On the Dynamics of Predator–Prey Models with the Beddington–DeAngelis Functional Response

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The dynamics of predator–prey models with the Beddington–DeAngelis functional response are analyzed, primarily from the viewpoint of permanence (uniform persistence). The Beddington–DeAngelis functional response is similar to the Holling type 2 functional response but contains an extra term describing mutual interference by predators. Both spatially homogeneous models based on ordinary differential equations and reaction–diffusion models are considered. Criteria for permanence and for predator extinction are derived. For systems without diffusion or with no-flux boundary conditions, criteria are derived for the existence of a globally stable coexistence equilibrium or, alternatively, for the existence of periodic orbits. © 2001 Academic Press

Key Words: predator–prey; reaction–diffusion; functional response; permanence; uniform persistence.

1. INTRODUCTION

The goal of this paper is to give a description of some of the basic dynamical properties of predator–prey models which incorporate the Beddington–DeAngelis functional response, with or without diffusion. The simplest version of a predator–prey model with Beddington–DeAngelis functional

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2. MATHEMATICAL PRELIMINARIES: PERMANENCE

Some of the conclusions of this paper are stated in terms of permanence, that is, uniform persistence plus dissipativity. A general discussion of permanence is given in [17], and the technical aspects of applying the idea in the context of reaction–diffusion system are treated in [1, 8, 9], so we shall give only a brief description of permanence here.

Suppose that Y is a complete metric space with $Y = Y_0 \cup \partial Y_0$ for an open set Y_0. We will typically choose Y_0 to be the positive cone in an ordered Banach space. A flow or semiflow on Y under which Y_0 and ∂Y_0 are forward invariant is said to be permanent if it is dissipative and if there is a number $\epsilon > 0$ such that any trajectory starting in Y_0 will be at least a distance ϵ from ∂Y_0 for all sufficiently large t. To state a theorem implying permanence we need a few definitions. An invariant set M for the flow or semiflow is said to be *isolated* if it has a neighborhood U such that M is the maximal invariant subset of U. Let $\omega(\partial Y_0) \subseteq \partial Y_0$ denote the union of the sets $\omega(u)$ over $u \in \partial Y_0$. (This differs from the standard definition of the ω-limit set of a set but is more convenient for our purposes; see [17] for a discussion.) The set $\omega(Y_0)$ is said to be *isolated* if it has a covering $M = \bigcup_{k=1}^{N} M_k$ of pairwise disjoint sets M_k which are isolated and invariant with respect to the flow or semiflow both on ∂Y_0 and on $Y = Y_0 \cup \partial Y_0$. The covering M is then called an *isolated covering*. Suppose the N_1 and N_2 are isolated invariant sets (not necessarily distinct). The set N_1 is said to be *chained* to N_2 (denoted $N_1 \rightarrow N_2$) if there exists $u \notin N_1 \cup N_2$ with $u \in W^u(N_1) \cap W^s(N_2)$. (As usual, W^u and W^s denote the unstable and stable manifolds, respectively.) A finite sequence $N_1, N_2, \ldots, N_k$ of isolated invariant sets is a *chain* if $N_1 \rightarrow N_2 \rightarrow N_3 \cdots \rightarrow N_k$. (This is possible for $k = 1$ if $N_1 \rightarrow N_1$.) The chain is called a *cycle* if $N_k = N_1$. The set $\omega(\partial Y_0)$ is said to be *acyclic* if there exists an isolated covering $\bigcup_{k=1}^{N} M_k$ such that no subset of $\{M_k\}$ is a cycle. We now state a theorem that can be used to establish permanence.

THEOREM 2.1 [14]. *Suppose that Y is a complete metric space with $Y = Y_0 \cup \partial Y_0$ where Y_0 is open. Suppose that a semiflow on Y leaves both Y_0 and ∂Y_0 forward invariant, maps bounded sets in Y to precompact sets for $t > 0$,*

response has the form (after rescaling)

$$\frac{du}{dt} = u(1-u) - \frac{Auv}{1+Bu+Cv}$$
$$\frac{dv}{dt} = \frac{Euv}{1+Bu+Cv} - Dv,$$

(1.1)

where u and v represent predator and prey densities, respectively. We shall consider both the system (1.1) and the analogous system with diffusion in what follows. The functional response in (1.1) was introduced by Beddington [2] and DeAngelis *et al.* [12]. It is similar to the well-known Holling type 2 functional response but has an extra term Cv in the denominator which models mutual interference between predators. It can be derived mechanistically via considerations of time utilization [2, 20] or spatial limits on predation [11]. In [6] we studied reaction–diffusion models with the Beddington–DeAngelis response from the viewpoint of practical persistence [5]. That approach is possible only because of the presence of mutual interference by the predators. In the present article we give a more complete discussion of the dynamics of (1.1) and analyze (1.1) and the corresponding diffusive model in terms of permanence (i.e., uniform persistence plus dissipativity.) Permanence typically yields sharper information on parameter dependence but less sharp information on the behavior of solutions than practical persistence, so the results of the present paper are somewhat complementary to those of [5, 6].

There has been considerable interest in ratio-dependent predator–prey models; see [11] and the references therein. A ratio-dependent version of (1.1) would have the form

$$\frac{du}{dt} = u(1-u) - \frac{Auv}{Bu+Cv}$$
$$\frac{dv}{dt} = \frac{Euv}{Bu+Cv} - Dv.$$

(1.2)

The ratio-dependent form (1.2) also incorporates mutual interference by predators, but it has somewhat singular behavior at low densities and has been criticized on other grounds. See [18] for a mathematical analysis and the references in [11] for some aspects of the debate among biologists about ratio dependence. The Beddington–DeAngelis form of functional response has some of the same qualitative features as the ratio-dependent form but avoids some of the behaviors of ratio-dependent models at low densities which have been the source of controversy.

In the next section we give a brief review of the notion of permanence; in Section 3 we examine the dynamics of (1.1) and give conditions for permanence, extinction, the presence of limit cycles, and the existence of

a globally attracting equilibrium. In Section 4 we extend the conditions for permanence and extinction to the corresponding model with diffusion under general boundary conditions. We also note that some of the more detailed observations on the dynamics of (1.1) extend to models with diffusion under no-flux (i.e., Neumann) boundary conditions. We end with a brief section on conclusions.

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and is dissipative. If in addition

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

    (ii) $W^s(M_k) \cap Y_0 = \varnothing$ *for all k, where* $\bigcup_{k=1}^{N} M_k$ *is the isolated covering used in the definition of acyclicity of* ∂Y_0,

then the semiflow is permanent; i.e., there exists $\epsilon > 0$ such that any trajectory with initial data in Y_0 will be bounded away from ∂Y_0 by a distance greater than ϵ for t sufficiently large.

Remarks. The notation used here is different than that of [14] because of the definition we have given for $\omega(\partial Y_0)$. For applications to ordinary differential equations Y_0 is usually taken to the positive orthant in $\mathbb{R}^m$; for reaction–diffusion systems Y_0 is usually taken to be a positive cone in a space of continuous or differentiable functions; see [1, 8, 9, 17].

A dynamical or semidynamical system is said to be dissipative if there is a fixed bounded set $X_0 \subseteq Y$ such that if $y(t)$ is any trajectory, $y(t) \in X_0$ for all sufficiently large t. How large t must be to insure that $y(t) \in X_0$ may depend on $y(0)$.

3. DYNAMICS ONLY: THE SPATIALLY HOMOGENEOUS CASE

In this section we shall examine the behavior of the system of ordinary differential equations which would describe the population dynamics in the spatially uniform case; namely

$$\frac{du}{dt} = u(1-u) - \frac{Auv}{1+Bu+Cv}$$
$$\frac{dv}{dt} = \left(\frac{Eu}{1+Bu+Cv} - D\right)v. \tag{3.1}$$

As is usual for population models, the system (3.1) leaves the first quadrant and the coordinate axes invariant. The isocline corresponding to $dv/dt = 0$ is the line $v = [(E-BD)u - D]/CD$. The isocline for $du/dt = 0$ is the hyperbola $v = (1-u)(1+Bu)/[A - C + Cu]$. The possible configurations of this isocline are shown in Fig. 3.1. Note that the isocline for $du/dt = 0$ has $v \leq 0$ for $u \geq 1$, with $v > 0$ when u is less than but close to one. If $A - C \geq 0$ then $v \geq 0$ for $0 \leq u \leq 1$; if $A - C < 0$ then $v > 0$ for $(C-A)/C < u < 1$, with $v \to \infty$ on the isocline as $u \downarrow (C-A)/C$. It is clear from an examination of the isoclines that there will be an equilibrium in the first quadrant if and only if the isocline for $dv/dt = 0$ becomes positive at some value $u < 1$, which will be true if and only if
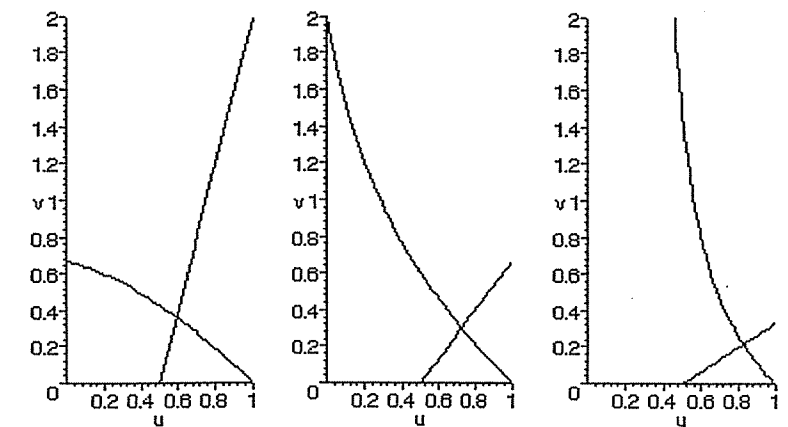
$$E > (B+1)D. \tag{3.2}$$

FIG. 3.1. The three graphs show the isoclines for the system 3.1 for small, medium, and large values of the parameter C, respectively. (Recall that C measures the amount of mutual interference by the predators.) Note that as C increases the slope of the predator isocline decreases, while the prey isocline goes from being concave to convex and then develops a vertical asymptote.

Elementary algebra shows that if there is a positive equilibrium then it is unique.

THEOREM 3.1. *The system* (3.1) *is always dissipative in the first quadrant. It is permanent if and only if* (3.2) *holds. If the inequality in* (3.2) *is reversed then $v \to 0$ as $t \to \infty$.*

Proof (sketch). Since $du/dt \leq u(1-u)$, it follows that for every $\epsilon > 0$ there is a t_1 (depending on $u(0)$) such that $u < 1 + \epsilon$ for $t > t_1$. If $u \leq 2$ then $dv/dt \leq \{[2E/(1+2B+Cv)] - D\}v$ so that there exists t_2 (depending on $v(0)$) so that $v \leq \{[2E - 2BD - D]/CD\} + \epsilon$ for $t > t_2$. Hence the system (3.1) is dissipative. If we take Y_0 to be the first quadrant then $\omega(\partial Y_0)$ consists of the equilibria $(0, 0)$ and $(1, 0)$. The stable manifold of $(0, 0)$ is the v-axis. All trajectories on the u-axis other than $(0, 0)$ approach $(1, 0)$. It follows from these structural features that the flow in $\partial(Y_0)$ is acyclic. If (3.2) holds then $dv/dt > 0$ for (u, v) with v small and u close to 1, so the stable manifold of $(1, 0)$ cannot intersect the interior of the first quadrant. In that case Theorem 2.1 implies permanence. If (3.2) fails then (3.1) cannot have a positive equilibrium and thus cannot be permanent. (Permanence implies the existence of a positive equilibrium; see [17].) If the inequality in (3.2) is reversed then for ϵ sufficiently small and for t large enough that $u \leq 1 + \epsilon$ we must have $dv/dt < 0$, so $v \to 0$ as $t \to \infty$.

LEMMA 3.2. *Suppose that* (3.2) *holds and that*

$$(B-1)(E-BD) - 2BD > 0. \tag{3.3}$$

If C is sufficiently small then the positive equilibrium of (3.1) *is unstable. If in addition E is sufficiently large then the equilibrium is an unstable spiral point and* (3.1) *has a limit cycle.*

Proof. The local stability properties of the equilibrium can be determined by direct computation. Let (u^*, v^*) be the positive equilibrium of (3.1); then

$$u^* = \frac{-[A(E-BD) - CE] + \sqrt{[A(E-BD) - CE]^2 + 4ACDE}}{2CE}$$

$$= \frac{2AD}{[A(E-BD) - CE] + \sqrt{[A(E-BD) - CE]^2 + 4ACDE}}. \tag{3.4}$$

It follows from (3.4) that as $C \to 0$, $u^* \to D/(E - BD)$. The local stability of (u^*, v^*) is determined by the Jacobian matrix J of the linearization of (3.1) around (u^*, v^*). Computing J from (3.1) and then simplifying using the equilibrium equations for (3.1) yields the value of the trace of J in terms of u^*; namely

$$\mathrm{Tr}\, J = -u^* + [(BD/E) - (CD/A)](1 - u^*).$$

If we let $C \to 0$ then

$$\mathrm{Tr}\, J \to \frac{D[(B-1)(E-BD) - 2BD]}{E(E-BD)}.$$

By (3.3), $\mathrm{Tr}\, J > 0$ for C sufficiently small. Since $\mathrm{Tr}\, J$ is the sum of the real parts of the eigenvalues of J, it follows that at least one eigenvalue must have a positive real part if (3.3) holds and C is small, so that (u^*, v^*) is unstable. If we compute the coefficients of the characteristic polynomial of J and compute the limit as $C \to 0$, a similar but messier calculation shows that the discriminant of the characteristic polynomial will be negative if E is sufficiently large relative to the remaining parameters in (3.1). It follows that for C small and E large the imaginary parts of the eigenvalues of J are nonzero, so that (u^*, v^*) is an unstable spiral point. In that case, a trajectory that starts near (u^*, v^*) will rotate around the equilibrium and intersect the radial ray along which it started at some point further away from (u^*, v^*). By connecting those two points on the ray with a line segment we can construct a neighborhood of (u^*, v^*) from which trajectories exit but do not return. Since (3.2) holds, the system (3.1) is permanent. Permanence implies that the system (3.1) has a compact attractor lying in the interior of the positive cone which is globally attracting for positive solutions; see [17]. The trajectories which leave the vicinity of (u^*, v^*) but do not return must have ω-limit sets in the attractor but distinct from

(u^*, v^*). By the Poincaré–Bendixson theorem, such ω-limit sets are necessarily either periodic orbits or equilibria. The equilibrium (u^*, v^*) is unique, so the attractor must contain at least one periodic orbit.

Remark. As $C \to 0$, the limiting system corresponding to (3.1) is a predator–prey model with a Holling type 2 functional response. Such models are known to have periodic orbits for some parameter values, so Lemma 3.2 may be considered as a type of perturbation result.

To conclude our discussion of the system (3.1) we give a sufficient condition for the global asymptotic stability of the positive equilibrium (u^*, v^*).

LEMMA 3.3.   *If*

$$B(1 - u^*) < 1 \tag{3.5}$$

then (u^*, v^*) *is globally asymptotically stable.*

Remark. If $B < 1$ then (3.5) holds automatically. For the instability condition (3.3) to hold it is necessary (but not sufficient) that $B > 1$. The value of u^* is given in (3.4). As $C \to \infty$, $u^* \to 1$ so (3.5) holds for large C.

If $B > 1$ then (3.5) may be rewritten as

$$C > \frac{AB[(B-1)E - B^2 D]}{E(B-1)}. \tag{3.6}$$

If

$$(B-1)E - B^2 D < 0 \tag{3.7}$$

then (3.6) holds automatically so that the equilibrium (u^*, v^*) is always stable. Thus, C is relevant in determining whether (u^*, v^*) is globally assymptotically stable only if (3.7) does not hold. (Note that $B < 1$ implies (3.7).) If condition (3.3) holds then C is crucial in determining the stability or instability of (u^*, v^*). Under condition (3.3), Lemma 3.2 implies that (u^*, v^*) is unstable for C small. However, even if (3.3) holds, Lemma 3.3 implies that (u^*, v^*) is globally asymptotically stable if C is large enough to satisfy (3.6). Note that (3.3) could be written $E(B-1) - B^2 D > BD$, so that (3.3) is stronger than the reverse of (3.7). If (3.7) is reversed but (3.3) does not hold we do not know whether (u^*, v^*) becomes unstable for C small, but (3.6) still implies global asymptotic stability for C large.

Proof. The proof is based on a Lyapunov function. Let $V_1 = u - u^* - u^* \ln(u/u^*)$ and $V_2 = v - v^* - v^* \ln(v/v^*)$. This sort of Lyapunov function has been widely used; see, e.g., [13]. It is easy to see that $\partial V_1/\partial u > 0$ for $u > u^*$ and $\partial V_1/\partial u < 0$ for $0 < u < u^*$, and similarly $\partial V_2/\partial v > 0$ for $v > v^*$ and $\partial V_2/\partial v < 0$ for $0 < v < v^*$. If we compute $dV_1(u(t))/dt$ via (3.1) we obtain

$$\frac{dV_1(u)}{dt} = \left(1 - \frac{u^*}{u}\right)\left[1 - u - \frac{Av}{1+Bu+Cv}\right]u$$

$$= (u - u^*)\left[u^* - u + \frac{Av^*}{1+Bu^*+Cv^*} - \frac{Av}{1+Bu+Cv}\right]$$

$$= -(u - u^*)^2 + \frac{(u-u^*)[ABv^*(u-u^*) - (ABu^* + A)(v-v^*)]}{(1+Bu^*+Cv^*)(1+Bu+Cv)}. \quad (3.8)$$

Similarly,

$$\frac{dV_2(v)}{dt} = \left(1 - \frac{v^*}{v}\right)\left[-D + \frac{Eu}{1+Bu+Cv}\right]v$$

$$= (v - v^*)\left[\frac{Eu}{1+Bu+Cv} - \frac{Eu^*}{1+Bu^*+Cv^*}\right]$$

$$= E(v - v^*)\left[\frac{(u-u^*) + Cv^*(u-u^*) + Cu^*(v^*-v)}{(1+Bu+Cv)(1+Bu^*+Cv^*)}\right]$$

$$= \frac{E(1+Cv^*)(v-v^*)(u-u^*) - CEu^*(v-v^*)^2}{(1+Bu+Cv)(1+Bu^*+Cv^*)}. \quad (3.9)$$

Define $V = V_1(u) + [A(1+Bu^*)/E(1+Cv^*)]V_2(v)$. Computing dV/dt via (3.8) and (3.9) yields

$$\frac{dV}{dt} = -(u - u^*)^2 + \frac{ABv^*(u-u^*)^2}{(1+Bu+Cv)(1+Bu^*+Cv^*)}$$

$$- \frac{ACu^*(1+Bu^*)(v-v^*)^2}{(1+Cv^*)(1+Bu+Cv)(1+Bu^*+Cv^*)}. \quad (3.10)$$

The coefficient of $(v - v^*)^2$ is always negative. The coefficient of $(u - u^*)^2$ is

$$-1 + \frac{ABv^*}{(1+Bu+Cv)(1+Bu^*+Cv^*)} \leq -1 + \frac{ABv^*}{1+Bu^*+Cv^*}$$

$$= -1 + B(1 - u^*).$$

It follows that if (3.5) holds then (3.10) implies $dV/dt < 0$ along all trajectories in the first quadrant except (u^*, v^*), so that (u^*, v^*) is globally asymptotically stable.

Biological Remarks. The system (3.1) could be viewed as a standard predator–prey model with a Holling type 2 functional response, but with an extra term Cv describing mutual feeding interference by predators. The parameter C measures the degree of mutual interference. It does not affect the criterion (3.2) for persistence of both species, but this observation must be used cautiously since C *does* affect the location and stability of the equilibrium (u^*, v^*). When C is small, the system behaves in roughly the same way as the corresponding system with $C = 0$. For small C the equilibrium (u^*, v^*) may be unstable and there may be periodic solutions. As $C \to \infty$ the equilibrium becomes stable, so in that sense increasing C stabilizes the system. However, $v^* \to 0$ as $C \to \infty$, so if demographic stochasticity were present the predator might be at risk of stochastic extinction if the degree of mutual interference held the predator population to a sufficiently low level. All of the other parameters in (3.1) are analogous to those in a standard Holling type 2 model and have the same general effects on the predictions of the model.

The qualitative description in the preceding paragraph can be sharpened by examining the stability and instability criteria more closely. By the discussion following Lemma 3.3, we can see that the equilibrium (u^*, v^*) for (3.1) will be globally asymptotically stable for all values of C provided that $(B-1)E - B^2D < 0$, which is true in particular if $B < 1$. In that case C can affect the size of u^* and v^* but not the stability of the equilibrium. On the other hand, if (3.3) holds then (u^*, v^*) is unstable for C small but globally asymptotically stable for C large, in particular if (3.6) holds. Thus, when (3.3) holds, C plays an important role in determining the stability of (u^*, v^*). In the proof of Lemma 3.2, which implies the instability of (u^*, v^*) for small C if (3.3) holds, one could solve the instability condition Tr $J > 0$ (i.e., $-u^* + [(BD/E) - (CD/A)](1 - u^*) > 0$) for C. However, this leads to a condition on C which is complicated and not very illuminating.

In addition to the effects of C on the size and stability of the equilibrium, having $C > 0$ can "stabilize" the system by reducing the extent to which trajectories can exhibit "boom–bust" behavior, where the predator population rises to high levels and then both populations decline dramatically. If C is relatively large, the methods of [5–7] can be used to obtain explicit bounds on trajectories. The effect of $C > 0$ is to introduce a self-limiting term into the predator equation which is roughly analogous to the logistic term in the prey equation. The presence of self-limitation reduces the extent to which the predator population can support a "boom."

4. DYNAMICS AND DIFFUSION

In this section we discuss the model

$$u_t = d_1 \nabla^2 u + u(1-u) - \frac{Auv}{1+Bu+Cv} \qquad \text{in } \Omega \times (0, \infty)$$

$$v_t = d_2 \nabla^2 u + \left(\frac{Eu}{1+Bu+Cv} - D \right)v \qquad \text{in } \Omega \times (0, \infty)$$
(4.1)

$$\beta u + (1-\beta)\frac{\partial u}{\partial n} = 0 \qquad \text{on } \partial\Omega \times (0, \infty)$$

$$\gamma v + (1-\gamma)\frac{\partial v}{\partial n} = 0 \qquad \text{on } \partial\Omega \times (0, \infty),$$

where $d_1, d_2 > 0$, $\Omega \subseteq \mathbb{R}^n$ is bounded with $\partial\Omega$ smooth, $\partial/\partial n$ denotes the outward normal derivative on $\partial\Omega$, and $\beta, \gamma \in [0, 1]$. The first observation is that in the case $\beta = \gamma = 0$ corresponding to no-flux (i.e., Neumann or reflecting) boundary conditions, any solution of (3.1) is also a solution of (4.1). Hence, (4.1) may have limit cycles, so we cannot expect persistence to be limited to cases where there is a globally attracting equilibrium. It follows that permanence or some related notion of persistence is appropriate.

The analysis of (4.1) uses a number of results about single reaction–diffusion equations and related eigenvalue problems which we shall state next.

LEMMA 4.1. *If $m(x)$ is continuous on Ω and positive on an open subset of Ω, the eigenvalue problem*

$$\nabla^2 \phi + \lambda m(x)\phi = 0 \qquad \text{on } \Omega$$

$$\beta\phi + (1-\beta)\frac{\partial\phi}{\partial n} = 0 \qquad \text{on } \partial\Omega$$
(4.2)

has a unique positive principal eigenvalue $\lambda_1^+(m, \beta)$ which admits a positive eigenfunction. The eigenvalue problem

$$d\nabla^2 \psi + m(x)\psi = \sigma\psi \qquad \text{in } \Omega$$

$$\beta\psi + (1-\beta)\frac{\partial\psi}{\partial n} = 0 \qquad \text{on } \partial\Omega$$
(4.3)

has a unique principal eigenvalue $\sigma_1(d, m, \beta)$ which admits a positive eigenfunction. We have $\sigma_1(d, m, \beta) > 0$ if and only if $d\lambda_1^+(m, \beta) < 1$.

Discussion. This result follows from general results given in [16]; see also [21] for the case of Neumann boundary conditions and [4, p. 1049] for the case of Dirichlet conditions.

LEMMA 4.2. *Suppose that $f(x, w)$ is smooth and is decreasing in w, with $f(x, 0) > 0$ on an open subset of Ω. Suppose further that there exists a constant K so that $f(x, w) < 0$ for $w > K$. Then the equation*

$$w_t = d\nabla^2 w + f(x, w)w \qquad \text{in } \Omega \times (0, \infty)$$

$$\beta w + (1-\beta)\frac{\partial w}{\partial n} = 0 \qquad \text{on } \partial\Omega \times (0, \infty)$$
(4.4)

has a unique positive equilibrium $\bar{w}$, which is globally attracting among positive solutions, if and only if $d\lambda_1^+(f(x, 0), \beta) < 1$ (equivalently $\sigma_1(d, f(x, 0), \beta) > 0$). If $d\lambda_1^+(f(x, 0), \beta) \geq 1$ then all positive solutions of (4.4) approach zero as $t \to \infty$.

Discussion. The case of Dirichlet boundary conditions is treated in [3, 4, 6]. The case of general boundary conditions follows from the same arguments as in [16].

Remark. The condition $d\lambda_1^+(f(x, 0), \beta) < 1$ is equivalent to $\sigma_1(d, f(x, 0), \beta) > 0$ by Lemma 4.1.

COROLLARY 4.3. *The problem*

$$u_t = d_1\nabla^2 u + u(1-u) \qquad \text{in } \Omega \times (0, \infty)$$

$$\beta u + (1-\beta)\frac{\partial u}{\partial n} = 0 \qquad \text{on } \partial\Omega \times (0, \infty)$$
(4.5)

has a unique equilibrium $\bar{u} > 0$ which is globally attracting among positive solutions if and only if $d_1\lambda_1^+(1, \beta) < 1$, or equivalently $\sigma_1(d_1, 1, \beta) > 0$. If $d_1\lambda_1^+(1, \beta) \geq 1$ then all solutions of (4.5) approach zero as $t \to \infty$.

To formulate a result on permanence we need to interpret (4.1) as a semidynamical system on an appropriate space. Let

$$X_\beta = \left\{ u \in C^1(\overline{\Omega}) : \beta u + (1-\beta)\frac{\partial u}{\partial n} = 0 \text{ on } \partial\Omega \right\}.$$

Let

$$X_\beta^+ = \begin{cases} \{u \in X_\beta : u > 0 \text{ on } \overline{\Omega}\} & \text{if } \beta < 1 \\ \left\{u \in X_\beta : u > 0 \text{ on } \Omega \text{and } \dfrac{\partial u}{\partial n} < 0 \text{ on } \partial\Omega\right\} & \text{if } \beta = 1. \end{cases}$$

Then let $Y_0 = X_\beta^+ \times X_\gamma^+$ and let $Y = Y_0 \cup \partial Y_0 \subseteq [C^1(\overline{\Omega})]^2$.

THEOREM 4.4. *The system (4.1) generates a dissipative semiflow on Y for which Y_0 and ∂Y_0 are forward invariant. If $d_1\lambda_1^+(1, \beta) \geq 1$ (equivalently $\sigma_1(d_1, 1, \beta) \leq 0$) then the system (4.1) is not permanent. If $d_1\lambda_1^+(1, \beta) < 1$ (equivalently $\sigma_1(d_1, 1, \beta) > 0$) the system is permanent if and only if*

$$\sigma_1\left(d_2, \frac{E\bar{u}}{1+B\bar{u}} - D, \gamma\right) > 0,$$
(4.6)

where $\bar{u}$ is the positive equilibrium of (4.5).

Discussion. The conclusion that (4.1) generates a semiflow on Y with Y_0 and ∂Y_0 forward invariant follows as in [8]; see also [16, 17]. Dissipativity follows as in Lemmas 4.1 and 4.3 of [8]. (See also [9, 17].) To see that (4.1) cannot be permanent if $d_1 \lambda_1^+(1, \beta) \geq 1$, note that if (u, v) is a nonnegative solution to (4.1) then u is a subsolution to (4.5). It follows that if $\tilde{u}$ is the solution to (4.5) with $\tilde{u}(x, 0) = u(x, 0)$ then $0 \leq u \leq \tilde{u}$ for all $t > 0$. However, by Corollary 4.3, $\tilde{u} \to 0$ as $t \to \infty$ if $d_1 \lambda_1^+(1, \beta) \geq 1$, so $u \to 0$ as $t \to \infty$ and hence (4.1) is not permanent. If $d_1 \lambda_1^+(1, \beta) < 1$ and (4.6) holds then permanence in (4.1) follows as in [8, Theorem 5.3]. Alternatively, the strong maximum principle implies that any solution of (4.1) which lies in ∂Y_0 must be of the form $(u, 0)$ or $(0, v)$. For solutions of the form $(0, v)$ we have $v_t = d_2 \nabla^2 v - Dv$ in $\Omega \times (0, \infty)$ so $v \to 0$ as $t \to \infty$; for solutions of the form $(u, 0)$ we have $u \to \tilde{u}$ as $t \to \infty$ by Corollary 4.3. Since $\omega(\partial Y_0)$ for (4.1) consists of $(0, 0)$ and $(\tilde{u}, 0)$ with solutions of the form $(u, 0)$ approaching $(\tilde{u}, 0)$ and solutions of the form $(0, v)$ approaching $(0, 0)$, permanence follows from Theorem 2.1 as in [9] if (4.6) holds. If (4.6) does not hold then (4.1) cannot have a positive equilibrium and thus cannot be permanent. (Permanence implies the existence of a positive equilibrium; see [8, 17].) If (u^*, v^*) is a positive equilibrium of (4.1) then u^* is a strict subsolution of (4.5), and since any sufficiently large constant K is a strict supersolution there must be a solution $\bar{u}$ with $u^* < \bar{u} < K$ on Ω. Since $\bar{u}$ is the unique positive solution of (4.5), $\bar{u} = \tilde{u}$ and hence $u^* < \tilde{u}$ on Ω. The equation for v^* is

$$d_2 \nabla^2 v^* + \left(\frac{E u^*}{1 + B u^* + C v^*} - D \right) v^* = 0 \quad \text{in } \Omega$$

$$\gamma v^* + (1 - \gamma) \frac{\partial v^*}{\partial n} = 0 \quad \text{on } \partial \Omega.$$

Since $v^* > 0$ in Ω we have $\sigma_1(d_2, [E u^*/(1 + B u^* + C v^*)] - D, \gamma) = 0$. However, $\tilde{u} > u^*$ and $v^* > 0$ so that on Ω we have $E \tilde{u}/(1 + B \tilde{u}) > E u^*/(1 + B u^* + C v^*)$. Standard monotonicity results for eigenvalues then imply

$$0 = \sigma_1(d_2, [E u^*/(1 + B u^* + C v^*)] - D, \gamma)$$
$$< \sigma_1(d_2, [E \tilde{u}/(1 + B \tilde{u})] - D, \gamma),$$

so permanence implies that (4.6) holds.

Remarks. (1) The condition (4.6) is analogous to (3.2). In the case $\beta = \gamma = 0$ (no flux boundary conditions) we have $\tilde{u} = 1$ and thus $\sigma_1(d_2, [E \tilde{u}/(1 + B \tilde{u})] - D, 0) = [E/(1 + B)] - D$ so that (4.6) reduces to (3.2).

(2) The biological interpretation of (4.6) is that if the system is at the equilibrium $(\tilde{u}, 0)$ with no predators and a small number of predators are

introduced then the number of predators can be expected to increase. In other words, (4.6) says that the system (4.1) with the prey at equilibrium and no predators is invasible by the predators. Thus, Theorem 4.4 can be interpreted as saying that both predator and prey populations can be expected to persist if the prey can sustain a positive equilibrium population in the absence of predators and the predators can invade the system with the prey at equilibrium.

To understand fully how the coefficients of (4.1) affect permanence, it is of interest to estimate the eigenvalue $\sigma_1(d_2, [E \tilde{u}/(1 + B \tilde{u})] - D, \gamma)$ in 4.6.

LEMMA 4.5.

$$\sigma_1\left(d_2, \frac{E \tilde{u}}{1 + B \tilde{u}} - D, \gamma\right) \leq \frac{E}{1 + B} - D - d_2 \lambda_1^+(1, \gamma). \tag{4.7}$$

Proof. By the strong maximum principle we have $\tilde{u} < 1$ in $\overline{\Omega}$. Monotonicity of eigenvalues then implies

$$\sigma_1\left(d_2, \frac{E \tilde{u}}{1 + B \tilde{u}} - D, \gamma\right) \leq \sigma_1\left(d_2, \frac{E}{1 + B} - D, \gamma\right)$$
$$= \frac{E}{1 + B} - D - d_2 \lambda_1^+(1, \gamma).$$

COROLLARY 4.6. *Hypothesis* (3.2) *is always necessary for permanence in* (4.1).

In general, loss of permanence does not imply deterministic extinction for either species. However, something close to that is true for (4.1).

PROPOSITION 4.7. *If* $d_1 \lambda_1^+(1, \beta) \geq 1$ *(i.e.,* $\sigma_1(d_1, 1, \beta) \leq 0$) *or if* $d_1 \lambda_1^+(1, \beta) < 1$ *and* $\sigma_1(d_2, [E \tilde{u}/(1 + B \tilde{u})] - D, \gamma) < 0$, *then* $v \to 0$ *as* $t \to \infty$.

Proof. We showed in the proof of Theorem 4.4 that if $d_1 \lambda_1^+(1, \beta) \geq 1$ then for any positive solution (u, v) of (4.1), $u \to 0$ as $t \to \infty$. If $u \leq D/(2E)$ then $v_t \leq d_2 \nabla^2 v - (D/2)v$ so $v \to 0$ as $t \to \infty$. If $d_1 \lambda_1^+(1, \beta) < 1$ then solutions of (4.5) approach $\tilde{u}$ as $t \to \infty$. Suppose $\tilde{u}$ satisfies (4.5) with $\tilde{u}(x, 0) = u(x, 0)$. Then, since u is a subsolution to (4.5), we have $u \leq \tilde{u}$. Because $\tilde{u} \to \tilde{u}$ as $t \to \infty$, we have $u \leq \tilde{u} \leq (1 + \epsilon)\tilde{u}$ for any $\epsilon > 0$ for sufficiently large t. Thus, for large t, v is a subsolution of

$$w_t = d_2 \nabla^2 w + \left(\frac{E \tilde{u}(1 + \epsilon)}{1 + B \tilde{u}(1 + \epsilon) + C w} - D \right) w \quad \text{in } \Omega \times (0, \infty)$$

$$\gamma w + (1 - \gamma) \frac{\partial w}{\partial n} = 0 \quad \text{on } \partial \Omega \times (0, \infty). \tag{4.8}$$

If $\sigma_1(d_2, [E\bar{u}/(1 + B\bar{u})] - D, \gamma) < 0$, then by continuity of eigenvalues we have

$$\sigma_1(d_2, [E\bar{u}(1 + \epsilon)/(1 + B\bar{u}(1 + \epsilon))] - D, \gamma) < 0 \qquad (4.9)$$

for $\epsilon > 0$ sufficiently small. Inequality (4.9) implies $d_2\lambda_1^+([E\bar{u}(1 + \epsilon)/(1 + B\bar{u}(1 + \epsilon))] - D, \gamma) > 1$ by Lemma 4.1, so by Lemma 4.2 all positive solutions of (4.8) approach zero as $t \to \infty$. Since v is a subsolution of (4.8) we must have $v \to 0$ as $t \to \infty$ as well.

In the case where the system (4.1) is permanent it is difficult to give a complete description of its dynamics. Permanence implies the existence of at least one positive equilibrium (u^*, v^*) but the equilibrium might be unstable. In general, permanence neither implies nor rules out the presence of additional equilibria. In this specific system there is no clear mechanism that would lead to multiple equilibria in the presence of diffusion, so there is no strong reason to suspect that there will be multiple equilibria, but we cannot rule out the possibility on the basis of our present analysis. We began this section with the observation that in the case of no-flux boundary conditions ($\beta = \gamma = 0$) solutions of (3.1) are solutions of (4.1). Thus, if $\beta = \gamma = 0$, the system (4.1) will have periodic solutions for certain parameter values, because (3.1) does. We have not attempted to show the existence of periodic solutions for $\beta, \gamma \in (0, 1]$ but we expect that such solutions will exist for certain parameter values, at least if β and γ are small. We conclude with an extension of Lemma 3.3 to the case of (4.1) with no-flux boundary conditions.

PROPOSITION 4.8. *Suppose that* (3.2) *holds so that the system* (3.1) *has a positive equilibrium* (u^*, v^*). *If* (3.5) *holds then* (u^*, v^*) *is globally asymptotically stable among positive solutions of* (4.1) *under no-flux boundary conditions* ($\beta = \gamma = 0$).

Proof. The Lyapunov function V used in the proof of Lemma 3.3 has the form $V = V_1(u) + kV_2(v)$ with $V_1''(u) = u^*/u^2$ and $V_2''(v) = v^*/v^2$ where k is a positive constant. Since the system (4.1) is dissipative it follows that all trajectories are eventually uniformly bounded in $L^\infty(\Omega)$ as in [8]. Hence, V_1'' and V_2'' are positive and bounded below for large t. Since we also have $V_1(u^*) = V_1'(u^*) = V_2(v^*) = V_2'(v^*) = 0$, it follows that for $(u, v) \in (0, U_0] \times (0, V_0]$ we have $V_1 \geq c_1(u - u^*)^2$ and $V_2 \geq c_2(v - v^*)^2$ for some positive constants c_1 and c_2. By the form of V and the convexity of V_1 and V_2 we have that

$$E(t) = \int_\Omega V(u(x, t), v(x, t))\, dx$$

is a Lyapunov function for (4.1) in the sense that $E'(t) < 0$ along trajectories except at (u^*, v^*) and $E(t) > 0$ except at (u^*, v^*); see [19], for example.

It follows that $E(t) \to 0$ as $t \to \infty$. Since all trajectories of (4.1) eventually must lie in $(0, U_0] \times (0, V_0]$, we have $(u, v) \to (u^*, v^*)$ in $[L^2(\Omega)]^2$. In general the issue of obtaining L^∞ bounds from L^p bounds in somewhat delicate (see [8, 10, 15, 19]) but since we already know that (4.1) is dissipative we may write it (for t sufficiently large) as

$$\begin{aligned} u_t - d_1\nabla^2 u &= p(x, t)u \\ v_t - d_2\nabla^2 v &= q(x, t)v \end{aligned} \qquad (4.10)$$

with p and q bounded in L^∞ independent of the particular trajectory (u, v). Because of the form of (4.10), standard "bootstrapping" arguments as used in [10, 15] as well as more sophisticated arguments of the same sort [8, 19] imply that $(u, v) \to (u^*, v^*)$ in $[L^\infty(\Omega)]^2$ as $t \to \infty$.

Biological remarks. The diffusive model (4.1) shares many of the features of the spatially homogeneous model (3.1). In particular, the condition (4.6) for permanence in (4.1) involves the parameters E, B, and D but not A or C. (In (4.6) the diffusion rates and boundary conditions also play a role, either directly or via $\bar{u}$.) Whenever (4.1) is permanent it must as a consequence have an equilibrium, and if the inequality (4.6) implying permanence is reversed then by Proposition 4.7 we have $v \to 0$ as $t \to \infty$ so no equilibrium is possible. Thus, as in the spatially homogeneous case, the conditions for permanence and the existence of a positive equilibrium are essentially the same. We have not analyzed the uniqueness or stability of the equilibrium in the general diffusive model. In the case of no-flux boundary conditions solutions to (3.1) are also solutions to (4.1) so (4.1) will sometimes have an unstable equilibrium and a periodic solution. We suspect that this is also the case for other boundary conditions but we have not tried to prove it. Although the coefficient C does not enter into the condition (4.6) for permanence, it may affect the stability of the equilibrium (e.g., in the no-flux case discussed in Proposition 4.8) and it may also affect the size of the equilibrium and the extent to which the predator population can experience "booms" resulting in later "busts." This is shown in the analysis in [6], which can then be combined with the methods of [7] to give bounds on trajectories. In theory, the coefficient C does not affect the prediction of permanence in (4.1). However, the model (4.1) does not account for demographic stochasticity. If (4.1) predicts coexistence of the predators and prey but the predicted densities are too low then the actual populations may be at risk of extinction because of stochastic effects. Since C *does* affect the size of possible equilibria [6] and some of the quantitative features of trajectories [6, 7], it can affect the predicted sizes of populations and hence the risk of stochastic extinctions.

5. CONCLUSIONS

The Beddington–DeAngelis functional response admits a range of dynamics which include the possibilities of extinction, persistence, stable or unstable equilibria, and limit cycles. The criteria for persistence are essentially the same as for systems with a Holling type 2 response, since they do not involve the extra parameter in the Beddington–DeAngelis response which describes mutual interference by predators. However, the presence of mutual interference by predators can stabilize the positive equilibrium and eliminate limit cycles. (It can also provide global bounds on the predator density which preclude extreme "boom–bust" cycles, because it provides a form of self-limitation by the predator and hence allows the use of comparison methods to obtain practical persistence; see [6, 7].) Since the Beddington–DeAngelis response can be generated by a number of natural mechanisms [2, 11, 20] and because it admits rich but biologically reasonable dynamics, it seems worthy of further study.

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