in Section 4 of [**14**]. We must require a self-regulatory mechanism for at least one of f_1 and f_2. For specificity, let us say that $f_1(x, v_1, v_2) < 0$ when $v_1 > M$ independent of choice of $x \in \overline{\Omega}$ and $v_2 \geq 0$. We then either require an analogous self-regulatory mechanism for f_2 or require that $f_2(x, v_1, v_2)$ be bounded above for v_1 bounded independent of choice of $x \in \overline{\Omega}$ and $v_2 \geq 0$ and that f_1 and f_2 satisfy a compatibility condition of the form (4.9) in [**14**]. This last alternative permits us to treat certain commonly arising predator-prey interactions that lack self-regulation on the predator (e.g., $f_2(x, v_1, v_2) = -d + m(x)v_1$). (It is worth noting at this point that in cases in which we hypothesize a self-regulation condition on both u_1 and u_2, dissipativity in the $[C(\overline{\Omega})]^2$ topology follows in much the same way as in a comparable system of ordinary differential equations, whereas the dissipativity arguments for predator-prey systems without self-limitation on the predator are considerably more complicated.) Once the dissipativity in the $[C(\overline{\Omega})]^2$ topology is established, the theory of reaction-diffusion equations allows us to deduce the point dissipativity of π in the $[C_0^1(\overline{\Omega})]^2$ topology in the case of zero Dirichlet boundary data as well as the compactness of $\pi(\cdot, t)$ for $t > 0$ (in whatever topology is suitable for the boundary data). See [**14**, Section 3]. In particular, we show there that if U is a $[C^m(\overline{\Omega})]^2$ bounded set for $m = 0$ or $m = 1$ and $t_0 > 0$, $\pi(U, t)$ is bounded in $[C^{m+1}(\overline{\Omega})]^2$ for $t > t_0$, with the bound in $[C^{m+1}(\overline{\Omega})]^2$ dependent only on t_0 and the $[C^m(\overline{\Omega})]^2$ bound on U. It follows immediately that $\pi(U, t)$ is compact in $[C^m(\overline{\Omega})]^2$ for $t > 0$ and that π is point dissipative in $[C_0^1(\overline{\Omega})]^2$ in the Dirichlet case. (We note in passing that there is a bounded set B in $[C^2(\overline{\Omega})]^2$ such that if $U \subseteq [C^1(\overline{\Omega})]^2$ is bounded, $\pi(U, t) \subseteq B$ for all $t \geq t_0$. Here t_0 depends upon the $[C^1(\overline{\Omega})]^2$ norm of U; in particular, t_0

is not equal to 1 for all U, as incorrectly stated in Theorem 3.3 of [**14**]. We thank one of the referees for this paper for calling our attention to this misstatement.)

Once the existence of the global attractor $\mathcal{A}$ is established, it is possible to formulate the criterion for permanence that we will use, as already noted, to explore the effect of spatial heterogeneity on the predictions for coexistence of the species modeled by (1.1). Since $\pi((u_1^0(x), u_2^0(x)), t)$ lies in the ε neighborhood $B(\mathcal{A}, \varepsilon)$ of $\mathcal{A}$ (relative to Y) for all t sufficiently large for any $(u_1^0(x), u_2^0(x)) \in Y$, it suffices to consider the compact forward invariant (with respect to π) set $X = \overline{\pi(B(A,\varepsilon),[1,\infty))}$. Observe that $X = (X \cap \operatorname{int} Y) \cup (X \cap \partial Y)$ with $X \cap \operatorname{int} Y$ and $X \cap \partial Y$ forward invariant under π. Let $S = X \cap \partial Y$. Then $X \cap \operatorname{int} Y = X - S$, and we say that π is permanent provided there is a set $U \subseteq X - S$ (notice that U is automatically bounded in Y) so that $\inf_{u \in U} \operatorname{dist}(u, \partial Y) > 0$ while $\lim_{t \to \infty} \operatorname{dist}(\pi((u_1^0, u_2^0), t), U) = 0$ for all $(u_1^0, u_2^0) \in X - S$. (Again, we remind the reader that this definition of permanence is shown in [**14**] to imply the one we state in this paper for permanence of (1.1).) S corresponds to the set of solutions to (1.1) in which at least one component vanishes identically. The single equation models which consequently arise, namely,

$$\begin{cases} u_t = \mu \Delta u + f(x,u)u & \text{in } \Omega \times (0,\infty), \\ Bu = 0 & \text{on } \partial\Omega \times (0,\infty), \\ u(x,0) = u^0(x) \end{cases} \tag{1.2}$$

have been considered in the context of population dynamics since the classical papers of Skellam [**29**] in 1951 and Kierstead and Slobodkin [**24**] in 1953 and subsequently widely studied. In particular, we note the advances of Aronson and Weinberger [**3**], in which several forms for the nonlinearity f were considered in the case of one space dimension, and Hess (see [**19**] and references therein), in which $f(x,0)$ is allowed to change signs as x varies through Ω. A rather complete analysis of (1.2) suitable to our present needs is given in [**8**] in the case of Dirichlet boundary data. In particular, under mild and biological reasonable assumptions on the growth law f (namely, that the intrinsic growth rate for u at low densities $f(x,0)$ be positive for at least some $x \in \Omega$ and that u be subject to the self-regulatory condition $f(x,u)$ decreasing in u with $f(x,u) < 0$ for $u \leq M$) there will be a critical value $\mu_0 > 0$ so that for all $\mu \in (0, \mu_0)$ there is a unique globally attracting positive equilibrium $\bar{u} = \bar{u}(\mu)$ for (1.2). If $\mu \geq \mu_0$, all solutions to (1.2) decay to 0 as $t \to \infty$. The critical value $\mu_0 = 1/\lambda_1(f(x,0))$, where $\lambda_1(f(x,0))$ denotes the unique positive eigenvalue for

$$\begin{cases} -\Delta w = \lambda f(x,0)w & \text{in } \Omega, \\ w = 0 & \text{on } \partial\Omega, \end{cases} \tag{1.3}$$

admitting a positive eigenvector. (In the case of Neumann boundary data, there are analogous results. However, their formulation in this setting is more complicated and there is to our knowledge no treatment of them in the literature quite suitable to our needs. Consequently, we include a brief treatment in the appendix of this paper, not only to facilitate our study of systems in which a u_i is subject to zero Neumann boundary conditions, but also because the results are of independent mathematical and biological interest.)

Now consider (1.1) and suppose that $\mu_1 > 0$ and $\mu_2 > 0$ are such that

$$\begin{cases} u_{1t} = \mu_1 \Delta u_1 + f_1(x, u_1, 0)u_1 & \text{in } \Omega \times (0,\infty), \\ B_1 u_1 = 0 & \text{on } \partial\Omega \times (0,\infty), \\ u_1(x,0) = u_1^0(x) \geq 0 & \text{in } \Omega \end{cases} \tag{1.4}$$

and

$$\begin{cases} u_{2t} = \mu_2 \Delta u_2 + f_2(x, 0, u_2)u_2 & \text{in } \Omega \times (0,\infty), \\ B_2 u_2 = 0 & \text{on } \partial\Omega \times (0,\infty), \\ u_2(x,0) = u_2^0(x) \geq 0 & \text{in } \Omega, \end{cases} \tag{1.5}$$

admit globally attracting positive equilibria $\bar{u}_1$ and $\bar{u}_2$, respectively. We now have the following, the main result of our previous article [**14**].

Theorem 1.1. *Suppose that $\mu_1 > 0$ and $\mu_2 > 0$ are as above, and suppose in addition that $f_1(x,0,0) \geq f_1(x,0,\bar{u}_2(x))$ for all $x \in \Omega$. Let σ_1 and σ_2 denote the unique eigenvalues, respectively, of*

$$\begin{cases} \mu_1 \Delta \psi_1 + f_1(x,0,\bar{u}_2)\psi_1 = \sigma\psi & \textit{in } \Omega, \\ B_1 \psi_1 = 0 & \textit{on } \partial\Omega \end{cases} \tag{1.6}$$

and

$$\begin{cases} \mu_2 \Delta \psi_2 + f_2(x,\bar{u}_1,0)\psi_2 = \sigma\psi_2 & \textit{in } \Omega, \\ B_2 \psi_2 = 0 & \textit{on } \partial\Omega \end{cases} \tag{1.7}$$

admitting positive eigenvectors. Then (1.1) *is permanent if* $\sigma_1 > 0$ *and* $\sigma_2 > 0$.

Now that the main result of [**14**] has been recalled, some clarification and amplification are in order. First of all, for μ_1 and μ_2 to be as in the statement of Theorem 1.1 requires $\mu_i < 1/\lambda_1(f_i(x,0,0))$. The conditions on f_i for such to be the case when zero Neumann data is imposed in the ith equation of (1.1) are detailed in Theorem A.1 of the Appendix. Second, the extra condition $f_1(x,0,0) \geq f_1(x,0,\bar{u}_2)$ is a weak formulation of a requirement that the u_2 species have a detrimental effect upon the u_1 species, as for example, would a competitor or a predator. Third, the omega limit set $\omega(S)$ of S in this case consists of the three equilibria $\{(\bar{u}_1,0),(0,\bar{u}_2),(0,0)\}$. Saying that $\sigma_1 > 0$, for example, gives an instability condition on the u_1 component of a solution pair at the equilibrium $(0,\bar{u}_2)$. It indicates growth in the u_1 component, forcing (u_1,u_2) away from S and into $X - S$ when $(u_1(x,t),u_2(x,t))$ is near $(0,u_2(x))$ in Y for some value of t. Such a phenomenon is called invasibility in the biological literature. It is widely believed that success of invasion is a necessary and sufficient condition for persistence. A case for this position is made in the context of systems such as (1.1) in a nonrigorous way in [**27**]. Our theorem asserts that invasibility of both species is sufficient to guarantee permanence in (1.1). Fourth, the statement of the theorem presupposes $f_i(x,0,0) > 0$ for some $x \in \Omega$ and, as well, a self-regulatory mechanism on u_i, $i = 1,2$. We may alter these requirements on u_2 and maintain the validity of the result. To do so, we assume $f_2(x,0,v) \leq 0$ for any $x \in \Omega$ and $v \geq 0$. In this case, for any $\mu_2 > 0$, all positive solutions to (1.5) decay to 0 as $t \to \infty$, and hence $\omega(S) = \{(\bar{u}_1,0),(0,0)\}$. Theorem 1.1 will still hold, provided we understand $\bar{u}_2 \equiv 0$ and that requiring $\sigma_2 > 0$ in (1.7) to be positive is the only constraint being placed upon $\mu_2 > 0$ (i.e., $\lambda_1(f_2(x,0,0))$ fails to exist in this situation and we make a convention that $1/\lambda_1(f_2(x,0,0,0)) = +\infty$). Finally, in the case of competition, an alternate approach to uniform persistence or permanence, called *compressibility* by Hess, is available. It is based upon monotone methods which are not applicable for (1.1) in general. See, for example, [**19**] and [**13**].

2. Interpreting permanence in terms of the system parameters. Theorem 1.1 provides a means for establishing permanence in (1.1) which is expressed in terms of the positivity of the eigenvalues σ of (1.6)–(1.7). Since positivity is the inequality "greater than zero," the criterion for permanence given in Theorem 1.1 is quantifiable and hence theoretically measurable. The eigenvalues σ are not themselves original parameters in the system (1.1). However, the coefficients in (1.6)–(1.7) are, and it is very useful to reformulate the requirement that the σ be positive in such a way that the underlying relationships among the parameters of (1.1) that we require to assert permanence for (1.1) become apparent. Consequently, we are then able to consider the impact of spatial heterogeneity and/or habitat geometry upon permanence. We illustrate with a reasonably simple Lotka-Volterra competition model having spatial variation in some but not all of its coefficients. Models of this type were recently employed by the first two co-authors in a study [**13**] (based on the work of D.H. Janzen [**22, 23**]) of the effects of diffusive interference from the outside upon a refuge. Our reformulation of the criteria that $\sigma_1 > 0$ and $\sigma_2 > 0$ in (1.6) and (1.7) rests upon the following result about inhomogeneous linear elliptic equations.

Lemma 2.1 (Positivity Lemma). *Suppose* $m \in L^\infty(\Omega)$ *and* $\{x \in \Omega : m(x) > 0\}$ *has positive measure. Consider the inhomogeneous boundary value problem*

$$\begin{cases} -\Delta u = \lambda m(x) u + h & \text{in } \Omega, \\ Bu = 0 & \text{on } \partial\Omega, \end{cases} \tag{2.1}$$

where $h \in C(\overline{\Omega})$ *and* $Bu = u$ *or* $Bu = \partial u/\partial\nu$. *Let* $\lambda_1(m)$ *be as in* (1.3). (*In case* $Bu = \partial u/\partial \nu$, *assume in addition that* $\int_\Omega m < 0$, *so that* $\lambda_1(m)$ *exists.*) *Then the following hold*:

(i) *If* $\lambda \in (0, \lambda_1(m))$, (2.1) *has a unique solution for all* $h \in C(\overline{\Omega})$. *Moreover, if* $h \geq 0$ *and* $h \not\equiv 0$, $u(x) > 0$ *on* Ω *when* $Bu = u$ *and* $u(x) > 0$ *on* $\overline{\Omega}$ *when* $Bu = \partial u/\partial\nu$.

(ii) *If* $\lambda \geq \lambda_1(m)$ *and* $h \geq 0$, (2.1) *can have a positive solution* u *only when* $\lambda = \lambda_1(m)$ *and* $h \equiv 0$. *In this case* u *is a positive eigenfunction for*

$$\begin{cases} -\Delta z = \lambda_1(m) m z & \text{in } \Omega, \\ Bz = 0 & \text{on } \partial\Omega. \end{cases}$$

Remark. When m is continuous, Lemma 2.1 is a special case of the results given in Propositions 2 and 3 of [**20**] in the case of homogeneous Dirichlet boundary data. In the Neumann case, it is a special case of the results given in Proposition 5 and 6 of [**28**]. If $m \in L^\infty(\Omega)\backslash C(\overline{\Omega})$,the existence of $\lambda_1(m)$ follows from [**25**] in the Dirichlet case and from [**7**] in the Neumann case. Once the existence of $\lambda_1(m) > 0$ is guaranteed, the arguments employed in [**20**] and [**28**] can be adapted to the situation $m \in L^\infty(\Omega)\backslash C(\overline{\Omega})$ to obtain Lemma 2.1.

Consider

$$\begin{cases} u_t = \mu_1 \Delta u + (m_1(x) - u - cv)u & \\ & \text{in } \Omega \times (0,\infty), \\ v_t = \mu_2 \Delta v + (m_2(x) - eu - v)v & \\ Bu = 0 = Bv & \text{on } \partial\Omega \times (0,\infty), \end{cases} \tag{2.2}$$

where $B\phi = \phi$ or $B\phi = \partial\phi/\partial\nu$ and c and e are positive constants. Assume that $m_i \in C^2(\overline{\Omega})$ and $m_i(x_0) > 0$ for some $x_0 \in \overline{\Omega}$ for $i = 1, 2$. If $B\phi = \partial\phi/\partial\nu$, assume for the moment also that $\int_\Omega m_i < 0$ for $i = 1, 2$. Suppose $\mu_i < 1/\lambda_1(m_i)$ for $i = 1, 2$, and let u^*, v^* denote the unique positive functions such that

$$\begin{cases} -\mu_1 \Delta u^* = (m_1(x) - u^*)u^* & \text{in } \Omega, \\ Bu^* = 0 & \text{on } \partial\Omega \end{cases} \tag{2.3}$$

and

$$\begin{cases} -\mu_2 \Delta v^* = (m_2(x) - v^*)v^* & \text{in } \Omega, \\ Bv^* = 0 & \text{on } \partial\Omega. \end{cases} \tag{2.4}$$

To achieve permanence for (2.2) via Theorem 1.1, we require that $\sigma > 0$ and $\gamma > 0$ in

$$\begin{cases} \mu_1 \Delta p + (m_1(x) - cv^*)p = \sigma p & \text{in } \Omega, \\ p > 0 & \text{in } \Omega, \\ Bp = 0 & \text{on } \partial\Omega \end{cases} \tag{2.5}$$

and

$$\begin{cases} \mu_2 \Delta q + (m_2(x) - eu^*)q = \gamma q & \text{in } \Omega, \\ q > 0 & \text{in } \Omega, \\ Bq = 0 & \text{on } \partial\Omega. \end{cases} \tag{2.6}$$

Observe that if c is such that $m_1(x) - cv^* \leq 0$ on Ω, the maximum principle implies that $\sigma < 0$ for any $\mu_1 > 0$. Likewise, if $m_2(x) - eu^* \leq 0$ on Ω, $\gamma < 0$ for any $\mu_2 > 0$. So we assume that the sets $\{x \in \Omega : (m_1 - cv^*)(x) > 0\}$ and $\{x \in \Omega : (m_2 - eu^*)(x) > 0\}$ have positive Lebesgue measure. We know in this case that $\lambda_1(m_1 - cv^*)$ and $\lambda_1(m_2 - eu^*)$ exist as positive numbers. (If $B\phi = \partial\phi/\partial\nu$, $\int_\Omega m_1 < 0$ and $\int_\Omega m_2 < 0$ guarantee that $\int_\Omega (m_1 - cv^*) < 0$ and $\int_\Omega (m_2 - eu^*) < 0$ since $c, e > 0$.) Moreover, $m_1 - cv^* < m_1$ and $m_2 - eu^* < m_2$ imply that $\lambda_1(m_1) < \lambda_1(m_1 - cv^*)$ and $\lambda_1(m_2) < \lambda_1(m_2 - eu^*)$. We may now establish the following.

Theorem 2.2. *Consider* (2.2)*. Assume* $m_i \in C^2(\overline{\Omega})$ *and* $m_i(x_0) > 0$ *for some* $x_0 \in \overline{\Omega}$ *for some* $i = 1, 2$. *(If* $B\phi = \partial\phi/\partial\nu$*, assume in addition that* $\int_\Omega m_i < 0$ *for* $i = 1, 2$.*) Suppose that* $\mu_i < 1/\lambda_1(m_i)$ *for* $i = 1, 2$*, and let* $u^*(\mu_1)$*,* $v^*(\mu_2)$ *denote the unique positive solutions of* (2.3) *and* (2.4)*, respectively. Then permanence obtains in* (2.2) *provided that the sets* $\{x \in \Omega : (m_1 - cv^*(\mu_2))(x) > 0\}$ *and* $\{x \in \Omega : (m_2 - eu^*(\mu_1))(x) > 0\}$ *have positive measure and provided that*

$$\mu_1 < \frac{1}{\lambda_1(m_1 - cv^*(\mu_2))} \tag{2.7}$$

and

$$\mu_2 < \frac{1}{\lambda_1(m_2 - eu^*(\mu_1))}. \tag{2.8}$$

Proof. The equation (2.5) can be written as

$$-\Delta p = \frac{1}{\mu_1}(m_1 - cv^*(\mu_2))p - \frac{\sigma}{\mu_1}p.$$

Letting $1/\mu_1 = \lambda$, $m = m_1 - cv^*(\mu_2)$ and $h = -(\sigma/\mu_1)p$, (2.5) is now of the form (2.1). It follows from Lemma 2.1 that $\sigma > 0$ if and only if $1/\mu_1 > \lambda_1(m_1 - cv^*(\mu_2))$ or, equivalently, $\mu_1 < 1/\lambda_1(m_1 - cv^*(\mu_2))$. The argument may be duplicated for equation (2.6), and the result follows from Theorem 1.1. □

Remark. In the case of Dirichlet boundary conditions, if for $i = 1, 2$, there are $x_0(i) \in \partial\Omega$ and $\varepsilon(i) > 0$ so that for any $\delta > 0$ the set $\{x \in \Omega \cap B(x_0(i);\delta) : m_i(x) \geq \varepsilon(i)\}$ has positive measure, then the sets $\{x \in \Omega : (m_1 - cv^*(\mu_2))(x) > 0\}$ and $\{x \in \Omega : (m_2 - eu^*(\mu_1))(x) > 0\}$ have positive measure for any $c, e > 0$. In the case of Neumann boundary conditions, u^* and v^* are positive on $\overline{\Omega}$ by the strong maximum principle, so there are c, $\varepsilon > 0$ so that $\{x \in \Omega : (m_1 - cv^*(\mu_2))(x) > 0\}$ and $\{x \in \Omega : (m_2 - eu^*(\mu_1))(x) > 0\}$ are of measure zero. But in either case, since $v^* \leq \sup_{\overline{\Omega}}(m_2)_+$ and $u^* \leq \sup_{\overline{\Omega}}(m_1)_+$ by the maximum principle, the sets will have positive measure for any $\mu_i < 1/\lambda_1(m_i)$ if $c < \sup_{\overline{\Omega}}(m_1)_+/\sup_{\overline{\Omega}}(m_2)_+$ and $e < \sup_{\overline{\Omega}}(m_2)_+/\sup_{\overline{\Omega}}(m_1)_+$.

Now suppose that we consider (2.2) with $B\phi = \partial\phi/\partial\nu$ and with $\int_\Omega m_i > 0$, $i = 1, 2$. Theorem A.1 guarantees that for any $\mu_1 > 0$ and $\mu_2 > 0$ there are unique positive u^* and v^* satisfying (2.3) and (2.4), respectively. Suppose now that $c > 0$ is such that $\int_\Omega (m_1 - cv^*(\mu_2)) > 0$. Let $w > 0$ satisfy

$$\begin{cases} \mu_1 \Delta w + (m_1(x) - cv^*(\mu_2)(x) - w)w = 0 & \text{in } \Omega, \\ \partial w/\partial\nu = 0 & \text{on } \partial\Omega \end{cases}$$

(w is guaranteed to exist by Theorem A.1). From (2.5), we have

$$\mu_1\left(\int_\Omega p\Delta w - w\Delta p\right) + \int_\Omega [(m_1 - cv^*(\mu_2) - w) - (m_1 - cv^*(\mu_2))]pw = -\sigma \int_\Omega pw$$

which implies

$$\int_\Omega pw^2 = \sigma \int_\Omega pw,$$

whence $\sigma > 0$. We may now give the following result.

Theorem 2.3. *Consider* (2.2) *with* $B\phi = \partial\phi/\partial\nu$. *Assume* $m_i \in C^2(\overline{\Omega})$ *and that* $\int_\Omega m_i > 0$ *for* $i = 1, 2$. *Suppose* $\mu_i > 0$ *for* $i = 1, 2$, *and let* $u^*(\mu_1), v^*(\mu_2)$ *denote the unique positive solutions of* (2.3) *and* (2.4), *respectively.*

(i) $\int_\Omega (m_1 - cv^*(\mu_2)) > 0$ *and* $\int_\Omega (m_2 - eu^*(\mu_1)) > 0$ *permanence obtains in* (2.2).

(ii) *If* $\int_\Omega (m_1 - cv^*(\mu_2)) < 0$ *and* $\int_\Omega (m_2 - eu^*(\mu_1)) < 0$ *permanence obtains in* (2.2) *provided the sets* $\{x \in \Omega : (m_1 - cv^*(\mu_2))(x) > 0\}$ *and* $\{x \in \Omega : (m_2 - eu^*(\mu_1))(x) > 0\}$ *have positive measure and provided the inequalities* (2.7) *and* (2.8) *are simultaneously satisfied.*

Remarks. (a) Theorem 2.3 (i) holds for any $\mu_1 > 0$, $\mu_2 > 0$ provided for instance $c < \int_\Omega m_1/(|\Omega| \sup m_2)$ and $e < \int_\Omega m_2/(|\Omega| \sup m_1)$. (In a spatially constant case, this is the same condition for persistence as in the case of ordinary differential equations.) In this case permanence holds in (2.2) for any $\mu_1 > 0$, $\mu_2 > 0$.

(b) The inequalities in Theorem 2.3 (i) can be nonstrict provided the sets $\{x \in \Omega : (m_1 - cv^*(\mu_2))(x) > 0\}$ and $\{x \in \Omega : (m_2 - eu^*(\mu_1))(x) > 0\}$ have positive measure.

(c) Theorem 2.3 (ii) still obtains with $\int_\Omega m_i = 0$ provided $\{x \in \Omega : m_i(x) > 0\}$ has positive measure.

(d) There are natural modifications of Theorems 2.2 and 2.3 when $\int_\Omega m_1 \geq 0$ and $\int_\Omega m_2 < 0$ or when $\int_\Omega m_1 < 0$ and $\int_\Omega m_2 \geq 0$. We shall leave these to the reader.

(e) For both Theorem 2.2 and Theorem 2.3, it is apparent from (2.7) and (2.8) that the spatial heterogeneity in (2.2) is a factor in determining permanence. The reader should note also that $\lambda_1(m)$, a quantity which occurs naturally and frequently in applications to mathematical biology, see, for example, [**6, 11, 12, 16**], depends not only on m but also on the geometry of Ω, so that habitat geometry is being taken into account as well.

Observe now that if the coefficients $m_1(x)$, $m_2(x)$ and c, e are held unchanged, it follows from the continuity of u^* upon μ_1, v^* upon μ_2 and $\lambda_1(m)$ upon m that the collection of ordered pairs (μ_1, μ_2) for which (2.7) and (2.8) are simultaneously satisfied is an open subset of the (μ_1, μ_2) plane $\mathbf{R}^2$. In applications, it frequently is of interest to know or at least to approximate the locus in $\mathbf{R}^2$ of $\{(\mu_1, \mu_2)$: (2.7) and (2.8) hold$\}$ and to track how the locus changes as some or all of the remaining coefficients in (2.2), i.e., $m_1(x)$, $m_2(x)$, c or e, are varied. For instance, consider our study [**13**] of the effect of outside interference upon a refuge. Our approach was to consider the population dynamics of two species that compete for resources. We assumed that inside a refuge each species had a growth rate that was *spatially independent*. We assumed also that the refuge was buffered from a completely hostile exterior by a surrounding region. We compared two situations: first, the case in which neither species could increase in numbers in the buffer zone, and second, the case in which one of the species could not increase in numbers in the buffer zone while the other had a growth rate in the buffer zone equal to its growth rate inside the refuge. The two situations appear at least reasonable biologically when both species can thrive in a pristine habitat but only one of them can increase in numbers in a secondary habitat. Then the first case corresponds to a management scheme of systematic clearing of the buffer zone surrounding the refuge, while in the second, secondary habitat (such as say brush surrounding a forest island) is essentially left alone. We employed (2.2) to model the population dynamics of the two competing species on the region Ω consisting of the refuge Ω_1 and surrounding buffer zone $\Omega - \Omega_1$, subject to zero Dirichlet boundary data to reflect the hostile exterior environment. In the case of a cleared buffer zone, we assumed that $m_1(x) = r_1\chi_{\Omega_1}(x)$ and $m_2(x) = r_2\chi_{\Omega_1}(x)$, where r_i is the growth rate of the ith species in the refuge and χ_{Ω_1} is the characteristic function of Ω_1, i.e., $\chi_{\Omega_1}(x) = 1$ if $x \in \Omega_1$ and 0 if $x \in \Omega - \Omega_1$, whereas, if the buffer zone is "left natural," we assumed that m_1 was as before but that $m_2(x) \equiv r_2$ on $\overline{\Omega}$. (Notice that since χ_{Ω_1} is discontinuous along the boundary of Ω_1, the hypotheses of Theorem 2.2 are not met. However, the result of Theorem 2.2 still obtains, as we demonstrated in [**13**]). Indeed, in [**13**] we were able to estimate $\{(\mu_1, \mu_2) \in \mathbf{R}^2\colon$ (2.7) and (2.8) hold$\}$ in both cases closely enough to conclude (by comparing the estimates) that for all competition rates c, e below a computable value there are open ranges in $\mathbf{R}^2$ of pairs of diffusion coefficients (μ_1, μ_2) for which an analysis of the model in the first case predicts long-term coexistence for both species; but for which the same analysis in the second case predicts the extinction of the first species. Since the change in the growth rate m_2 in the buffer zone is the only difference in the model from the first case to the second, the change in prediction can be attributed to the second species gaining a competitive advantage in the buffer zone which becomes a competitive advantage inside the refuge due to diffusion from the buffer zone into the refuge. Of course, these are only theoretical models, but they do support Janzen's assertion [**22, 23**] that the first management scheme, i.e., clearing the buffer zone, can sometimes be the more desirable.

The preceding discussion provides evidence of the utility of mathematical analysis of the relationships among the coefficients of (1.1) that are employed to assert permanence and also of the utility of allowing spatial heterogeneity in such models. It should also indicate that the more specific information available about the coefficients, the better the estimates of parameter ranges guaranteeing permanence and the more applicable the results. But, on the other hand, what kind of observations can be made in general? Consider (2.7) and (2.8) again. Suppose, for instance, that the competition coefficient c is increased. Notice that $v^*(\mu_2)$ arises from equation (2.4) which is independent of c. So increasing c increases $cv^*(\mu_2)$ and hence decreases $m_1(x) - cv^*(\mu_2)$. Decreasing $m_1(x) - cv^*(\mu_2)$ in turn increases $\lambda_1(m_1(x) - cv^*(\mu_2))$ and hence decreases $1/\lambda_1(m_1(x) - cv^*(\mu_2))$. Consequently, (2.7) becomes a more stringent requirement upon the diffusion coefficient μ_1, and the collection of ordered pairs (μ_1, μ_2) so that permanence is guaranteed by Theorem 2.2 is reduced, which of course agrees with one's natural intuition.

In addition to observations regarding the change in size of the set $\{(\mu_1, \mu_2) : (2.7) \text{ and } (2.8) \text{ hold}\}$ due to monotonic changes in the coefficients of (2.2), we may also give in general information regarding the spatial location of the set. To illustrate, assume additionally when $Bu = u$ that for $i = 1, 2$ $\{x \in \Omega : m_i(x) \leq 0\}$ has positive measure. The maximum principle guarantees that for any $\mu_i < (1/\lambda_1(m_i))$, $u^*(\mu_1) \leq ||(m_1)_+||_\infty$ and $v^*(\mu_2) \leq ||(m_2)_+||_\infty$. Consequently, if $c < (\int_\Omega (m_1)_+/|\Omega|)(1/||(m_2)_+||_\infty)$, $m_1(x) - cv^*(\mu_2)(x) \geq m_1(x) - \int_\Omega (m_1)_+/|\Omega| > 0$ for x in a set of positive measure since $\int_\Omega (m_1)_+/|\Omega| \leq ||(m_1)_+||_\infty |\Omega'|/|\Omega| < ||(m_1)_+||_\infty$ where $\Omega' = \{x \in \Omega : m_1(x) > 0\}$. Hence, $\lambda_1(m_1 - cv^*(\mu_2)) \leq \lambda_1(m_1 - \int_\Omega (m_1)_+/|\Omega|)$, or equivalently,

$$\frac{1}{\lambda_1(m_1 - \int_\Omega (m_1)_+/|\Omega|)} \leq \frac{1}{\lambda_1(m_1 - cv^*(\mu_2))}.$$

It follows that if $c < (\int_\Omega (m_1)_+/|\Omega|)(1/||(m_2)_+||_\infty)$ and

$$\mu_2 < \frac{\lambda_1(m_1)}{\lambda_1(m_2)} \frac{1}{\lambda_1(m_1 - \int_\Omega (m_1)_+/|\Omega|)}$$

$(< (1/\lambda_1(m_2))$ since $m_1 - \int_\Omega (m_1)_+/|\Omega| < m_1)$, $(\lambda_1(m_2)/\lambda_1(m_1))\mu_2 < 1/(\lambda_1(m_1 - cv^*(\mu_2)))$. Consequently, if $c < (\int_\Omega (m_1)_+/|\Omega|)(1/||(m_2)_+||_\infty)$

and

$$\mu_2 < \frac{\lambda_1(m_1)}{\lambda_1(m_2)} \frac{1}{\lambda_1(m_1 - \int_\Omega (m_1)_+/|\Omega|)}$$

and $\mu_1 \le (\lambda_1(m_2)/\lambda_1(m_1))\mu_2$, then (μ_1, μ_2) satisfies (2.7), or put another way, the boundary curve of the region in (μ_1, μ_2)-space described by (2.7), namely,

$$\mu_1 = \frac{1}{\lambda - 1(m_1 - cv^*(\mu_2))}, \tag{2.9}$$

lies to the right of the line $\mu_2 = (\lambda_1(m_1)/\lambda_1(m_2))\mu_1$. Similarly, if $e < (\int_\Omega (m_2)_+/|\Omega|)(1/||(m_1)_+||_\infty)$ and

$$\mu_1 < \frac{\lambda_1(m_2)}{\lambda_1(m_1)} \frac{1}{\lambda_1(m_2 - \int_\Omega (m_2)_+/|\Omega|)},$$

$$\left(\text{again} \quad \frac{\lambda(m_2)}{\lambda_1(m_1)} \frac{1}{\lambda_1(m_2 - \int_\Omega (m_2)_+/|\Omega|)} < \frac{1}{\lambda_1(m_1)}\right),$$

then $(\lambda_1(m_1)/\lambda_1(m_2))\mu_1 < 1/(\lambda_1(m_2 - eu^*(\mu_1))$. Hence, if $e < (\int_\Omega (m_2)_+/|\Omega|)(1/||(m_1)_+||_\infty)$ and

$$\mu_1 < \frac{\lambda_1(m_2)}{\lambda_1(m_1)} \frac{1}{\lambda_1(m_2 - \int_\Omega (m_2)_+/|\Omega|)},$$

the boundary curve to the region described by (2.8),

$$\mu_2 = \frac{1}{\lambda_1(m_2 - eu^*(\mu_1))} \tag{2.10}$$

lies above the line $\mu_2 = (\lambda_1(m_1)/\lambda_1(m_2))\mu_1$. Thus the line $\mu_2 = (\lambda_1(m_1)/\lambda_1(m_2))\mu_1$ connecting the origin in (μ_1, μ_2) parameter space to the "critical" point $(1/\lambda_1(m_1), 1/\lambda_1(m_2))$ separates (2.9) and (2.10) when

$$c < \frac{\int_\Omega (m_1)_+}{|\Omega|} \frac{1}{||(m_2)_+||_\infty}, \qquad e < \frac{\int_\Omega (m_2)_+}{|\Omega|} \frac{1}{||(m_1)_+||_\infty},$$

$$\mu_1 < \frac{\lambda_1(m_2)}{\lambda_1(m_1)} \frac{1}{\lambda_1(m_2 - \int_\Omega (m_2)_+/|\Omega|)},$$

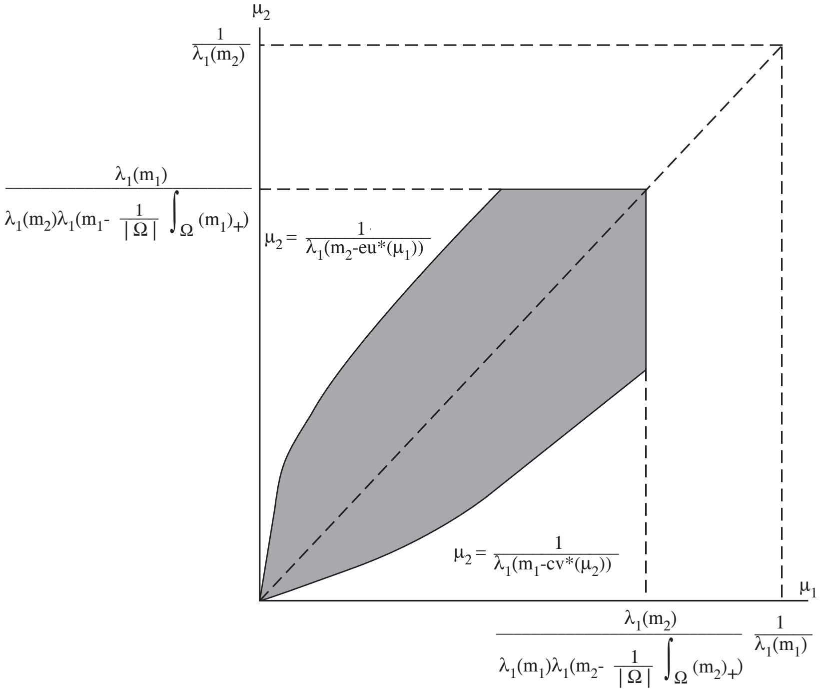

FIGURE 2.1. Permanence in (2.2) is guaranteed in the shaded region under the hypotheses of Theorem 2.1 when $c < \int_\Omega (m_1)_+/(|\Omega|\,||(m_2)_+||_\infty)$ and $e < \int_\Omega (m_2)_+/(|\Omega|\,||(m_1)_+||_\infty)$.

$$\mu_2 < \frac{\lambda_1(m_1)}{\lambda_1(m_2)} \frac{1}{\lambda_1(m_1 - \int_\Omega (m_1)_+/|\Omega|}.$$

Permanence for (2.2) obtains for (μ_1, μ_2) lying between these two curves, as indicated in Figure 2.1.

3. Examples: explicit and approximate criteria for permanence. In the previous section we noted how conditions such as (2.7)–(2.8) show the interplay among diffusion, spatial heterogeneity, species interaction and habitat geometry that will guarantee permanence in (1.1). We described in detail the significance in a problem of genuine applied interest of analyzing mathematically such conditions, and also observed how to think of (2.7)–(2.8) as relations between diffusion coefficients which depend on the remaining parameters in the problem. We made some observations in general regarding the locus of the set of pairs of diffusion coefficients satisfying (2.7)–(2.8) and its dependence on the remaining coefficients. Of course, condition (2.7)–(2.8) is in general quite difficult to analyze mathematically. There are certain rather significant reasons why. First of all, understanding how the quantity $\lambda_1(m)$ (which appears in both (2.7) and (2.8)) varies as $m(x)$ varies in a nonmonotonic fashion is a challenging mathematical problem of current research interest. There are some results on the problem in [**8, 10**], but nothing approaching a complete understanding. Moreover, expressions such as $\lambda_1(m_1 - cv^*)$, even when m_1 is known, have as part of their arguments solutions to nonlinear differential equations which are usually not known explicitly. Consequently, one is led to numerical approximation in order to study conditions such as (2.7)–(2.8). Fortunately, the numerical approximations are of a rather standard nature involving a linear problem for which fairly straightforward techniques are available. Nevertheless, there are some examples which can be resolved explicitly. Such examples serve to aid biological intuition and perhaps suggest approaches toward the analysis of conditions such as (2.7)–(2.8) in general. For instance, consider a predator-prey problem of Lotka-Volterra type, the governing equations being of the form

$$\partial u/\partial t = \mu\Delta u + u[a - bu - cv] \quad \text{in } \Omega \times (0,\infty) \tag{3.1}$$

$$\partial v/\partial t = \beta\Delta v + v[-d + eu - fv] \quad \text{in } \Omega \times (0,\infty) \tag{3.2}$$

with boundary conditions

$$\partial u/\partial\nu = 0, \qquad v = 0 \quad \text{on } \partial\Omega \times (0,\infty). \tag{3.3}$$

Consequently, there is no prey migration across the boundary, but the predator can "leak" since the boundary is assumed lethal to it. Notice that if a and b are constants, the prey has positive equilibrium $u^* \equiv a/b$ in the absence of the predator.

Example 3.1. Suppose that the coefficients a, b, c, d, e are strictly positive constants and that $f \geq 0$. Since u satisfies a zero Neumann condition, in the absence of its predator all solutions (not identically zero) approach $u^* = a/b$, the carrying capacity of the prey. However, the zero Dirichlet condition on v means that it is to be expected from a biological point of view that, for a given area A of Ω, permanence is more likely for small values of the perimeter l of Ω, since then the predator leakage is reduced. We can test the actual strength of this effect by taking Ω to be a rectangle with sides r, s. (Strictly speaking, the boundary should be smooth, but clearly by "rounding" its corners our results hold to a very good approximation).

It is easy to see that the principal eigenvalue λ_1 of $-\Delta$ on Ω subject to zero Dirichlet conditions is given by

$$\lambda_1 = \pi^2\left(\frac{1}{r^2} + \frac{1}{s^2}\right) = \frac{\pi^2}{4A^2}(l^2 - 8A).$$

Of course, the eigenvalues of the Laplacian on various domains have been studied extensively, see [**4, 28**] for example, and these are known in several cases, and in many other examples good approximate methods are available for finding them. From Theorem 1.1, permanence holds if $(-d + u^*e)/\beta > \lambda_1$. (The principle eigenvalue for (3.1) linearized at (0,0) is clearly $a > 0$.) This condition is thus

$$u^*e > d + \beta\pi^2(l^2 - 8A)/4A^2. \tag{3.4}$$

Such confirms the argument above, and shows that the perimeter is indeed a strong factor, appearing quadratically in (3.4) in determining permanence.

Notice also that, as the diffusion rate β in (3.2) tends to 0, the condition for permanence in (3.1)–(3.3) tends to

$$u^*e > d, \tag{3.5}$$

which is the criterion for permanence in the constant coefficient system of ordinary differential equations

$$\frac{du}{dt} = u[a - bu - cv], \qquad \frac{dv}{dt} = v[-d + eu - fv]. \tag{3.6}$$

In general it is a very difficult problem to assert that dynamics of a system such as (3.1)–(3.3), which necessarily take place in an infinite dimensional space, approximate the dynamics of the corresponding system (3.6) of ordinary differential equations as $\mu \to 0$ and $\beta \to 0$, since the perturbation is singular. However, permanence techniques do allow us to assert that the relationship (3.4) among the parameters a, b, d and e that guarantees coexistence in (3.1)–(3.3) does approximate the relationship among the parameters that guarantees coexistence in the limiting system (3.6). This phenomenon is yet a further indication of the benefits of the permanence concept. We ask for less than a complete analysis of the dynamics of (3.1)–(3.3) but derive enough information nevertheless to make biologically meaningful comparisons with (3.6) as $\mu \to 0$ and $\beta \to 0$.

Example 3.2. The object of this example is to show that in some cases, even with coefficients varying with position, the permanence question is tractable in terms of well-known special functions. Consider (3.1)–(3.3), but now with $\Omega = (-1, 1)$. The assumptions on the coefficients are as in Example 3.1 except that e, which governs the utilization of prey by the predator, is allowed to vary spatially, with

$$e(x) = \gamma - \delta x^2$$

with γ, δ constants satisfying $\gamma > \delta > 0$.

The equation for the prey in the absence of the predator still has $u^* = a/b$ as its stable positive equilibrium. To apply Theorem 1.1 again, we must examine the value of σ such that the equation

$$\beta v'' + [-d + (\gamma - \delta x^2)u^*]v = \sigma v \tag{3.7}$$

has a solution which is a positive on $(-1, 1)$ and satisfies $v(-1) = 0 = v(1)$. Permanence will hold if $\sigma > 0$. The change of variable $x = \alpha y$ with $\alpha^4 = \beta/4\delta u^*$ reduces (3.7) to the form

$$\frac{d^2v}{dy^2} - \left[g + \frac{1}{4}y^2\right]v = 0 \tag{3.8}$$

where $g = -\alpha^2(\gamma u^* - d - \sigma)/\beta = -(\gamma u^* - d - \sigma)/(4\gamma\delta u^*)^{1/2}$. Now (3.8) is the equation for parabolic cylinder functions, and from [**1**, Section 19], the even solution of (3.7) is

$$e^{-x^2/4\alpha^2} M\left(\frac{1}{2}g + \frac{1}{4}, \frac{1}{2}, \frac{x^2}{2\alpha^2}\right)$$

where M is a confluent hypergeometric function. There are tables available [**1**, Table 13.1] which enable us to determine the parameters g and α so that $M((1/2)g + 1/4, 1/2, x^2/(2\alpha^2))$ will be zero for the first time at $x = 1$. Then the definitions of g and α may be employed to express the condition $\sigma > 0$ in terms of the original parameters of the system a, b, β, d, γ, and δ. Consequently, the permanence question can be completely resolved in this case.

There are other possibilities of this nature. For example, if $e(x) = \gamma - \delta \cos x$, the eigenvalue problem will involve Mathieu functions, a well-known class with documented properties. See [**1**, Section 20] for further details.

A rather different line of inquiry is suggested by again taking zero Neumann conditions on the prey but now assuming that $a = a(x)$ is spatially dependent, and assuming that μ is very large (which is possible whenever $a(x)$ in (3.1) is such that $\int_\Omega a \geq 0$). It is reasonable to expect in the case of μ large that $u^*(\mu)$ is approximately a constant (even though the prey equation is spatially dependent), and hence examples akin to those above are possible. We will not pursue this line of inquiry further, other than to verify that $u^*(\mu)$ is approximately constant as $\mu \to +\infty$. Since this result is largely technical, we present it as Theorem A.2 in the Appendix.

4. Conditions for permanence when diffusion rates are small. As a final example, we observe some approximate conditions for permanence in the case of diffusive competitive Lotka-Volterra systems with small diffusion rates. First notice that our results for (2.2) can readily be extended to systems of the form

(4.1)
$$\begin{cases} u_{1t} = \mu_1 \Delta u_1 + (m_1(x) - b_{11}(x)u_1 - b_{12}(x)u_2)u_1 & \text{in } \Omega \times (0,\infty) \\ u_{2t} = \mu_2 \Delta u_2 + (m_2(x) - b_{21}(x)u_1 - b_{22}(x)u_2)u_2 & \text{in } \Omega \times (0,\infty) \end{cases}$$

$$Bu_i = 0 \quad \text{on } \partial\Omega \times (0,\infty), \tag{4.2}$$

$i = 1, 2$, where $B\phi = \phi$ or $B\phi = \partial\phi/\partial\nu$ and b_{ij} is smooth and of one sign on $\overline{\Omega}$. For the sake of specificity, we shall assume m_i and b_{ij} are positive and smooth on $\overline{\Omega}$, $i = 1, 2$, so that we consider a competitive system, and also that $B\phi = \phi$.

When $\mu_i < 1/\lambda_1(m_i)$, there are steady-state solutions $(\bar{u}_1, 0)$ and $(0, \bar{u}_2)$, where $\bar{u}_i$ is the positive, globally attracting equilibrium for

$$\begin{cases} u_{it} = \mu_i \Delta u_i + (m_i(x) - b_{ii}(x) u_i) u_i & \text{in } \Omega \times (0,\infty) \\ u_i = 0 & \text{on } \partial\Omega \times (0,\infty). \end{cases} \tag{4.3}$$

The conditions (1.6)–(1.7) for permanence become that $\sigma_i > 0$ in

$$\begin{cases} \mu_i \Delta \psi_i + [m_i(x) - b_{ij}(x)\bar{u}_j]\psi_i = \sigma_i \psi_i & \text{in } \Omega, \\ \psi_i = 0 & \text{on } \partial\Omega, \\ \psi_i > 0 & \text{in } \Omega, \end{cases} \tag{4.4}$$

where $i, j = 1, 2$ and $i \neq j$. Since

$$\mu_i \Delta \bar{u}_i + [m_i(x) - b_{ii}(x)\bar{u}_i]\bar{u}_i = 0,$$

an integration by parts argument shows that

$$\int_\Omega (b_{ii}\bar{u}_i - b_{ij}\bar{u}_j)\bar{u}_i \psi_i = \sigma_i \int_\Omega \bar{u}_i \psi_i. \tag{4.5}$$

It is evident that the condition

$$b_{ii}\bar{u}_i - b_{ij}\bar{u}_j > 0 \quad \text{in } \Omega \tag{4.6}$$

guarantees that $\sigma_i > 0$ and that permanence obtains in (4.1)–(4.2). Since there is a positive number k_{ij} (depending on μ_i and μ_j) so that $\bar{u}_i > k_{ij}\bar{u}_j$, the condition $b_{ii}k_{ij} - b_{ij} > 0$ is sufficient to guarantee permanence. Qualitatively, the condition is that the interaction terms b_{ij} not be too large compared to the self-regulation terms b_{ii}. Such is similar to the analysis at the end of Section 2. Moreover, since k_{ij} depends on μ_i and μ_j, the condition is also somewhat implicit if we only require that $\mu_i < 1/\lambda_1(m_i)$.

A slightly weaker condition than (4.6) for permanence is that

$$\int_\Omega (b_{ii}\bar{u}_i - b_{ij}\bar{u}_j)\bar{u}_i^2 > 0, \tag{4.7}$$

$i = 1, 2$, $i \neq j$. To see that such is the case, we note that an implicit function theorem argument along the lines of the one used in [**11**] guarantees that the solution $\psi_i(s)$ and eigenvalue $\alpha_i(s)$ for

$$\tag{4.8}\begin{cases} \mu_i \Delta\psi_i(s) + [m_i - (1-s)b_{ii}\bar{u}_i - sb_{ij}\bar{u}_j]\psi_i(s) = \alpha_i(s)\psi_i(s) & \text{in } \Omega, \\ \psi_i > 0 & \text{in } \Omega, \\ \psi_i = 0 & \text{on } \partial\Omega, \\ \int_\Omega \psi_i^2(s) = 1, \end{cases}$$

depend differentiably on $s \in [0,1]$. Note that $\psi_i(0) = \bar{u}_i/||\bar{u}_i||_{L^2(\Omega)}$ and $\alpha_i(0) = 0$. If we differentiate (4.8) with respect to s, it is not difficult to see that $\psi_i' = \psi_i'(s)$ and $\alpha_i' = \alpha_i'(s)$ satisfy

$$\tag{4.9}\begin{cases} \mu_i \Delta\psi_i' + [m_i - (1-s)b_{ii}\bar{u}_i - sb_{ij}\bar{u}_j]\psi_i' + (b_{ii}\bar{u}_i - b_{ij}\bar{u}_j)\psi_i & \\ \quad = \alpha_i\psi_i' + \alpha_i'\psi_i & \text{in } \Omega, \\ \psi_i' = 0 & \text{on } \partial\Omega. \end{cases}$$

Multiplying (4.9) by ψ_i and integrating by parts yields

$$\tag{4.10} \alpha_i' = \alpha_i' \int_\Omega \psi_i^2 = \int_\Omega (b_{ii}\bar{u}_i - b_{ij}\bar{u}_j)\psi_i^2.$$

Notice now that (4.8) can be written

$$\tag{4.11} \mu_i\Delta\psi_i + (m_i - b_{ii}\bar{u}_i)\psi_i + s(b_{ii}\bar{u}_i - b_{ij}\bar{u}_j)\psi_i = \alpha_i\psi_i$$

in Ω. Since $\bar{u}_i > 0$ and $\mu_i\Delta\bar{u}_i + (m_i - b_{ii}u_i)\bar{u}_i \equiv 0$, the variational characterization of eigenvalues implies that

$$\tag{4.12} \inf_{\substack{\phi \in W_0^{1,2}(\Omega) \\ \phi \not\equiv 0}} \left\{ \frac{\int_\Omega \mu_i |\nabla\phi|^2 - (m_i - b_{ii}\bar{u}_i)\phi^2}{\int_\Omega \phi^2} \right\} = 0.$$

Multiplying (4.11) by $-\psi_i$, integrating by parts and applying (4.12), we find that

$$-s\int_\Omega (b_{ii}\bar{u}_i - b_{ij}\bar{u}_j)\psi_i^2 \leq -\alpha_i \int_\Omega \psi_i^2 = -\alpha_i.$$

Hence, from (4.10), we have

$$\alpha_i'(s) \geq \frac{\alpha_i(s)}{s} \tag{4.13}$$

for $s \in (0,1]$. From (4.10), $\alpha_i'(0) = \int_\Omega (b_{ii}\bar{u}_i - b_{ij}\bar{u}_j)\bar{u}_i^2/||\bar{u}_i||^2_{L^2(\Omega)}$ and $\alpha_i'(0) > 0$ if $\int_\Omega (b_{ii}\bar{u}_i - b_{ij}\bar{u}_j)\bar{u}_i^2 > 0$. Since $\alpha_i(0) = 0$, $\alpha_i(s)$ is positive for $s > 0$ and sufficiently small. From (4.13), it follows that $\alpha_i(s)$ remains positive as s increases. In particular, $\alpha_i = \alpha_i(1) > 0$, and the condition $\int_\Omega (b_{ii}\bar{u}_i - b_{ij}\bar{u}_j)\bar{u}_i^2 > 0$, $i = 1, 2$, $j \neq i$, guarantees permanence in (4.1)–(4.2), as asserted.

Let us now examine (4.7) under the assumption $\mu_i \ll 1$. To this end, consider

$$\varepsilon^2\bar{\mu}_i\Delta\bar{u}_i(\varepsilon) + [m_i(x) - b_{ii}(x)\bar{u}_i(\varepsilon)]\bar{u}_i(\varepsilon) = 0 \tag{4.14}$$

and

$$\varepsilon^2\bar{\mu}_i\Delta\psi_i(\varepsilon) + [m_i(x) - b_{ij}\bar{u}_j(\varepsilon)]\psi_i(\varepsilon) = \sigma_i(\varepsilon)\psi_i(\varepsilon) \tag{4.15}$$

with the same conditions on $\bar{u}_i$ and ψ_i as before and $\bar{\mu}_i > 0$ fixed. Suppose that $\bar{u}_1(\varepsilon)$ and $\bar{u}_2(\varepsilon)$ converge to $\bar{u}_1(0)$ and $\bar{u}_2(0)$, respectively, in $L^p(\Omega)$ for any $p < \infty$ as $\varepsilon \to 0$. Since $\sigma_i(\varepsilon) > 0$ if $\int_\Omega (b_{ii}\bar{u}_i(\varepsilon) - b_{ij}\bar{u}_j(\varepsilon))\bar{u}_i^2(\varepsilon) > 0$, we obtain permanence for $\varepsilon > 0$ small provided

$$\int_\Omega (b_{ii}\bar{u}_i(0) - b_{ij}\bar{u}_j(0))\bar{u}_i^2(0) > 0, \tag{4.16}$$

$i = 1, 2$, $i \neq j$. We establish that $\bar{u}_i(\varepsilon)$ converges in L^p for any $p < \infty$ via an analysis based on the following singular perturbation result, due to DeSanti [**17**].

Theorem 4.1 [**17**, p. 313]. *Suppose that* $\Omega \subseteq \mathbf{R}^m$ *is a bounded domain so that* $\partial\Omega = F^{-1}(\{0\})$, *where* $F \in C^2(\mathbf{R}^m)$ *and* $\nabla F \neq 0$ *on* $\partial\Omega$. *Let* $h(x,w) \in C^2(\Omega \times \mathbf{R})$, *and suppose that*

$$V(x,w) = \int_0^w h(x,s)\,ds$$

satisfies the following.

(i) *There exists* $g(x) \in C^2(\Omega)$ *such that* $V_w(x, g(x)) \equiv h(x, g(x)) = 0$ *for* $x \in \Omega$.

(ii) $V_{ww}(x, g(x)) = h_w(x, g(x)) > K$ *for some* $K > 0$ *and all* $x \in \Omega$.

(iii) $[V(x,w) - V(x, g(x))][f(x) - g(x)] > 0$ *for* $x \in \partial\Omega$ *and* $w \in (g(x), f(x)]$ *or* $[f(x), g(x))$.

Then for $\varepsilon > 0$ *and sufficiently small*

$$\begin{cases} \varepsilon^2 \Delta w = h(x,w) & \textit{in } \Omega, \\ w = f(x) & \textit{on } \partial\Omega, \end{cases}$$

admits a solution w *which converges uniformly to* $g(x)$ *as* $\varepsilon \to 0$ *on each closed subset of* Ω.

To apply Theorem 4.1, consider the problem

$$\begin{cases} \varepsilon^2 \Delta w = (-m_i(x) w - b_{ii} w^2)/\bar{\mu}_i & \text{on } \Omega, \\ w = 0 & \text{on } \partial\Omega. \end{cases} \tag{4.17}$$

We know that $-\bar{u}_i(\varepsilon)$ is the unique negative solution to (4.17) for ε sufficiently small. As a consequence, we may choose $V = (-(m_i(x)w^2/2) - (b_{ii}(x)w^3/3))/\bar{\mu}_i$, $f(x) = 0$ and $g(x) = -m_i(x)/b_{ii}(x)$ to conclude that $\bar{u}_i(\varepsilon)$ converges to $m_i(x)/b_{ii}(x)$ uniformly on compact subsets of Ω as $\varepsilon \to 0$. For details, see [**8**, Section 4]. We note here only that the arguments employed there are local in that they focus on arbitrarily small subdomains Ω' of Ω having the property that $\overline{\Omega}' \subset \Omega$. For this reason, the proofs in [**8**, Section 4] can be adapted to the case of homogeneous Neumann boundary data on Ω, and we could have just as easily chosen $B\phi = \partial\phi/\partial\nu$ in (4.2). Consequently, since $\bar{u}_i(\varepsilon) \le \sup_{x\in\overline{\Omega}} (m_i/b_{ii})(x)$ for all $\varepsilon > 0$, $\bar{u}_i(\varepsilon) \to m_i/b_{ii}$ in $L^p(\Omega)$ for any $p < \infty$ as $\varepsilon \to 0$, and we obtain permanence for $\varepsilon > 0$ sufficiently small if (4.16) obtains. Since now (4.16) becomes

$$\int_\Omega \left(m_i - \frac{b_{ij} m_j}{b_{jj}} \right) \left(\frac{m_i}{b_{ii}} \right)^2 > 0 \tag{4.18}$$

for $i, j = 1, 2$, $i \neq j$, we have the following result.

Theorem 4.2. *Consider* (4.1)–(4.2), *assume that all coefficients are smooth and positive and that* $B\phi = \phi$. *Then for any fixed* $(\bar{\mu}_1, \bar{\mu}_2)$

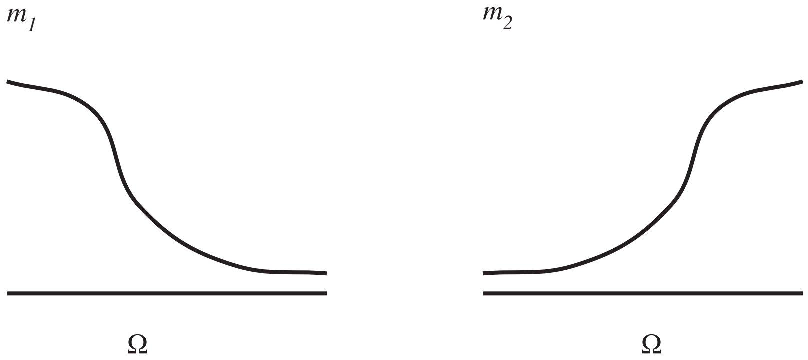

FIGURE 4.1. Profiles of growth rates for which permanence obtains in (4.1)–(4.2) for small diffusion rates under the assumption that $b_{ij} \equiv 1$ (strong competition).

with $\bar{\mu}_1 > 0$, $\bar{\mu}_2 > 0$, *permanence obtains in* (4.1)–(4.2) *for* $(\mu_1, \mu_2) = (\varepsilon^2 \bar{\mu}_1, \varepsilon^2 \bar{\mu}_2)$ *for* ε *sufficiently small provided* (4.18) *holds.*

It is clear that (4.18) holds whenever b_{ij}, $i \neq j$, is relatively small. It will also obtain even if b_{ij}, $i \neq j$, is large provided that m_i is large where m_j is small, and vice versa. For instance, suppose that $b_{ij} \equiv 1$ for $i, j = 1, 2$. (Under these assumptions in a spatially homogeneous case, u_i will exclude u_j if $m_i > m_j$; if $m_i = m_j$, coexistence is possible.) Then (4.18) reduces to

$$\int_\Omega (m_1 - m_2) m_1^2 > 0 \tag{4.19}$$

and

$$\int_\Omega (m_2 - m_1) m_2^2 > 0. \tag{4.20}$$

Suppose m_1 and m_2 are as in Figure 4.1. Then m_1^2 is large when $m_1 - m_2 > 0$ and small when $m_1 - m_2 < 0$, and similarly, m_2^2 is large when $m_2 - m_1 > 0$ and small when $m_2 - m_1 < 0$. Thus, we can expect (4.18) to hold even under severe competition, *provided* it occurs only in small geographical regions attractive to each species in the absence of the other. Such a condition complements the usual one that competition is weak but may be universal.

Appendix

Theorem A.1. *Suppose that* $f(x,u)$ *is Lipschitz in* x *on* $\overline{\Omega}$ *and continuously differentiable in* u *with* $\partial f/\partial u < 0$ *for* $u > 0$, $f(x,u) \leq 0$ *for all* $x \in \overline{\Omega}$ *and* $u \geq l$, *where* l *is a positive constant, and* $f(x_0, 0) > 0$ *for some* $x_0 \in \Omega$. *Consider the eigenvalue problem*

$$(*) \qquad \begin{cases} -\Delta\phi = \lambda f(x,0)\phi & \text{in } \Omega, \\ \partial\phi/\partial\nu = 0 & \text{on } \partial\Omega. \end{cases}$$

If $\int_\Omega f(x,0)\,dx < 0$, *let* $\lambda_1(f(x,0))$ *be the principal positive eigenvalue of* $(*)$, *and if* $\int_\Omega f(x,0)\,dx \geq 0$, *set* $\lambda_1(f(x,0)) = 0$. *Then the problem*

$$(**) \qquad \begin{cases} u_t = \mu\Delta u + f(x,u)u & \text{in } \Omega \times (0,\infty), \\ \partial u/\partial\nu = 0 & \text{on } \partial\Omega \times (0,\infty) \end{cases}$$

has a unique positive steady-state $\bar{u}$ *which is a global attractor for nonnegative nontrivial solutions when* $0 < \mu < 1/\lambda_1(f(x,0))$. *When* $\mu \geq 1/\lambda_1(f(x,0))$, *there is no positive steady-state for* $(**)$, *and all nonnegative solutions to* $(**)$ *decay to* 0 *as* $t \to \infty$.

Remarks. (i) When $\int_\Omega f(x,0)\,dx \geq 0$ and $\lambda_1(f(x,0)) = 0$, $1/\lambda_1(f(x,0))$ is to be interpreted as $+\infty$.

(ii) The self-regulation hypotheses of Theorem A.1 make it essential that $f(x,0)$ be positive somewhere in Ω. If not, $f(x,u) < 0$ for $u \geq 0$ and all $x \in \overline{\Omega}$, and hence all solutions to $(**)$ decay to 0 as $t \to \infty$.

(iii) It is reasonable to view $\int_\Omega f(x,0)\,dx/|\Omega|$ as a measure of average environmental quality, where $|\Omega|$ denotes the Lebesgue measure of Ω. Theorem A.1 can be understood to say that when the boundary of the habitat acts as a barrier, the average environmental quality needs to be negative in order for the diffusion rate of the population to affect long-term survival of the population. This contrasts with the Dirichlet case, where the diffusion rate always plays a role in the long-term survival of the population.

(iv) Theorem A.1 is an analogue for the case of zero Neumann boundary data to the results of Section 2 of [**8**]. Our proof of Theorem A.1 is divided into two cases, depending on whether $\int_\Omega f(x,0)\,dx < 0$ or $\int_\Omega f(x,0)\,dx \geq 0$. We treat the former case first and make an argument based on the implicit function theorem and the well-known result of Crandall and Rabinowitz on bifurcation from simple eigenvalues [**15**, Theorem 1.7], which was employed in a similar context in [**9**]. When $\int_\Omega f(x,0)\,dx \geq 0$, we use the results for the case where $\int_\Omega f(x,0)\,dx < 0$ along with the method of upper and lower solutions. In the former case, the proof that all nonnegative solutions to $(**)$ decay to 0 when $\mu \geq 1/\lambda_1(f(x,0))$ is the same as that of [**8**, Theorem 4.9], so we do not repeat the argument here.

Proof. Consider

$$\text{(A1)} \qquad \begin{cases} \partial u/\partial t = \mu\Delta u + f(x,0)u + \tilde{f}(x,u)u & \text{in } \Omega \times (0,\infty), \\ \partial u/\partial \nu = 0 & \text{on } \partial\Omega \times (0,\infty), \end{cases}$$

where $\tilde{f}(x,u) = f(x,u) - f(x,0)$, and the corresponding elliptic problem

$$\text{(A2)} \qquad \begin{cases} -\mu\Delta u = [f(x,0) + \tilde{f}(x,u)]u & \text{in } \Omega, \\ \partial u/\partial \nu = 0 & \text{on } \partial\Omega. \end{cases}$$

Suppose first that $\int_\Omega f(x,0)\,dx < 0$. Then the linear problem

$$\text{(A3)} \qquad \begin{cases} -\Delta z = \lambda f(x,0) z & \text{in } \Omega, \\ \partial z/\partial \nu = 0 & \text{on } \partial\Omega, \end{cases}$$

has a unique positive eigenvalue $\lambda_1 = \lambda_1(f(x,0))$ admitting a positive eigenfunction [**7**]. Let $p > N$, where $\Omega \subseteq \mathbf{R}^N$, and let $V = \{w \in W^{2,p}(\Omega) : \partial w/\partial \nu = 0 \text{ on } \partial\Omega\}$, where $W^{2,p}(\Omega)$ is the Sobolev space of twice weakly differentiable functions on Ω having the property that the function and its weak derivatives lie in $L^p(\Omega)$. $W^{2,p}(\Omega)$ is a Banach algebra (see [**2**]) and V is a closed subspace. Define $F : V \times \mathbf{R} \to L^p(\Omega)$ by

$$F(u,\lambda) = -\Delta u - \lambda(f(x,0) + \tilde{f}(x,u))u.$$

Then $F(u,\lambda) = 0$ for $\lambda > 0$ is equivalent to u being a solution to (A2) for $\mu = 1/\lambda$. $D_u F(u,\lambda)w = -\Delta w - \lambda(f(x,0)w + (\partial\tilde{f}/\partial u)(x,u)uw + \tilde{f}(x,u)w)$. In particular, $D_u F(0,\lambda)w = -\Delta w - \lambda f(x,0)w$, a Fredholm operator of index 0 from V to $L^p(\Omega)$. Since $F(0,\lambda) = 0$ for all λ and λ_1 is a simple eigenvalue of (A3), the Crandall-Rabinowitz bifurcation theorem [**15**] implies that there will be a branch of positive solutions to (A2) emanating from $(0, 1/\lambda_1)$ provided $D_{\lambda u}F(0,\lambda_1)z_0 \notin R(F_u(0,\lambda_1))$ where z_0 solves (A3) with $||z_0||_{W^{2,p}(\Omega)} = 1$. Moreover, in this case, the limit of $u/||u||_{W^{2,p}(\Omega)}$ along such a branch as $||u||_{W^{2,p}(\Omega)} \to 0$ is z_0. To verify that $D_{\lambda u}F(0,\lambda_1)z_0 \notin R(F_u(0,\lambda_1))$, observe that $D_{\lambda u}F(0,\lambda)\phi = -f(x,0)\phi$. If $-\Delta w - \lambda_1 f(x,0)w = -f(x,0)z_0$ in Ω with $\partial w/\partial\nu = 0$ on $\partial\Omega$, an application of integration by parts via the divergence theorem yields that $\int_\Omega f(x,0)z_0^2 = 0$. However, in the proof of the existence of λ_1 [**7**] it is shown that $\int_\Omega f(x,0)z_0^2 > 0$. As a consequence, $D_{\lambda u}F(0,\lambda_1)z_0 \notin R(F_u(0,\lambda_1))$, and there is a branch of positive solutions to (A2) emanating from $(0, 1/\lambda_1)$, as asserted.

Next observe that if $u > 0$ solves (A2) for some $\mu > 0$, then $F(u, 1/\mu) = 0$ and $1/\mu = \lambda_1(f(x,0) + \tilde{f}(x,u))$. But since $u > 0$, $\tilde{f}(x,u) < 0$. We know from [**28**] that $\lambda_1(m)$ decreases as m increases. Hence, $\lambda_1(f(x,0) + \tilde{f}(x,u)) > \lambda_1(f(x,0))$. Therefore, $\mu < 1/\lambda_1(f(x,0))$, and we conclude that there can be no positive steady-state for (A1) when $\mu \geq 1/\lambda_1(f(x,0))$.

Consider now the eigenvalue problem obtained from the linearization about a positive solution u of $F(u,\bar{\lambda}) = 0$ for some $\bar{\lambda} > 0$:

$$\begin{cases} -\Delta z - \bar{\lambda}(f(x,0)z + (\partial\tilde{f}/\partial u)(x,u)uz + \tilde{f}(x,u)z) = \alpha z & \text{in } \Omega, \\ \partial z/\partial\nu = 0 & \text{on } \partial\Omega. \end{cases}$$

Since $F(u,\bar{\lambda}) = 0$, $y = u$ and $\gamma = 0$ are eigenfunction and eigenvalue, respectively, for

$$\begin{cases} -\Delta y - \bar{\lambda}(f(x,0)y + \tilde{f}(x,u)y) = \gamma y & \text{in } \Omega \\ \partial y/\partial\nu = 0 & \text{on } \partial\Omega; \end{cases}$$

since $-\bar{\lambda}(\partial\tilde{f}/\partial u)(x,u)u > 0$, it follows from a comparison argument that $\alpha > 0$. Consequently, u is locally asymptotically stable as a solution to (A1) for $\mu = 1/\bar{\lambda}$, and moreover, the implicit function theorem guarantees the continuability of positive solutions to $F(u,\lambda) = 0$ in a neighborhood $(\bar{\lambda} - \delta, \bar{\lambda} + \delta)$ for some $\delta > 0$. Since $||u||_\infty \leq l$ for any positive solution of $F(u,\lambda) = 0$ corresponding to a $\lambda > 0$, and since for such a solution

$$u = (-\Delta + 1)^{-1}(\lambda f(x,u) + 1)u,$$

the positive solutions to $F(u,\lambda)=0$ are uniformly bounded in $W^{2,p}(\Omega)$ (hence precompact in $L^p(\Omega)$) for λ contained in bounded intervals. It follows that there are nonnegative solutions to $F(u,\lambda)=0$ when $\lambda=\bar{\lambda}-\delta$ and $\lambda=\bar{\lambda}+\delta$. So the branch of solutions to (A2) which emanates from $(0,1/\lambda_1)$ is an arc (in terms of μ) and must continue for all $\mu<1/\lambda_1$. Moreover, since the Crandall-Rabinowitz theorem [**15**] guarantees the uniqueness of the branch in a neighborhood of $(0,1/\lambda_1)$, the uniqueness argument employed in [**9**] is applicable here, and there is in fact a unique arc of positive solutions to (A2) for $0<\mu<1/\lambda_1$. Finally, that each of these solutions is a *global* attractor for nonnegative nontrivial solutions of (A1) follows from dynamical system principles.

Suppose now that $\int_\Omega f(x,0)\,dx \geq 0$. Then there is no positive eigenvalue for (A3) admitting a positive eigenfunction. Consequently, the bifurcation theoretic arguments employed to establish existence and uniqueness of the positive solutions to (A2) when $\int_\Omega f(x,0)\,dx<0$ are no longer available. We replace these arguments with ones based on the method of upper and lower solutions. Once we obtain existence and uniqueness of the positive solutions to (A2), the stability properties asserted for these solutions follow as in the case $\int_\Omega f(x,0)\,dx<0$.

So now let $\bar{\lambda}>0$ be fixed. Let $\Omega'\subset\subset\Omega$ be an open ball in Ω so that the Lebesgue measures of $\{x\in\Omega' : f(x,0)>0\}$ and $\Omega-\Omega'$ are positive. As ε increases beyond $\int_\Omega f(x,0)\,dx/|\Omega-\Omega'|$, $\int_\Omega(f(x,0)-\varepsilon\chi_{\Omega-\Omega'}(x))\,dx$ becomes negative while $f(x,0)-\varepsilon\chi_{\Omega-\Omega'}(x)>0$ in Ω'. Hence,

$$\begin{cases} -\Delta z=\lambda(f(x,0)-\varepsilon\chi_{\Omega-\Omega'}(x))z & \text{in } \Omega,\\ \partial z/\partial\nu=0 & \text{on } \partial\Omega \end{cases}$$

admits a positive principal eigenvalue $\lambda_1=\lambda_1(\varepsilon)$, and consequently,

$$\text{(A4)}\qquad \begin{cases} -\Delta w=\lambda(f(x,0)-\varepsilon\chi_{\Omega-\Omega'}(x)+\tilde{f}(x,w))w & \text{in } \Omega,\\ \partial w/\partial\nu=0 & \text{on } \partial\Omega \end{cases}$$

admits a unique positive solution for $\lambda>\lambda_1(\varepsilon)$. (The argument in the preceding case remains valid even though $f(x,0)-\varepsilon\chi_{\Omega-\Omega'}(x)$ is discontinuous.) Moreover, as $\varepsilon\to\int_\Omega f(x,0)\,dx/|\Omega-\Omega'|$, $\lambda_1(\varepsilon)\to 0$, so that we can choose $\varepsilon>\int_\Omega f(x,0)\,dx/|\Omega-\Omega'|$ with $\lambda_1(\varepsilon)<\bar{\lambda}$. So (A4) admits a unique positive solution $w_{\bar{\lambda}}$ when $\lambda=\bar{\lambda}$. Notice that if $\alpha\in(0,1)$, $\alpha w_{\bar{\lambda}}<w_{\bar{\lambda}}$, and thus $\tilde{f}(x,\alpha w_{\bar{\lambda}})>\tilde{f}(x,w_{\bar{\lambda}})$. Hence $\alpha w_{\bar{\lambda}}$ is a lower solution for

$$\text{(A5)} \qquad \begin{cases} -\Delta u = \bar{\lambda}(f(x,0) + \tilde{f}(x,u))u & \text{in } \Omega, \\ \partial u/\partial \nu = 0 & \text{on } \partial\Omega. \end{cases}$$

Any sufficiently large constant is an upper solution. Since $(-\Delta + C)^{-1}$ is realized as integration against a positive kernel (the Green's function) for any $C > 0$ and $f(x,0) \in L^\infty(\Omega)$, the method of upper and lower solutions guarantees the existence of $u > 0$ so that $F(u, \bar{\lambda}) = 0$. Moreover, since there is no bifurcation from the zero solution at $\bar{\lambda}$ and $\alpha w_{\bar{\lambda}}$ is a lower solution to (A5) for any $\alpha \in (0,1)$, there is a minimal positive solution u_1 to (A5). If $u_2 > u_1$ is another solution of $F(u, \bar{\lambda}) = 0$,

$$\begin{aligned} -\Delta(u_2 - u_1) &= \bar{\lambda}\{f(x,u_2)u_2 - f(x,u_1)u_1\} \\ &= \bar{\lambda}\{(\partial f/\partial u)(x,\theta)\theta + f(x,\theta)\}(u_2 - u_1) \end{aligned}$$

in Ω, with $\partial(u_2 - u_1)/\partial\nu = 0$ and $\theta > u_1$. So $y = u_2 - u_1 > 0$ and $\gamma = 0$ satisfy

$$-\Delta y - \bar{\lambda} f(x,u_1)y - \bar{\lambda}\{(\partial f/\partial u)(x,\theta)\theta + f(x,\theta) - f(x,u_1)\}y = \gamma y$$

in Ω. Since $\theta > u_1 > 0$, $(\partial f/\alpha u)(x,\theta) < 0$ and $f(x,\theta) - f(x,u_1) < 0$. Consequently, the principal eigenvalue of

$$\text{(A6)} \qquad \begin{cases} -\Delta z - \bar{\lambda} f(x,u_1)z = \alpha z & \text{in } \Omega, \\ \partial z/\partial \nu = 0 & \text{on } \partial\Omega \end{cases}$$

must be negative. But since $z = u_1$ is an eigenfunction for (A6) corresponding to $\alpha = 0$, we have a contradiction which establishes the uniqueness of u_1 and hence completes the proof.

Theorem A.2. *Consider* (A1) *in the special case* $f(x,u) = m(x) - u$, *where* $\int_\Omega m(x) \geq 0$. *For* $\mu > 0$, *let* $u^*(\mu)$ *denote the unique positive steady state to* (A1). *Then* $\lim_{\mu\to\infty} u^*(\mu) = \int_\Omega m/|\Omega|$, *where the limit is in the topology of* $C^{1+\alpha}(\overline{\Omega})$.

Proof. Let $V = \{w \in W^{2,p}(\Omega) : \partial w/\partial\nu = 0 \text{ on } \partial\Omega\}$ as in the proof of Theorem A.1, and let $W = \{w \in V : \int_\Omega w = 0\}$. Define $H : \mathbf{R} \times W \times$

$\mathbf{R} \to L^p(\Omega)$ by $H(c, w, \lambda) = -\Delta w - \lambda(m(x)(c + w) - (c + w)^2)$ where c is now an arbitrary parameter. Notice that $H(c, w, \lambda) = F(c + w, \lambda)$, where

$$F(u, \lambda) = -\Delta u - \lambda(m(x)u - u^2).$$

Notice that if $\lambda = 0$, $F(u, 0) = 0$ implies that $u = c$. Since $V = \mathbf{R} \otimes W$, we can examine the solution set to $F(u, \lambda) = 0$ for λ near 0 by examining $H(c, w, \lambda) = 0$ for λ near 0.

Letting $DH(c, w, \lambda)$ denote the Fréchet derivative of H with respect to (w, λ), we find that

$$\begin{aligned} DH(c, w, \lambda)(v, \sigma) = -\Delta v - \lambda m(x)v + 2\lambda(c + w)v \\ - \sigma\{m(x)(c + w) - (c + w)^2\}. \end{aligned}$$

In particular, $DH(c, 0, 0)(v, \sigma) = -\Delta v - \sigma\{m(x)c - c^2\}$. If $DH(c, 0, 0)$ $(v, \sigma) = 0$, $\sigma = 0$ or $c \int_\Omega m = c^2|\Omega|$. As a consequence, if $\bar{c} \neq 0$ and $\bar{c} \neq \int_\Omega m/|\Omega|$, $DH(\bar{c}, 0, 0)$ is a linear homeomorphism from $W \times \mathbf{R}$ onto $L^p(\Omega)$, and the line of constants $\{(c, 0, 0) : c \in \mathbf{R}\}$ is the only branch of solutions to $H(c, w, \lambda) = 0$ in a neighborhood of $(\bar{c}, 0, 0)$.

Suppose now that $\int_\Omega m > 0$ and that $\bar{c} = \int_\Omega m/|\Omega|$. Then

$$DH\bigg(\int m/|\Omega|, 0, 0\bigg)(v, \sigma) = -\Delta v - \sigma\bigg\{m\bigg(\int_\Omega m/|\Omega|\bigg) - \bigg(\int_\Omega m\bigg)^2/|\Omega|^2\bigg\}.$$

As $\int_\Omega [m(\int_\Omega m/|\Omega|) - (\int_\Omega m)^2/|\Omega|^2] = 0$, there is a unique $v^* \in W$ so that $-\Delta v^* = ((\int_\Omega m)/|\Omega|)m - (\int_\Omega m)^2/|\Omega|^2$ and hence $\ker DH(\int_\Omega m/|\Omega|, 0, 0) = \{(sv^*, s) : s \in \mathbf{R}\}$. The Crandall-Rabinowitz constructive bifurcation theorem [**15**] can be applied to obtain a unique curve of solutions to $H(c, w, \lambda)$ bifurcating from the constant solutions at $(\int_\Omega m/|\Omega|, 0, 0)$ if

$$\text{(A7)} \quad \begin{aligned} D_c DH\bigg(\bigg(\int_\Omega m/|\Omega|\bigg), 0, 0\bigg)(v^*, 1) \\ \notin R\bigg(DH\bigg(\bigg(\int_\Omega m/|\Omega|\bigg), 0, 0\bigg)\bigg) \quad \text{as } H \text{ is } C^2 \end{aligned}$$

and $DH(\int_\Omega m/|\Omega|, 0, 0)$ is Fredholm of index 0. Notice that

$$D_c DH\bigg(\bigg(\int_\Omega m/|\Omega|\bigg), 0, 0\bigg)(v, \sigma) = -\sigma\bigg(m(x) - 2\bigg(\int_\Omega m/|\Omega|\bigg)\bigg).$$

So if (A7) fails, there is a $(y, \gamma) \in W \times \mathbf{R}$, so that

$$-\Delta y-\gamma\left\{\left(\int_\Omega m/|\Omega|\right)m-\left(\int_\Omega m\right)^2/|\Omega|^2\right\} = -\left(m(x)-\left(2\int_\Omega m/|\Omega|\right)\right).$$

But since $\int_\Omega[\gamma\{((\int_\Omega m)/|\Omega|)m-(\int_\Omega m)^2/|\Omega|^2\}-(m(x)-2(\int_\Omega m/|\Omega|))]=\int_\Omega m > 0$, there can be no such (y, γ) and (A7) holds.

If now $\int_\Omega m > 0$ and $\bar{c} = 0$, $DH(0,0,0)(v,\sigma) = -\Delta v$. Consequently, $\ker DH(0,0,0) = \{(0,s) : s \in \mathbf{R}\}$. As $D_c DH(0,0,0)(v,\sigma) = -\sigma m(x)$, the condition

$$D_c DH(0,0,0)(0,1) \notin R(DH(0,0,0))$$

becomes the insolvability of the linear problem

$$\begin{cases} -\Delta y = -m(x) & \text{in } \Omega \\ \partial y/\partial \nu = 0 & \text{on } \partial\Omega. \end{cases}$$

Since $\int_\Omega m > 0$, the problem has no solution, and the Crandall-Rabinowitz theorem [**15**] may be invoked to obtain a unique curve of solutions to $H(c, w, \lambda) = 0$ bifurcating from the line of solutions $(c, 0, 0)$ at $(0, 0, 0)$. Clearly, this curve can only be the line of trivial solutions $(0, 0, \lambda)$. We may conclude that if $u^*(\mu)$ denotes the unique positive equilibrium for (A1), then $\lim_{\mu\to\infty} u^*(\mu)$ in $W^{2,p}(\Omega)$ (and hence in $C^{1+\alpha}(\overline{\Omega})$) is the constant $\int_\Omega m/|\Omega|$ if $\int_\Omega m > 0$.

Finally, suppose $\int_\Omega m = 0$. Then for any $\bar{c} \neq 0$, we know that the line of constants $(c, 0, 0)$ is the only branch of solutions to $H(c, w, \lambda) = 0$ in a neighborhood of $(\bar{c}, 0, 0)$. But for $\lambda = 1/\mu$, $u = u^*(\mu)$ satisfies

$$u = (-\Delta + 1)^{-1}[u + \lambda(mu - u^2)] \tag{A8}$$

with $||u||_\infty \leq \operatorname{ess\,sup}_\Omega m_+$. Then, for any sequence $\lambda_n \to 0^+$, there is a subsequence λ_{n_k} such that the corresponding solution u_{n_k} of (A8) converges in $W^{2,p}(\Omega)$ to a solution $\tilde{u}$ of

$$\begin{cases} -\Delta u = 0 & \text{in } \Omega, \\ \partial u/\partial \nu = 0 & \text{on } \partial\Omega. \end{cases}$$

$\tilde{u}$ is necessarily a constant, and from the above the only possible constant is 0. So $u_{n_k} \to 0$ in $W^{2,p}(\Omega)$ (and hence in $C^{1+\alpha}(\overline{\Omega})$). Consequently, if $\int_\Omega m = 0$, $\lim_{\mu\to\infty} u^*(\mu) = 0$.

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