Bounds on Trajectories in Diffusive Predator-Prey Models

R.S. Cantrell and C. Cosner
Department of Mathematics and Computer Science
University of Miami
Coral Gables, FL 33124
U.S.A.

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Abstract

For an ecological model to predict persistence it should have a positive attractor. However, the transient behavior of trajectories as they approach the attractor may be relevant in some cases. An example is the scenario where a new predator is introduced at low density into a region with an established prey population. In some cases the system may maintain both populations at moderate densities. In other cases there may be an explosion in the predator population followed by collapses in the prey and then the predator populations. We give conditions under which the first alternative is predicted by a diffusive predator-prey system. The analysis is based on comparisons with diffusive logistic equations and leads to bounds on trajectories in terms of those for associated logistic equations. The methods can be applied to many other sorts of models.

§1. Introduction.

One of the most basic questions that can be asked about a population model is whether it predicts persistence or extinction for the populations it describes. In the long term persistence can sometimes be inferred from the presence of a positive globally attracting positive equilibrium or more generally from the presence of a globally attracting positive set, i.e. from uniform persistence or permanence (see [4,10]). On the other hand, simple deterministic models ignore many effects including demographic stochasticity, so a robust prediction of long term persistence may require some estimates on the location of the positive attracting sets, specifically lower bounds on the densities in the attracting set. Furthermore, sometimes the short term behavior of a model is relevant. One scenario where that is the case is where a new predator is introduced into a region where there is a prey population. In some cases the predator population may increase dramatically, causing a crash in the prey population, which in turn causes a crash in the predator population. These crashes may lead to the extinction of the predator and perhaps the prey; see [12, p.236-237] for a biological discussion of this point. The phenomenon of crashes may be seen in simple mathematical models. To be specific, consider the simple predator-prey model $du/dt = (a - bu - cv)u$, $dv/dt = (-d + eu)v$ where u =prey density, v =predator density, and a, b, c, d, e are positive constants. For some parameter values the system has an equilibrium with both components positive and large, but trajectories starting with $u = a/b$ (the logistic prey equilibrium) and v small have v becoming very large and u and then v later becoming very small. It turns out that this effect will be reduced or eliminated if a self-regulation term is incorporated into the predator equation, so that $dv/dt = (-d + eu - fv)u$. In this article we obtain bounds on trajectories corresponding to an equivalent scenario for a predator-prey model with diffusion and with spatial and temporal heterogeneity in the coefficients.

In the case of reaction-diffusion models with constant coefficients and no-flux (i.e. reflecting, i.e. Neumann) boundary conditions, trajectories can often be bounded by comparisons with systems of ordinary differential equations via the method of contracting rectangles; see [1,11]. In the case of models which are order preserving, e.g. cooperative systems and models for two competing species, it is often possible to bound the dynamics of solutions via comparisons with sub- and super-solutions of the system. This sort of idea is discussed in [2,4,6,9] among many other references. In a recent paper [3] we devised a method of using successive comparisons with single logistic equations to obtain bounds for the attractors of nonmonotone systems with spatially and temporally varying coefficients. That method is described in [4] and extended to other sorts of models (including discrete time models and density dependent matrix models) in [5]. It turns out that the same comparison approach also can yield time dependent bounds on trajectories. We consider a relatively simple and specific scenario, namely the situation described above where the prey is established in an environment and a predator is introduced at a low density. However, the methods could in principle be applied to obtain time dependent bounds on trajectories in any of the many sorts of models discussed in [3,5].

This paper is organized as follows: in Section 2 we state the necessary background results about diffusive logistic equations; in Section 3 we derive the estimates on trajectories; in Section 4 we show how more explicit estimates can be obtained in a relatively simple example; and in Section 5 we briefly discuss the biological implications of our results in relatively nonmathematical terms.

§2. Preliminaries.

Our analysis will be based on comparisons between solutions of the predator-prey model of interest and those of related diffusive logistic equations. All equations will be defined on $\Omega \times (0,\infty)$ where $\Omega \subseteq \mathbb{R}^n$ is a bounded domain with smooth boundary. The form of logistic model we shall use is

$$\begin{aligned} w_t &= Lw + r(x,t)w - g(x,t)w^2 && \text{in } \Omega \times (0,\infty) \\ Bw &= 0 && \text{on } \partial\Omega \times (0,\infty) \end{aligned} \tag{2.1}$$

where

$$Lw \equiv \sum_{i,j=1}^{n} A_{ij}(x,t)\frac{\partial^2 w}{\partial x_i \partial x_j} + \sum_{i=1}^{n} A_i(x,t)\frac{\partial w}{\partial x_i} \tag{2.2}$$

is uniformly elliptic for each t with $A_{ij} = A_{ji}$ and

$$Bw = \alpha(x)w + \beta(x)\frac{\partial w}{\partial n} \tag{2.3}$$

where $\alpha, \beta \geq 0$, $\alpha + \beta > 0$ ($\partial/\partial n$ denotes the outward normal derivative). We shall assume that r, g, and the coefficients of L are Hölder continuous of class $C^{\theta,\theta/2}$ in (x,t) and T-periodic in t. (If the coefficients do not depend on t they can be viewed as T-periodic for all T.) The coefficient g in (2.1) is assumed to be bounded below by a positive constant. We have the following

Theorem 2.1 ([9]): The eigenvalue problem

$$
(2.4) \qquad \begin{aligned} \phi_t - L\phi - r(x,t)\phi &= \mu\phi && \text{on } \Omega \times I\!R \\ B\phi &= 0 && \text{on } \partial\Omega \times I\!R, \\ \phi &\text{ is } T-\text{periodic} \end{aligned}
$$

has a unique principal eigenvalue μ_1 characterized by an eigenfunction ϕ which is positive on $\Omega \times I\!R$. If $\mu_1 < 0$, then (2.1) has a unique positive T-periodic steady state w^* which is globally attracting among nontrivial nonnegative solutions in the $C^{1+\theta}(\overline{\Omega})$ norm. If $\mu_1 \geq 0$ then all positive solutions of (2.1) approach zero as $t \to \infty$.

Discussion: This Theorem follows from results of Hess; see [9, §I.14 and Theorem 28.1].

Remark: If L and r are independent of t, then $\mu_1 = -\sigma_1$ where σ_1 is the principal eigenvalue of $L\phi + r\phi = \sigma\phi$ in Ω, $B\phi = 0$ on $\partial\Omega$.

We shall need the following comparison theorem.

Theorem 2.2: Suppose that $\overline{w}$, $\underline{w} \in C^{2,1}(\Omega \times (0,\infty)) \cap C(\overline{\Omega} \times [0,\infty))$ (with $\overline{w}, \underline{w} \in C^1(\overline{\Omega} \times (0,\infty))$ if $\beta \neq 0$ in (2.3)) and

$$
(2.5) \qquad \begin{aligned} \overline{w}_t - L\overline{w} - r\overline{w} + g\overline{w}^2 &\geq \underline{w}_t - L\underline{w} - r\underline{w} + g\underline{w}^2 && \text{on } \Omega \times (0,\infty) \\ B\overline{w} &\geq B\underline{w} && \text{on } \partial\Omega \times (0,\infty) \\ \overline{w}(x,0) &\geq \underline{w}(x,0). \end{aligned}
$$

Then $\overline{w}(x,t) \geq \underline{w}(x,t)$ on $\overline{\Omega} \times [0,\infty)$ and either $\overline{w}(x,t) > \underline{w}(x,t)$ on $\Omega \times (0,\infty)$ or $\overline{w} \equiv \underline{w}$.

Discussion: This is a standard comparison result for parabolic equations; see [9, §III.21] or [8,11].

Definition: If

$$
(2.6) \qquad \begin{aligned} \overline{w}_t - L\overline{w} - r\overline{w} + g\overline{w}^2 &\geq 0 && \text{on } \Omega \times (0,\infty) \\ B\overline{w} &\geq 0 && \text{on } \partial\Omega \times (0,\infty) \end{aligned}
$$

then $\overline{w}$ is a *supersolution* of (2.1). If $\underline{w}$ satisfies the reverse inequalities of (2.6) then $\underline{w}$ is a *subsolution.* It follows from Theorem 2.2 that if $w(x,0) \leq \overline{w}(x,0)$ and w is a solution of (2.1) then $w(x,t) \le \overline{w}(x,t)$. (Any solution of (2.1) is both a subsolution and a supersolution.)

§3. Analysis of trajectories in a predator-prey model.

We shall consider a scenario where a prey species is in an established persistent state and a predator is introduced at low densities. The predator-prey model we shall study is a mild generalization of a Lotka-Volterra model; however, the methods could be applied to many other types of models; see [3,5]. Let u denote the density of the prey and v the density of the predator. The model is

$$\begin{aligned} u_t &= L_1 u + [a(x,t,u,v) - b(x,t,u,v)u - c(x,t,u,v)v]u \\ u &= L_2 v + [d(x,t,u,v) + e(x,t,u,v)u - f(x,t,u,v)v]v \end{aligned} \qquad \text{in } \Omega \times (0,\infty) \tag{3.1}$$

$$B_1 u = 0, \ B_2 v = 0 \qquad \text{on } \partial\Omega \times (0,\infty)$$

where L_1, L_2 are as in (2.2) and B_1, B_2 as in (2.3). We shall assume that there are T-periodic Hölder continuous functions $\underline{a}, \overline{a}, \underline{b}, \overline{b}, \underline{c}, \overline{c}, \underline{d}, \overline{d}, \underline{e}, \overline{e}, \underline{f}, \overline{f}$ independent of u, v and positive constants b_0 and f_0 such that

$$\begin{aligned} &\underline{a} \le a \le \overline{a}, \quad b_0 \le \underline{b} \le b \le \overline{b}, \quad 0 \le \underline{c} \le c \le \overline{c}, \quad \underline{d} \le d \le \overline{d}, \\ &0 \le \underline{e} \le e \le \overline{e}, \quad f_0 \le \underline{f} \le f \le \overline{f} \quad \text{on } \overline{\Omega} \times (0,\infty). \end{aligned} \tag{3.2}$$

We are only interested in nonnegative solutions of (3.1); however, the set $u \ge 0, v \ge 0$ is positively invariant by standard arguments (see e.g. [9,11]). We note that d will be negative if the predator cannot survive without the prey, but might be positive if the predator has alternate food sources.

We envision a scenario where the prey is established and the predator is introduced at low densities. Thus, we must have the prey existing at a state analogous to a positive equilibrium at $t = 0$. For that to be possible, we must require that $\overline{a}$ is positive somewhere, and in fact that $\overline{a}$ is sufficiently positive on a large enough subset of $\Omega \times [0,T]$ that the principal eigenvalue of

$$\begin{aligned} \phi_t - L_1\phi - \overline{a}\phi &= \mu\phi && \text{in } \Omega \times I\!R \\ B_1\phi &= 0 && \text{on } \partial\Omega \times I\!R, \\ \phi \ &\text{is } T-\text{periodic} \end{aligned} \tag{3.3}$$

is negative. This is needed because if u is a solution of (3.1) then u is a subsolution of

$$\text{(3.4)} \qquad \begin{aligned} u_t &= L_1 u + (\overline{a} - \underline{b}u)u && \text{on } \Omega \times (0,\infty) \\ B_1 u &= 0 && \text{on } \partial\Omega \times (0,\infty), \end{aligned}$$

so by Theorem 2.2 we have $u \le \overline{u}$ where $\overline{u}$ is the solution of (3.4) with $\overline{u}(x,0) = u(x,0)$. If the principal eigenvalue of (3.3) is nonnegative then $\overline{u} \to 0$ as $t \to \infty$ by Theorem 2.1, so $u \to 0$ for all nonnegative solutions of (3.1) and the prey cannot be viewed as being established. On the other hand, if the principal eigenvalue of (3.3) is negative then we still have $u \le \overline{u}$ but now by Theorem 2.1 there is a unique positive T-periodic solution u^* of (3.4) which attracts all positive solutions, so that $\overline{u} \to u^*$ as $t \to \infty$. (In the case of a genuine Lotka-Volterra model, u^* is the steady-state for the prey in the absence of the predator.) The periodic solution u^* provides a natural upper bound for an established prey population. We shall assume also that there is a natural lower bound in the absence of the predator. Hence we assume that there is a negative principal eigenvalue for

$$\text{(3.5)} \qquad \begin{aligned} \phi_t - L_1\phi - \underline{a}\phi &= \mu\phi && \text{in } \Omega \times I\!R \\ B_1\phi &= 0 && \text{on } \partial\Omega \times I\!R, \\ \phi \ \text{ is } T &- \text{periodic}, \end{aligned}$$

so that there is a unique positive T-periodic globally attracting solution $\tilde{u}$ of

$$\text{(3.6)} \qquad \begin{aligned} u_t &= L_1 u + (\underline{a} - \overline{b}u)u && \text{in } \Omega \times (0,\infty) \\ B_1 u &= 0 && \text{on } \partial\Omega \times (0,\infty). \end{aligned}$$

(Since $\underline{a} \le \overline{a}$, the negativity of the principal eigenvalue in (3.5) implies the negativity of the one in (3.3).) If u satisfies (3.1) with $v \equiv 0$ then u is a supersolution to (3.6) so that by Theorem 2.2, $u(x,t) \ge w(x,t)$ where w satisfies (3.6) with $w(x,0) = u(x,0)$. By Theorem 2.1, $w \to \tilde{u}$ as $t \to \infty$. Since $w \le u \le \overline{u}$ it follows that $\tilde{u} \le u^{**}$ for all t. Thus, when interpreting u as "being established" it is reasonable to assume

$$\text{(3.7)} \qquad \tilde{u}(x,0) \le u(x,0) \le u^*(x,0).$$

(In a T-periodic Lotka-Volterra model, $\underline{a} = \overline{a}$ and $\underline{b} = \overline{b}$ so $\tilde{u} = u^*$.) As the predator is introduced the upper bound $u(x,t) \le u^*(x,t)$ will remain valid but the lower bound on u in (3.7) may fail.

The hypothesis (3.7) and its implication $u(x,t) \leq u^*(x,t)$ begin our sequence of bounds on trajectories of (3.1). The next bound is the following:

Theorem 3.1: If (u, v) satisfies (3.1) with $0 \leq u(x,0) \leq u^*(x,0)$, $u(x,0) \not\equiv 0$, and $v(x,0) \geq 0$, then $v(x,t) \leq \overline{v}(x,t)$ where $\overline{v}(x,t)$ is the solution to

$$\begin{aligned} v_t &= L_2 v + [\overline{d} + \overline{e}u^* - \underline{f}v]v && \text{in } \Omega \times (0,\infty) \\ B_2 v &= 0 && \text{on } \partial\Omega \times (0,\infty) \end{aligned} \tag{3.8}$$

with $v(x,0) = \overline{v}(x,0)$. If the principal eigenvalue of

$$\begin{aligned} \phi_t - L_2\phi - [\overline{d} + \overline{e}u^*]\phi &= \mu\phi && \text{on } \Omega \times I\!R \\ B_2\phi &= 0 && \text{on } \partial\Omega \times I\!R \\ \phi \text{ is } T-\text{periodic}, \end{aligned} \tag{3.9}$$

is nonnegative then $\overline{v} \to 0$ as $t \to \infty$ and hence $v \to 0$ as $t \to \infty$. If the principal eigenvalue of (3.9) is negative then there exists a unique positive T-periodic solution v^* of (3.8) and v^* is globally attracting among nonnegative nontrivial solutions, so $\overline{v} \to v^*$ as $t \to \infty$. If $v(x,0) \leq v^*(x,0)$, then $v(x,t) \leq v^*(x,t)$.

Proof: By the discussion prior to Theorem 3.1, $0 \leq u(x,0) \leq u^*(x,0)$ implies $u(x,t) \leq u^*(x,t)$ for $t > 0$. Since any solution v of the second equation in (3.1) with $u \leq u^*$ is a subsolution of (3.8), the inequality $v(x,t) \leq \overline{v}(x,t)$ follows from Theorem 2.2. Theorem 2.1 implies the existence of a principal eigenvalue for (3.9), and that $\overline{v} \to 0$ as $t \to \infty$ if that eigenvalue is nonnegative; but v^* exists and $\overline{v} \to v^*$ as $t \to 0$ if the eigenvalue is negative. Since v^* is a solution of (3.8) and v is a subsolution, it follows from Theorem 2.2 that $v(x,t) \leq v^*(x,t)$ if $v(x,0) \leq v^*(x,0)$.

Once we have the upper bounds $u \leq u^*$ and $v \leq \overline{v} \leq v^*$ we can look for a lower bound on u.

Theorem 3.2: Suppose that (3.7) holds, $v \leq \overline{v} \leq v^*$ and that the principal eigenvalue of

$$\begin{aligned} \phi_t - L_1\phi - [\underline{a} - \overline{c}v^*]\phi &= \mu\phi && \text{in } \Omega \times I\!R \\ B_1\phi &= 0 && \text{on } \partial\Omega \times I\!R \\ \phi \text{ is } T-\text{periodic}, \end{aligned} \tag{3.10}$$

is negative. Let $\underline{u}$ be the solution of

$$(3.11) \qquad \begin{aligned} u_t &= L_1 u + [\underline{a} - \overline{c}v^* - \overline{b}u]u && \text{in } \Omega \times (0,\infty) \\ B_1 u &= 0 && \text{on } \partial\Omega \times (0,\infty). \end{aligned}$$

with $\underline{u}(x,0) = u(x,0)$. There exists a unique positive T-periodic solution u^{**} of (3.11), and $u(x,t) \geq \underline{u}(x,t) \geq u^{**}(x,t)$.

Remark: If the principal eigenvalue in (3.10) is negative, so is the principal eigenvalue in (3.5). It is also the case that $\tilde{u} \geq u^{**}$; we shall discuss this point further in the proof of Theorem 3.2.

Proof: The existence of u^{**} follows from Theorem 2.1. Furthermore, all nontrivial nonnegative solutions of (3.11) converge to u^{**} as $t \to \infty$. Let $\tilde{w}$ be the solution to (3.11) with $\tilde{w}(x,0) = \tilde{u}(x,0) \leq u(x,0) = \underline{u}(x,0)$. Then since $\tilde{w}$ satisfies (3.11), $\tilde{w}$ is a subsolution of (3.6) so by Theorem 2.2, $\tilde{w} \leq \tilde{u}$. Also, $\tilde{w} \to u^{**}$ as $t \to \infty$ by Theorem 3.1. Hence $\tilde{u} \geq u^{**}$. Also, by Theorem 2.2, $u^{**} \leq \underline{u}$ since u^{**} and $\underline{u}$ are solutions of (3.11) but $\underline{u}(x,0) = u(x,0) \geq \tilde{u}(x,0) \geq u^{**}(x,0)$. Finally, if (u,v) satisfies (3.1) with $v \leq v^*$ then u is a supersolution of (3.11), and since $u(x,0) = \underline{u}(x,0)$ we have $u(x,t) \geq \underline{u}(x,t)$ by Theorem 2.2.

Remark: In fact, $\tilde{u}$ is a strict supersolution of (3.11) so by results of [9], the sequence $\tilde{w}(x,t+nT)$ is strictly decreasing in n and approaches a T-periodic steady state of (3.11). Since $\tilde{w}(x,0) \geq u^{**}(x,0)$ and u^{**} is a T-periodic steady-state of (3.11) we must have $\tilde{u}(x,t) \geq \tilde{w}(x,t) > \tilde{w}(x,t+T) > u^{**}(x,t+T) = u^{**}(x,t)$ on Ω. Hence $\tilde{u}$ is strictly greater than u^{**}.

Having established the lower bound $\underline{u}(x,t)$ on the prey population trajectory with $\underline{u} \geq u^{**}$ we can now give a lower bound on the predator population trajectory. This lower bound will necessarily be affected by the initial predator density, which is assumed to be small.

Theorem 3.3: Suppose that (u,v) is a solution of (3.1) with $u(x,0) \geq \tilde{u}(x,0)$ and that the principal eigenvalue of the problem

$$(3.12) \qquad \begin{aligned} \phi_t - L_2\phi - [\underline{d} + \underline{e}u^{**}]\phi &= \mu\phi && \text{in } \Omega \times I\!R \\ B_2\phi &= 0 && \text{on } \partial\Omega \times I\!R \\ \phi &\ \text{is } T-\text{periodic}, \end{aligned}$$

is negative. Let $\underline{v}(x,t)$ be the solution of

$$\text{(3.13)} \qquad \begin{aligned} v_t &= L_2 v + (\underline{d} + \underline{e}u^{**} - \overline{f}v)v && \text{on } \Omega \times (0,\infty) \\ B_2 v &= 0 && \text{on } \partial\Omega \times (0,\infty). \end{aligned}$$

with $\underline{v}(x,0) = v(x,0)$. There exists a unique positive T-periodic solution v^{**} of (3.13), and $v(x,t) \geq \underline{v}(x,t)$ with $\underline{v}(x,t) \to v^{**}(x,t)$ as $t \to \infty$.

Proof: The existence of v^{**} and the convergence of $\underline{v}$ to v^{**} as $t \to \infty$ follow from Theorem 2.1. Any solution (u,v) with $u(x,0) \geq \tilde{u}(x,0)$ has $u(x,t) \geq u^{**}(x,t)$ by Theorem 3.2. Thus, for any such solution of (3.1) $v(x,t)$ is a supersolution of (3.13) so that $v \geq \underline{v}$ by Theorem 2.2.

Remark: Suppose that $v(x,0) \geq \varepsilon\phi_1$ where $\phi_1 > 0$ is an eigenfunction for (3.12) with sup $\phi_1 = 1$. Since $\varepsilon\phi_1$ is a strict subsolution of (3.13) for ε small, if we let $\tilde{v}$ be the solution of (3.13) with $\tilde{v}(x,0) = \varepsilon\phi_1(x,0)$ we have the sequence $\tilde{v}(x,t+nT)$ increasing in n with $\tilde{v}(x,t+nT) \to v^{**}(x,t)$ as $n \to \infty$ by results of [9]. Also, since v is a supersolution of (3.13) and $\tilde{v}$ is a solution, we have $v \geq \tilde{v}$ by Theorem 2.2. The point is that in some cases fairly explicit estimates of the growth of $\tilde{v}$ in time can be obtained, so that in turn the lower bound on the trajectory v can be made more explicit as well. We shall illustrate this in an example in the next section.

§4. An example.

Here we consider the simple Lotka-Volterra model

$$\text{(4.1)} \qquad \begin{aligned} u_t &= D_1\Delta u + (a - bu - cv)u \\ v_t &= D_2\Delta v + (d + eu - fv)v \end{aligned} \quad \text{in } \Omega \times (0,\infty)$$
$$\frac{\partial u}{\partial n} = 0, \quad v = 0 \qquad \text{on } \partial\Omega \times (0,\infty)$$

where a, b, c, d, e, f are constants, with a, b, c, e, and f positive (d may be positive or negative). In this case the functions $u^*, \tilde{u}, \overline{u}, \underline{u}, u^{**}$, and $v^*, \overline{v}, \underline{v}$, and v^{**} are all either solutions of diffusive logistic equations with constant coefficients or can be bounded by such solutions. Simple diffusive logistic equations have been widely studied [3,6,9] so the estimates they provide are fairly explicit. We digress briefly to recall or derive some results about them.

If $\underline{r} \leq r(x,t) \leq \overline{r}$ and $\overline{g} \geq g(x,t) \geq \underline{g}$, then any solution of

$$
(4.2) \qquad \begin{aligned} u_t &= D\Delta u + (r - gu)u \qquad \text{in } \Omega \times (0, \infty) \\ Bu &= 0 \end{aligned}
$$

is a subsolution of

$$
(4.3) \qquad u_t = D\Delta u + (\overline{r} - \underline{g}u)u \quad \text{in } \Omega \times (0, \infty)
$$

and a supersolution of

$$
(4.4) \qquad u_t = D\Delta u + (\underline{r} - \overline{g}u)u \quad \text{in } \Omega \times (0, \infty)
$$

under the same boundary conditions. Thus, any solution of (4.2) is bounded between solutions of (4.3) and (4.4) with the same boundary and initial data by Theorem 2.2. In the case of constant coefficients $r(x,t) \equiv r_0$, $g(x,t) \equiv g_0$ and the Neumann boundary conditions $\partial u/\partial n = 0$ (i.e. no flux or reflecting boundary conditions), solutions of the logistic equation $dp/dt = (r_0 - g_0 p)p$ are also solutions of (4.2) and the equilibrium of (4.2) is $u \equiv r_0/g_0$. In the case of Dirichlet (i.e. absorbing) boundary conditions with $r(x,t) \le \overline{r}$, $g(x,t) \ge \underline{g}$ where $\overline{r}$ and $\underline{g}$ are constant, solutions of (4.2) are subsolutions of (4.3) when (4.3) is equipped with Neumann boundary conditions so u can be bounded above by solutions of $dp/dt = (\overline{r} - \underline{g}p)p$. For lower bounds we have the following:

Theorem 4.1. Suppose that u satisfies (4.2) with $Bu = u$, $r = r(x)$, and $g = g_0$. Suppose the principal eigenvalue μ_1 of

$$
(4.5) \qquad -D\Delta\phi - r(x)\phi = \mu\phi \quad \text{in } \Omega, \quad \phi = 0 \text{ on } \partial\Omega
$$

is negative and let ϕ_1 be the positive principal eigenfunction normalized by $\sup \phi_1 = 1$. Let $\sigma_1 = -\mu_1 > 0$. If $u(x,0) \ge \varepsilon\phi_1(x)$ then $u(x,t) \ge p(t)\phi_1(x)$ where $p(0) = \varepsilon$ and p satisfies the logistic equation

$$
(4.6) \qquad \frac{dp}{dt} = (\sigma_1 - g_0 p)p.
$$

Proof: Let $w = p(t)\phi_1(x)$. Then

$$
\begin{aligned}
w_t - D\Delta w - r(x)w + g_0 w^2 &= p'\phi_1 + p[-D\Delta\phi_1 - r\phi_1 + g_0\phi_1^2 p] \\
&= p'\phi_1 + p[-\sigma_1\phi_1 + g_0\phi_1^2 p] \\
&\le p'\phi_1 + p[-\sigma_1\phi_1 + g_0\phi_1 p] \\
&= \phi_1[p' - [\sigma_1 p + g_0 p^2]] = 0
\end{aligned}
$$

so w is a subsolution of (4.1). Since $w(x,0) \le u(x,0)$ and $u = w = 0$ on $\partial\Omega$, $w(x,t) \le u(x,t)$.

Remark: $p(t) = \varepsilon\sigma_1/[\varepsilon g_0 + (\sigma_1 - \varepsilon g_0)e^{-\sigma_1 t}] \to \sigma_1/g_0$ as $t \to \infty$. If $r(x) = r_0$ then $\mu_1 = D\lambda_1 - r_0$ (so $\sigma_1 = r_0 - D\lambda_1$) and $\phi_1 = \psi_1$ where λ_1 and ψ_1 are the principal eigenvalue and eigenfunction of

(4.7) $$-\Delta\psi = \lambda\psi \text{ on } \Omega, \quad \psi = 0 \text{ on } \partial\Omega$$

and ψ is normalized by $\sup \psi_1 = 1$. In simple geometries (e.g. Ω an interval, rectangle, or circular disc) the eigenvalue and eigenfunction in (4.7) can be explicitly computed.

We can now examine a detailed scenario for (4.1). First, we have $a = \underline{a} = \overline{a}$ and $b = \underline{b} = \overline{b}$ with a, b constant, so for the first equation in (4.1) we have $\tilde{u} = u^{**} = a/b$. The principal eigenvalue for the problem corresponding to (3.9) will then be $\mu_1 = D_2\lambda_1 - d - ea/b$; if $\mu_1 > 0$ then $v \to 0$ as $t \to \infty$, and if $\mu_1 < 0$ then $v \le \overline{v}$ where $\overline{v}$ is the solution of

(4.8) $$
\begin{aligned}
\overline{v}_t &= D_2\Delta\overline{v} + [d + (ea/b) - f\overline{v}]\overline{v} && \text{on } \Omega \times (0,\infty), \\
\overline{v} &= 0 && \text{on } \partial\Omega \times (0,\infty), \\
\overline{v}(x,0) &= v(x,0).
\end{aligned}
$$

As $t \to \infty$, $\overline{v} \to v^*$ where v^* is the unique positive equilibrium of (4.8). We have $\overline{v} \le \overline{p}$ where $d\overline{p}/dt = [d + (ea/b) - f\overline{p}]\overline{p}$, $\overline{p}(0) = \sup_{\overline{\Omega}} \overline{v}(x,0)$; hence $v^* \le [d + (ea/b)]/f$, and $v \le [d + (ea/b)]/f$ if $v(x,0) \le [d + (ea/b)]/f$. It follows that if $v(x,0)$ is small and $a - c[d + (ea/b)]/f > 0$ then $\underline{u}$ satisfying (3.11) and hence u satisfying (4.1) is a supersolution of

$$
(4.9)\qquad \begin{aligned} u_t &= D_1\Delta u + [a - (c[d + (ea/b)]/f) - bu]u && \text{on } \Omega \times (0,\infty) \\ \frac{\partial u}{\partial n} &= 0 && \text{on } \partial\Omega \times (0,\infty), \\ u(x,0) &= a/b. \end{aligned}
$$

Also,

$$
(4.10)\qquad u(x,0) = u^*(x,0) = a/b \geq \{a - (c[d + (ea/b)]/f)\}/b \equiv \underline{u}^{**},
$$

where $\underline{u}^{**}$ is the equilibrium of (4.9), so we also have $u^{**} \geq \underline{u}^{**}$. Finally, since $u^{**} \geq \underline{u}^{**}$, it follows that the principal eigenvalue $\overline{\mu}_1$ of

$$
(4.11)\qquad \begin{aligned} -D_2\Delta\phi - [d + e\underline{u}^{**}]\phi &= \mu\phi && \text{on } \Omega \\ \phi &= 0 && \text{on } \partial\Omega \end{aligned}
$$

is larger than the principal eigenvalue μ_1 of (3.12), which in this case reduces to

$$
\begin{aligned} -D_2\Delta\phi - [d + eu^{**}]\phi &= \mu\phi && \text{in } \Omega \\ \phi &= 0 && \text{on } \partial\Omega. \end{aligned}
$$

(The relation between eigenvalues follows from classical eigenvalue comparison results based on the variational formulation of eigenvalue problems; see [7].) With $\underline{u}^{**}$ defined as in (4.10) the eigenvalue $\overline{\mu}_1$ in (4.11) is $D_2\lambda_1 - [d + e\underline{u}^{**}]$ with λ_1 as in (4.7). If $D_2\lambda_1 - [d + e\underline{u}^{**}] < 0$ then we can obtain a lower bound on v.

Theorem 4.2: Let $\underline{u}^{**}$ be as in (4.10) and λ_1, ψ_1 as in (4.7). If $D_2\lambda_1 - [d + e\underline{u}^{**}] < 0$ then $v(x,t) \geq \underline{w}(x,t)$ where

$$
(4.12)\qquad \begin{aligned} \underline{w}_t &= D_2\Delta\underline{w} + [d + e\underline{u}^{**}\underline{w} - f\underline{w}]\underline{w} && \text{in } \Omega \times (0,\infty), \\ \underline{w} &= 0 && \text{on } \partial\Omega \times (0,\infty), \\ \underline{w}(x,0) &= v(x,0). \end{aligned}
$$

If $v(x,0) \geq \varepsilon\psi(x)$ then $v \geq \underline{w} \geq p(t)\psi_1(x)$ where

$$
\frac{dp}{dt} = [d + e\underline{u}^{**} - D_2\lambda_1 - fp]p, \quad p(0) = \varepsilon.
$$

If $v(x,0) \geq 0$, $v(x,0) \neq 0$ then $v \geq \underline{w}$ with $\underline{w} \to \underline{w}^{**}$ as $t \to \infty$, where $\underline{w}^{**}$ is the positive equilibrium of (4.12). A lower bound for $\underline{w}^{**}$ is given by $\underline{w}^{**}(x) \geq [(d + e\underline{u}^{**} - D_2\lambda_1)/f]\psi_1(x)$.

Proof: Since $u \geq u^{**} \geq \underline{u}^{**}$, the solution v of (4.1) is a supersolution for (4.12). The behavior of $\underline{w}$ is then described by Theorem 2.1 and Theorem 4.1. Finally, the lower bound on $\underline{w}^{**}$ is well known; see for example [6].

Remarks: Explicit estimates on $\underline{w}$ can be obtained as in the remarks following Theorem 4.1.

§5. Discussion and conclusions.

Our results imply that for simple predator-prey models where the predator population is logistically self-regulating and the interaction terms between the predator and prey are relatively small compared to the prey growth rate, some trajectories can be bounded above and below by trajectories of diffusive logistic equations. Those in turn can be bounded explicitly in simple cases by expressions involving solutions of the ordinary logistic equation. The sort of trajectories we have estimated correspond to a scenario where the prey is established and the predator is introduced at low densities. In principle the methods could be applied to many other scenarios and many other sorts of models. Any of the systems discussed in [3,5] could be treated in this way. It would also be possible to give time dependent estimates on extinction rates in certain situations. A critical element in drawing a conclusion of persistence, i.e. in obtaining good lower bounds on trajectories, is the presence of some type of self-regulation on the predator. The self-regulation need not be logistic (see [5]) but must be present for the analysis to go through. This requirement is reasonable from a biological point of view because in the absence of predator self-regulation the predator population might explode, causing a crash in the prey population followed by a crash in the predator population. A natural speculation is that perhaps the stabilizing effect of predator self-regulation is partly responsible for the evolution of regulatory mecahnisms such as territoriality. That is only a speculation, but the stabilizing effect of predator self-regulation on the behavior of trajectories in predator-prey models is a rigorous consequence of the present analysis.

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