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ON THE STEADY-STATE PROBLEM FOR THE VOLTERRA-LOTKA COMPETITION MODEL WITH DIFFUSION

Robert Stephen Cantrell and Chris Cosner

1. **Introduction.** The Volterra-Lotka model for two competing species, with diffusion, is given by the system

$$(1.1)\quad \begin{aligned} U_t &= K_1 \Delta U + U[A - BU - CV] \\ V_t &= K_2 \Delta V + V[D - EU - FV] \end{aligned}$$

where U and V denote the population densities of two competing species; the equations are assumed to hold for $(x,t) \in \Omega \times (0,\infty)$ with $\Omega \subseteq R^n$ a smooth, bounded domain. The terms A, B, C, D, E, F, K_1, K_2 are all positive. In the present article we will consider the case where they are constants; however, for some interpretations of the model they may occur as functions. The values of K_1 and K_2 describe the diffusion rates of the two species, A and D the rates of reproduction, B and F the self-regulation of each species, and C and E the interaction of the species.

The model (1.1) has been investigated widely; see [2], [3], [5], [8], [9], [11], [13], [14]. A partial survey of the literature is given in [5]. It is natural to study (1.1) by examining the possible steady states; however, only the positive ones are of physical interest. States in which both U and V are positive are called coexistence states. In the present article, those are the states we shall investigate.

We study the system

$$(1.2)\quad \begin{aligned} 0 &= K_1 \Delta U + U[A - BU - CV] \\ 0 &= K_2 \Delta V + V[D - EU - FV] \\ &\text{in } \Omega,\ U|_{\partial\Omega} = 0,\ V|_{\partial\Omega} = 0. \end{aligned}$$

We note that the corresponding system with homogeneous Neumann boundary conditions was investigated in [3], [11], where rather precise conditions were given for the existence and stability of coexistence states. In that case, such states are constant on Ω.

In the case of (1.2), sufficient conditions for the existence of coexistence states are given in [8] and [11]; in the special case $K_1 = K_2$ and $A = D$, necessary and sufficient conditions for the existence of such states are given in [5]. In [2], a bifurcation analysis is performed on the system (1.2) when either A or D is varied while the remaining parameters are held fixed. Solutions to (1.2) with both U and V positive are shown in [2] to bifurcate from the semi-trivial solutions where one component is positive and the other is zero; hence coexistence states arise via secondary bifurcation, since the states with one component zero and the other positive can be viewed as bifurcating from the zero state. In [11], the conditions $A > K_1\lambda_1$ and $D > K_2\lambda_1$ (where λ_1 is the first eigenvalue for $-\Delta$ with homogeneous Dirichlet boundary conditions on Ω) are shown to be necessary for the existence of coexistence states.

In the present article, we sharpen known necessary conditions for the existence of coexistence states by extending some results of [5] to systems where $K_1 \neq K_2$ and/or $A \neq D$. We also perform a local bifurcation analysis which is somewhat more detailed than that of [2]; specifically, we obtain fairly precise quantitative estimates of where bifurcation can occur, determine in some cases the direction of bifurcation, and obtain additional qualitative information about the bifurcating solutions by viewing (1.2) as a two-parameter bifurcation problem in A and D. The bifurcation analysis also gives additional information on necessary conditions for the existence of coexistence states.

We use integration by parts via the divergence theorem to obtain many of our bounds on the regions of nonexistence for coexistence states and on the values of A and D for which bifurcation can occur. The bifurcation analysis is based on the result of Crandall and Rabinowitz [6] on bifurcation from a simple eigenvalue. In addition, much of our work relies on the theory of the single equation

$$(1.3)\quad 0 = \Delta w + w[a - q(x) - w] \text{ in } \Omega,$$
$$w > 0 \text{ in } \Omega,\ w|_{\partial\Omega} = 0$$

and its linearization.

To facilitate our analysis, we rescale the system (1.2). Dividing out K_1 and K_2, letting $u = \alpha U$ and $v = \beta V$, and making the appropriate choices of α and β rescales the system (1.2) to the form

$$(1.4)\quad \begin{aligned} -\Delta u &= u[a - u - cv] \\ -\Delta v &= v[d - eu - v] \\ \text{in } \Omega,\ u|_{\partial\Omega} &= 0,\ v|_{\partial\Omega} = 0. \end{aligned}$$

In what follows we shall restrict our attention to (1.4).

As noted above, we require some information about (1.3). The necessary results are summarized in the following lemma:

LEMMA (1.1). *Suppose that* $q(x)$ *is a smooth function from* Ω *to* R. *Then the lowest eigenvalue,* $\lambda_1(q)$, *of the problem*

$$(1.5)\quad -\Delta\Psi + q(x)\Psi = \lambda\Psi \text{ in } \Omega,\ \Psi|_{\partial\Omega} = 0$$

is simple, with positive eigenfunction. Furthermore, the following statements hold:

(i) *If* $q_1(x) < q_2(x)$ *for all* $x \in \Omega$, $\lambda_1(q_1) < \lambda_1(q_2)$.

(ii) *Equation* (1.3) *has a unique positive solution for* $a > \lambda_1(q)$ *and no positive solutions for* $a \leqslant \lambda_1(q)$.

(iii) *If* $a_1 \geqslant a_2$, $q_1(x) \leqslant q_2(x)$, *and* w_1, w_2 *are positive solutions to* (1.3) *corresponding to* a_1, q_1, *and* a_2, q_2, *respectively, then* $w_1 \geqslant w_2$.

REMARKS. 1. The assertions of the lemma are all either standard results or follow directly from the theory of sub- and super-solutions, as discussed in [12]. A discussion is given in [2], §2.

2. Another implication of Lemma (1.1) and the theory of sub- and super-solutions is that given any positive value of a for which there exists a subsolution $\underline{w}$ to (1.3) with $0 < \underline{w} \leqslant a$, then since $\underline{w} = a$ is a super-solution, there exists a solution $w > 0$ for that value of a. Since positive solutions only exist for $a > \lambda_1(q)$, it follows that sub-solutions can only exist for $a > \lambda_1(q)$.

3. We will frequently refer to the solution of equation (1.3) with $q(x) \equiv 0$. Following [5], we denote that solution by θ_a. That $\lim_{a\to\lambda_1^+} \theta_a = 0$ follows from a bifurcation argument.

We shall also make use of the following lemma:

LEMMA (1.2). *Consider the function* $g\colon R_+ \times (\lambda_1, \infty) \to R$ *given by* $g(e,a) =$

$\lambda_1(e\theta_a)$. *Then* g *has the following properties*:

(i) $e < e' \to g(e,a) < g(e',a)$.

(ii) $a < a' \to g(e,a) < g(e,a')$.

(iii) $g(1,a) = a$ *for all* $a > \lambda_1$.

(iv) $\frac{\partial g}{\partial e}(e,a)$: $R_+ \times \{a\} \to R$ *is continuous. Furthermore, if* $a > \lambda_1$ *is fixed and* $h: R_+ \to C_0^{2+\alpha}(\bar{\Omega})$ *is given by* $h(e) = \Psi_e$, *where*

$$-\Delta\Psi_e + e\theta_a\Psi_e = \lambda_1(e\theta_a)\Psi_e,\ \Psi_e > 0, \textit{ and } \int_\Omega \Psi_e^2 = 1,$$

then $h': R_+ \to C_0^{2+\alpha}(\bar{\Omega})$ *is also continuous.*

PROOF. (i) and (ii) are consequences of Lemma (1.1). (iii) follows from the definition of θ_a. There are a number of ways of establishing (iv). We have chosen to present a particularly elegant proof, due to our colleague Alan Lazer [7], and based on the Implicit Function Theorem. To this end, let $E = C_0^{2+\alpha}(\bar{\Omega}) \times R$ and $F = C_0^{\alpha}(\bar{\Omega}) \times R$, $0 < \alpha < 1$, and consider a mapping $\Phi: E \times R \to F$ given by $\Phi(v,s,e) = (-\Delta v + e\theta_a v - sv, \|v\|^2_{L^2(\Omega)} - 1)$. Note that Φ is a continuous map and that the linearization of Φ with respect to E at (v,s,e), denoted $D_1\Phi(v,s,e)$, is given by

$$D_1\Phi(v,s,e)(w,t) = (-\Delta w + e\theta_a w - sw - tv,\ 2\int_\Omega vw).$$

If $v_0 = \Psi_{e_0}$ and $s_0 = \lambda_1(e_0)$, $D_1\Phi(v_0,s_0,e_0)$: $E \to F$ is a linear homeomorphism. That such is the case will follow from the open mapping theorem, provided we show that $D_1\Phi(v_0,s_0,e_0)$ is a bijection. Suppose then that $D_1\Phi(\Psi_{e_0},\lambda_1(e_0),e_0)(w,t) = (0,0)$. Then $-\Delta w + e_0\theta_a w - \lambda_1(e_0)w = t\Psi_{e_0}$, $w|_{\partial\Omega} = 0$, and $\int_\Omega w\Psi_{e_0} = 0$. The Fredholm alternative implies $\int_\Omega t\Psi_{e_0}^2 = 0$. Hence $t = 0$ and $w = c\Psi_{e_0}$. Since $\int_\Omega w\Psi_{e_0} = 0$, $c = 0$ and so $w = 0$.

Consider now the pair of equations

(1.6) $-\Delta w + e_0\theta_a w - \lambda_1(e_0)w - t\Psi_{e_0} = h$

(1.7) $2\int_\Omega w\Psi_{e_0} = r$.

Let $t = -\int_\Omega h\Psi_{e_0}$. Then $\int_\Omega (t\Psi_{e_0} + h)\Psi_{e_0} = 0$. Hence (1.6) has solutions w of the form $z + k\Psi_{e_0}$, where z is uniquely determined and $\int_\Omega z\Psi_{e_0} = 0$. We may then obtain a solution to (1.6) - (1.7) by choosing $k = r/2$. Hence $D_1\Phi(v_0,s_0,e_0)$ is a linear homeomorphism, and (iv) follows from the Implicit Function Theorem.

As we have indicated, one of our aims is to give quantitative information on the locus in a-d parameter space of the secondary bifurcation phenomena. We pause briefly to note the significance of such information. If the parameters c and e in (1.4) are held fixed, it is a consequence of the results of [2] that coexistence states emanate from the semi-trivial (extinction) states $(a,d,\theta_a,0)$ and $(a,d,0,\theta_d)$ along the curves $\Gamma_e = \{(a,\lambda_1(e\theta_a)): a \geqslant \lambda_1\}$ and $\Gamma_c = \{(\lambda_1(c\theta_d),d): d \geqslant \lambda_1\}$ in a - d parameter space. By Lemma (1.2), these curves are strictly monotonic. Suppose now that $a > \lambda_1$ is fixed. Blat and Brown show that a global continuum of coexistence states emanates from $(a,d,\theta_a,0)$ when $d = \lambda_1(e\theta_a) > \lambda_1$, and, furthermore, that the only global possibility is that the continuum links to the sheet $(a,d,0,\theta_d)$. The strict monotonicity of the curves Γ_e and Γ_c guarantees that there is only one $d^* > \lambda_1$ such that $\lambda_1(c\theta_{d^*}) = a$. Thus coexistence states must exist for (a,d) with d in the open interval joining $\lambda_1(e\theta_a)$ and d^*. Hence coexistence states exist in the region bounded by Γ_c and Γ_e, and investigating quantitatively the locus of these sets in a - d parameter has obvious significance.

Now let $D = \{(a,d) \in R^2: a > \lambda_1, d > \lambda_1\}$, and let $D_+ = \{(a,d) \in D: d > a\}$ and $D_- = \{(a,d) \in D: d < a\}$. The following result is a consequence of Lemma 1.2, and is perhaps the most basic observation on the location of Γ_e and Γ_c.

PROPOSITION 1.3. (i) *If* $e < 1$, $\Gamma_e \subseteq D_-$; *if* $e > 1$, $\Gamma_e \subseteq D_+$.

(ii) *If* $c < 1$, $\Gamma_c \subseteq D_+$; *if* $c > 1$, $\Gamma_c \subseteq D_-$.

Finally, we note that in contrast to the case of (1.3), the questions of uniqueness and direction of bifurcation of solutions to (1.4) remain largely open. Some results on those questions are obtained in [5] and the present article, but much remains to be done.

2. Estimates. In this section we derive various estimates on the ranges of parameters for which coexistence states exist and on the eigenvalues of the linearized problems that occur in the bifurcation analysis. We will assume that the system has been scaled so that it has the form (1.4), that is

$$\Delta u + u[a - u - cv] = 0 \text{ in } \Omega$$

$$\Delta v + v[d - eu - v] = 0$$

$$u = v = 0 \text{ on } \partial\Omega,\ u,v > 0 \text{ in } \Omega.$$

As is noted in [5], it follows from results of Pao [11] that (1.4) can have no solutions unless $a > \lambda_1$, $d > \lambda_1$. The maximum principle implies that $u < a$ and $v < d$. The following result provides additional information on the values of the parameters a, c, d, and e for which solutions to (1.4) cannot exist.

THEOREM (2.1). *If* a, c, d, e *are positive constants, the system* (1.4) *cannot have solutions unless one of the following conditions holds*:

(i) $c \leq 1$, $e \leq 1$, $d \leq a/c$, *and* $d \geq ae$. *(If the inequalities for* c *and* e *are made strict, then* a *and* d *must satisfy the strict versions of the inequalities, also.)*

(ii) $e \leq 1 < c$, $d < a$, $d > ae/c$,

(iii) $c \leq 1 < e$, $d < ae/c$, $d > a$,

(iv) $c > 1$, $e > 1$, $d < ae$, $d > a/c$.

REMARKS. Some of the conclusions of this theorem were noted in [2] and [5]. In particular, it was shown in [5] that no solution for (1.4) is possible if $a = d$ and $e < 1 < c$ or $c < 1 < e$; and it was shown in [2] that if $c = e = 1$ then (1.4) has solutions only if $a = d$. This first result follows from (ii) or (iii) above, the second from (i). The proof of the theorem uses ideas similar to those used in proving Theorem 3.1 of [5]; specifically, the proof is based on integration by parts.

PROOF. We multiply the first equation in (1.4) by v and the second by u and integrate over Ω. Integrating by parts using the divergence theorem and subtracting the second equation from the first yields

$$(2.1)\quad 0 = \int_\Omega uv[(a-d) - (1-e)u + (1-c)v].$$

If the expression $D = [(a-d) - (1-e)u + (1-c)v]$ is strictly positive or strictly negative on Ω, then by (2.1) we cannot have a solution of (1.4). Hence we must have $\sup_\Omega D \geq 0$ and $\inf_\Omega D \leq 0$. Suppose $c, e < 1$. Then $\sup_\Omega D < a - d + (1-c)d = a - cd$ since $u \geq 0$ and $v < d$ on $\bar{\Omega}$. So $0 \leq \sup_\Omega D < a - cd$. Similarly, $0 \geq \inf_\Omega D > a - d - (1-e)a = ae - d$. Thus, when $c, e < 1$, we must have $d < a/c$ and $d > ae$ for any solution to exist for (1.4). If $c, e \leq 1$ then a and d must satisfy the corresponding nonstrict inequalities. If $e \leq 1 < c$, then on $\bar{\Omega}$, $D > a - d - (1-e)a + (1-c)d = ae - cd$, so $0 > \inf_\Omega D > ae - cd$ or $d > ae/c$. Also from (2.1) we have

$$(a-d)\int_\Omega uv = (1-e)\int_\Omega u^2 v + (c-1)\int_\Omega uv^2 > 0,$$

so since $uv > 0$ in Ω, $a - d > 0$ or $d < a$. Similarly, if $c \leqslant 1 < e$, then $d > a$ and $d < ae/c$. Finally, if $c,e > 1$, then on $\bar{\Omega}$ we have $D \geqslant (a - d) + (1 - c)v > a - dc$, so $0 \geqslant \inf_{\Omega} D > a - dc$ and so $d > a/c$; also, $D \leqslant (a - d) - (1 - e)u < ae - d$ on $\bar{\Omega}$, so $0 \leqslant \sup_{\Omega} D < ae - d$ or $d < ae$. This last estimate completes the proof.

In a later theorem we will obtain a somewhat sharper version of the estimates for the case $e,c < 1$. First, however, we must study the eigenvalue problem

(2.2) $-\Delta\Psi + e\theta_a\Psi = \lambda\Psi$ in Ω, $\Psi = 0$ on $\partial\Omega$.

As in Lemma 1.1, we denote the first eigenvalue by $\lambda_1(e\theta_a)$, or by $\lambda_1(e)$ when a is held fixed, and the first eigenfunction by Ψ_e, where Ψ_e is normalized via

(2.3) $\int_{\Omega}\Psi_e^2 = 1.$

We obtain the following result:

THEOREM 2.2. *If* $a > \lambda_1(0)$, *then* $\lambda_1(e\theta_a)$ *satisfies the estimates*:

(i) *If* $0 \leqslant e < 1$, *then*

$$ae + \lambda_1(0)(1 - e) \leqslant \lambda_1(e\theta_a) \leqslant \min(ae + \lambda_1(0), a)$$

(and in fact $\lambda_1(e\theta_a) < a$*)*

(ii) *If* $e = 1$, *then*

$$\lambda_1(\theta_a) = a$$

(iii) *If* $e > 1$, *then*

$$a < \lambda_1(e\theta_a) \leqslant ae + (1 - e)\lambda_1(0).$$

PROOF. In the introduction we showed that when $a > \lambda_1(0)$, we have $\lambda_1(e) \leqslant a$ for $0 \leqslant e < 1$, $\lambda_1(1) = a$, and $\lambda_1(e) \geqslant a$ for $e > 1$. If we fix $e = e_1$ in (2.2), multiply by Ψ_{e_2}, and integrate by parts via the divergence theorem, we obtain

(2.4) $$\begin{aligned}\lambda_1(e_1)\int_{\Omega}\Psi_{e_1}\Psi_{e_2} &= \int_{\Omega}\Psi_{e_2}(-\Delta\Psi_{e_1}) + e_1\int_{\Omega}\theta_a\Psi_{e_1}\Psi_{e_2} \\ &= \int_{\Omega}(-\Delta\Psi_{e_2})\Psi_{e_1} + e_1\int_{\Omega}\theta_a\Psi_{e_1}\Psi_{e_2} \\ &= \lambda_1(e_2)\int\Psi_{e_1}\Psi_{e_2} + (e_1 - e_2)\int_{\Omega}\theta_a\Psi_{e_1}\Psi_{e_2}.\end{aligned}$$

If we let $e_1 = e$ and $e_2 = 0$ in (2.4) and use the fact that $\theta_a < a$, we obtain the estimate

$$\lambda_1(e)\int_{\Omega}\Psi_e\Psi_0 \leqslant (\lambda_1(0) + ae)\int_{\Omega}\Psi_e\Psi_0$$

so that $\lambda_1(e) \leqslant ae + \lambda_1(0)$ for any $e \geqslant 0$. Also, (2.3) may be rewritten as

(2.5) $[\lambda_1(e_1) - \lambda_1(e_2)]/(e_1 - e_2) = (\int_\Omega \theta_a \Psi_{e_1} \Psi_{e_2})/(\int_\Omega \Psi_{e_1} \Psi_{e_2})$.

As noted in the introduction, $\lambda_1(e)$ and Ψ_e depend differentiably on e; so if we take $e_1 = e$, let $e_2 \to e$, and use (2.3) then (2.5) yields

(2.6) $\lambda_1'(e) = \int_\Omega \theta_a \Psi_e^2 > 0$.

It follows immediately from (2.6) that $\lambda_1(e) > a$ for $e > 1$ and $\lambda_1(e) < a$ for $e < 1$. Also, it follows from (2.2) and (2.6) that

$$\lambda_1'(e) = (1/e) \int_\Omega [\Psi_e \Delta \Psi_e + \lambda_1(e) \Psi_e^2],$$

or

(2.7) $\lambda_1'(e) - \lambda_1(e)/e = -(1/e) \int_\Omega |\nabla \Psi_e|^2$.

Since the variational formula for the first eigenvalue of the Laplacian together with (2.3) imply the bound

$$\int_\Omega |\nabla \Psi_e|^2 \geqslant \lambda_1(0),$$

it follows from (2.7) that $\lambda_1'(e) - \lambda_1(e)/e \leqslant -\lambda_1(0)/e$, or

(2.8) $[\lambda_1(e)/e]' \leqslant -\lambda_1(0)/e^2$.

If $e < 1$ then we may integrate (2.8) from e to 1, obtaining $a - \lambda(e)/e \leqslant \lambda_1(0)(1 - 1/e)$ or $\lambda_1(e) \geqslant ae + (1 - e)\lambda_1(0)$. If $e > 1$, then integrating (2.8) from 1 to e yields the reverse inequality, $\lambda_1(e) \leqslant ae + (1 - e)\lambda_1(0)$, which completes the proof.

We may now obtain a sharper version of one of the estimates in Theorem (2.1).

THEOREM (2.3). *If* a, c, *and* e *are fixed, with* $c, e < 1$, *and if* $d \leqslant a$ *is such that a solution to* (1.4) *exists, then*

(2.9) $u \geqslant [(1 - c)/(1 - ce)]\theta_a$, $v \leqslant [(1 - e)/(1 - ce)]\theta_a$

and

(2.10) $d \geqslant \lambda_1([e(1 - c)/(1 - ce)]\theta_a) \geqslant [ae(1 - c) + \lambda_1(0)(1 - e)]/(1 - ce)$.

REMARKS. This theorem, like Theorem (2.1), gives information on how far solutions bifurcating from $d = \lambda_1(e\theta_a)$ can "bend backward."

PROOF. If u and v satisfy (1.4), then since $u > 0$, it follows from Lemma (1.1) that $v \leqslant w$, where w is the solution to $\Delta w + w[d - w] = 0$ in Ω, $w = 0$ on $\partial\Omega$, $w > 0$ in Ω; that is, $w = \theta_d$. Since $d < a$, $v \leqslant \theta_a$. Then, again by Lemma (1.1), $u \geqslant z$, where z is the solution to

(2.11) $\Delta z + z[a - c\theta_a - z] = 0$ in Ω, $z > 0$ in Ω, $z = 0$ on $\partial\Omega$.

However, the unique solution to (2.11) is $z = (1 - c)\theta_a$, so $u \geqslant (1 - c)\theta_a$. We can repeat the argument; in general, if $k \leqslant 1$ and $u \geqslant k\theta_a$ then v is a subsolution to $\Delta w + w[d - ek\theta_a - w] = 0$, $w > 0$ in Ω, $w = 0$ on $\partial\Omega$ and hence to $\Delta w + w[a - ek\theta_a - w] = 0$, $w > 0$ in Ω, $w = 0$ on $\partial\Omega$. Then Lemma (1.1) implies that $d \geqslant \lambda_1(ek\theta_a)$ and that $v \leqslant (1 - ek)\theta_a$. It then follows that $u \geqslant y = (1 - c + cek)\theta_a$, since y is the solution to $\Delta y + y[a - c(1 - ek)\theta_a - y] = 0$ in Ω, $y = 0$ on $\partial\Omega$, $y > 0$ in Ω. Starting with $k = 1 - c$, we obtain $u \geqslant [1 - c + ce(1 - c)]\theta_a$ or $u \geqslant (1 - c)[1 + ce]\theta_a$. Letting $k = (1 - c)[1 + ce]$, we obtain $u \geqslant (1 - c + ce(1 - c)[1 + ce])\theta_a = (1 - c)[1 + ce + c^2e^2]\theta_a$. Proceeding by induction, we have $u \geqslant (1 - c)\, \Sigma_{k=0}^{\infty}(ce)^k\theta_a = [(1 - c)/(1 - ce)]\theta_a$. Then $v \leqslant [(1 - e)/(1 - ce)]\theta_a$ and $d \geqslant \lambda_1([e(1 - c)/(1 - ce)]\theta_a)$. By Theorem (2.2) we have $d \geqslant [ae(1 - c) + \lambda_1(0)(1 - e)]/(1 - ce)$.

3. **Bifurcation results.** In this section we consider the local character of the componentwise positive solutions to (1.4) which bifurcate from the sheets $\{(a,d,\theta_a,0)$: $a > \lambda_1$, $d \in R$ and $(a,d,0,\theta_d)$: $a \in R$, $d > \lambda_1\}$ along $\Gamma_e = \{(a,\lambda_1(e\theta_a),\theta_a,0)$: $a > \lambda_1\}$ and $\Gamma_c = \{(\lambda_1(c\theta_d),d,0,\theta_d)$: $d > \lambda_1\}$, respectively. To this end, consider again the system (1.4), i.e.

$$\begin{cases} -\Delta u = au - u^2 - cuv \\ -\Delta v = dv - v^2 - euv. \end{cases}$$

The substitution $w = u - \theta_a$, $v = v$ gives rise to the equivalent system

$$(3.1) \quad \begin{cases} -\Delta w + (2\theta_a - a)w = -c\theta_a v - w^2 - cwv \\ -\Delta v + e\theta_a v = dv - v^2 - ewv. \end{cases}$$

A computation shows that the linearization of (3.1) about $(w,v) = (0,0)$ is given by

$$(3.2) \quad \begin{cases} -\Delta x + (2\theta_a - a)x = -c\theta_a y \\ -\Delta y + e\theta_a y = dy. \end{cases}$$

Observe that if $-\Delta z + (2\theta_a - a)z = \lambda z$, with $z > 0$ on Ω, $\int_\Omega z^2 = 1$,

$$\int_\Omega(-\Delta z)\theta_a + \int_\Omega(2\theta_a^2 - a\theta_a)z = \lambda \int_\Omega z\theta_a$$

or

$$\int_\Omega z(-\Delta\theta_a) + \int_\Omega (2\theta_a^2 - a\theta_a)z = \lambda \int_\Omega z\theta_a.$$

Hence $\int_\Omega \theta_a^2 z = \lambda \int_\Omega z\theta_a$ whence it follows that $\lambda > 0$. Thus by [1], $[-\Delta + (2\theta_a - a)]^{-1}$ exists and is a compact positive operator.

Thus (3.2) is equivalent to the system

$$(3.3)\quad \begin{cases} x = [-\Delta + (2\theta_a - a)]^{-1}(-c\theta_a y) \\ y = d[-\Delta + e\theta_a]^{-1}y. \end{cases}$$

Let $A_1 = [-\Delta + eu_a]^{-1}$, $A_2 = [-\Delta + (2\theta_a - a)]^{-1}$, and $M_{ca}z = -c\theta_a z$. Then (3.3) may be equivalently expressed as

$$(3.4)\quad \binom{x}{y} = d\begin{pmatrix} 0 & 0 \\ 0 & A_1 \end{pmatrix}\binom{x}{y} + \begin{pmatrix} 0 & A_2M_{ca} \\ 0 & 0 \end{pmatrix}\binom{x}{y}.$$

If we now let $B_1 = \begin{pmatrix} 0 & 0 \\ 0 & A_1 \end{pmatrix}$ and $B_2 = \begin{pmatrix} 0 & A_2M_{ca} \\ 0 & 0 \end{pmatrix}$, B_1 and B_2 are compact on the Banach space $E = [C_0^{1,\alpha}(\overline{\Omega})]^2$. Thus $I - dB_1 - B_2$ is a Fredholm operator on E, with index 0. Furthermore, since $\ker(I - \lambda_1(e\theta_a)B_1 - B_2)$ has dimension 1, $\lambda_1(e\theta_a)$ will be a simple eigenvalue of the pair $(I - B_2, B_1)$ (see [4]) provided

$$(3.5)\quad B_1\phi \notin R(I - B_2 - \lambda_1(e\theta_a)B_1),$$

where $\langle\phi\rangle = \ker(I - \lambda_1(e\theta_a)B_1 - B_2)$. Suppose then

$$\begin{cases} x = [-\Delta + (2\theta_a - a)]^{-1}(-cu_a y) \\ y = \lambda_1(e\theta_a)[-\Delta + e\theta_a]^{-1}y \end{cases}$$

and $y \neq 0$. Then

$$B_1\binom{x}{y} = \binom{0}{A_1 y} = \binom{0}{(-\Delta+e\theta_a)^{-1}y} = \binom{0}{(1/\lambda_1(e\theta_a))y}.$$

But

$$(I - B_2 - dB_1)\binom{x^*}{y^*} = \begin{pmatrix} x^* - [-\Delta+(2\theta_a - a)]^{-1}(-c\theta_a y^*) \\ \{I - d[-\Delta+e\theta_a]^{-1}\}y^* \end{pmatrix}.$$

Hence if $B_1\binom{x}{y} \in R(I - B_2 - \lambda_1(e\theta_a)B_1)$, $y \in R(I - \lambda_1(e\theta_a)[-\Delta + e\theta_a]^{-1})$. However, $\langle y\rangle = \ker(I - \lambda_1(e\theta_a)[-\Delta + e\theta_a]^{-1})$, a contradiction.

From [4], the preceding analysis justifies an application of the Crandall-Rabinowitz Constructive Bifurcation Theorem [6]. Let $a > \lambda_1$, $c > 0$, and

$e > 0$ be fixed. Then $(a,d,\theta_a,0)$ is a solution of (1.4) for all $d \in R$. From [6], there are $\delta_0 > 0$ and smooth functions d: $(-\delta_0,\delta_0) \to R$, u: $(-\delta_0,\delta_0) \to C_0^{1,\alpha}(\bar{\Omega})$, v: $(-\delta_0,\delta_0) \to C_0^{1,\alpha}(\bar{\Omega})$ such that

$$d(0) = \lambda_1(e\theta_a),$$

$$u(s) = \theta_a + sw_0 + \tilde{w}(s)$$

$$v(s) = sv_0 + \tilde{v}(s),$$

where

$$\langle v_0 \rangle = \ker(I - \lambda_1(e\theta_a)[-\Delta + e\theta_a]^{-1}),$$

$$v_0(x) > 0 \text{ if } x \in \Omega,$$

$$\int_\Omega v_0^2 = 1,$$

$$w_0 = [-\Delta + (2\theta_a - a)]^{-1}(-c\theta_a v_0),$$

$$\|\tilde{w}(s)\|_{C_0^{1,\alpha}(\bar{\Omega})} = o(|s|),$$

and

$$\|\tilde{v}(s)\|_{C_0^{1,\alpha}(\bar{\Omega})} = o(|s|).$$

Furthermore, in a sufficiently small neighborhood of $(a,\lambda_1(e\theta_a),\theta_a,0)$ (in $\{a\} \times R \times C_0^{1,\alpha}(\bar{\Omega}) \times C_0^{1,\alpha}(\bar{\Omega})$), the four-tuples $(a,d(s),u(s),v(s))$, $|s| \leqslant \delta_0$ are the only solutions to (1.4) other than $(a,d,\theta_a,0)$. In particular, we have componentwise positive solutions to (1.4) when $s > 0$.

We now let $\lambda(s) = d(s) - d(0)$ and calculate $\lambda'(0)$ (cf. [10]). To do so, we need only consider the equation

(3.6) $-\Delta v(s) = d(s)v(s) - v^2(s) - eu(s)v(s)$.

Equation (3.6) is equivalent to

$$(3.7)\quad [-\Delta + e\theta_a - d(0)](sv_0 + \tilde{v}(s)) = \lambda(s)(sv_0 + \tilde{v}(s)) - (sv_0 + \tilde{v}(s))^2$$
$$- e(sv_0 + \tilde{v}(s))(\theta_a + sw_0 + \tilde{w}(s) - \theta_a).$$

Differentiating (3.7) with respect to s yields

$$(3.8)\quad [-\Delta + e\theta_a - d(0)](\tilde{v}'(s)) = \lambda'(s)(sv_0 + \tilde{v}(s)) + \lambda(s)(v_0 + \tilde{v}'(s))$$
$$- 2(sv_0 + \tilde{v}(s))(v_0 + \tilde{v}'(s))$$

$$- e(v_0 + \widetilde{v}'(s))(sw_0 + \widetilde{w}(s))$$
$$- e(sv_0 + \widetilde{v}(s))(w_0 + \widetilde{w}'(s)).$$

If $s = 0$, the right hand side of (3.8) is zero. Hence $[-\Delta + e\theta_a - d(0)]\widetilde{v}'(0) = 0$. However, from [6], it follows that $(\widetilde{w}(s),\widetilde{v}(s))$ may be assumed to lie in $R(I - d(0)B_1 - B_2)$. As a consequence, $\widetilde{v}(s) \in R(I - \lambda_1(e\theta_a)[-\Delta + e\theta_a]^{-1})$, or, equivalently $\int_\Omega \widetilde{v}(s)v_0 = 0$. Hence $\int_\Omega \widetilde{v}'(0)v_0 = 0$ and so $\widetilde{v}'(0) = 0$. Thus $v'(0) = v_0$ and $\widetilde{v}''(0) = v''(0)$.

If we differentiate with respect to s once more and evaluate at $s = 0$, we obtain

(3.9) $(-\Delta + e\theta_a - d(0))\widetilde{v}''(0) = 2\lambda'(0)v_0 - 2v_0^2 - 2ev_0(w_0 + \widetilde{w}'(0)),$

and a computation will show $\widetilde{w}'(0) = 0$. Thus

(3.9) $\int_\Omega(-\Delta + e\theta_a - d(0))\widetilde{v}''(0)v_0 = 2\lambda'(0)\int_\Omega v_0^2 - 2\int_\Omega v_0^3 - 2e\int_\Omega v_0^2 w_0.$

Since $(-\Delta + e\theta_a - d(0))$ is self-adjoint, (3.9) yields

(3.10) $\lambda'(0) = \int_\Omega v_0^3 + e\int_\Omega v_0^2 w_0.$

Let ϕ_0 be defined by $\phi_0 = [-\Delta + (2\theta_a - a)]^{-1}(\theta_a v_0)$. Then (3.10) may be expressed

(3.11) $\lambda'(0) = \int_\Omega v_0^3 - ec\int_\Omega v_0^2\phi_0.$

Since $v_0 > 0$ on Ω and $\int_\Omega v_0^2 = 1$, v_0 and consequently ϕ_0 are determined as functions of e. The following result is then an immediate corollary of formula (3.11).

THEOREM 3.1. *If* $e > 0$ *is given,* $\lambda'(0) = 0$ *if and only if*

(3.12) $c = \frac{1}{e}\int_\Omega v_0^3(e) / \int_\Omega v_0^2(e)\phi_0(e).$

We may give some further results on the sign of $\lambda'(0)$ in terms of c and e. From Lemma (1.2) $\lim_{e\to 0}\int_\Omega v_0^3(e) = \int_\Omega \gamma^3$ where $-\Delta\gamma = \lambda_1\gamma$, $\gamma > 0$ on Ω, and $\int_\Omega \gamma^2 = 1$. Furthermore, $\lim_{e\to 0}\int_\Omega v_0^2(e)\phi_0(e) = \int_\Omega \gamma^2[-\Delta + (2\theta_a - a)]^{-1}(\theta_a\gamma)$. Then $\lim_{e\to 0} e\int_\Omega v_0^2(e)\phi_0(e) = 0$. The following result obtains

THEOREM (3.2) *There exist* $e_0 \in (0,1)$ *such that* $0 < e < e_0$ *implies* $\int_\Omega v_0^3(e) > e\int_\Omega v_0^2(e)\phi_0(e)$. *Then if* $e \in (0,e_0)$ *and* $c \in (0,1)$, $\lambda'(0) > 0$.

Assume in that which follows that $e < 1$. Then

(3.13) $-\Delta v_0 + (2\theta_a - a)v_0 = (\lambda_1(e\theta_a) - a)v_0 + (2 - e)\theta_a v_0.$

From the definition of ϕ_0, it follows from (3.13) that

(3.14) $[-\Delta + (2\theta_a - a)](e\phi_0 + v_0) = (2\theta_a + \lambda_1(e\theta_a) - a)v_0.$

Since $e < 1$, $\lambda_1(e\theta_a) < a$. Hence

$$\begin{aligned} 0 \leqslant e\phi_0 + v_0 &= [-\Delta + (2\theta_a - a)]^{-1}(2\theta_a + \lambda_1(e\theta_a) - a)v_0 \\ &\leqslant [-\Delta + (2\theta_a - a)]^{-1}(2\theta_a v_0) \\ &= 2\phi_0. \end{aligned}$$

Thus $v_0 \leqslant (2 - e)\phi_0$. The following result now obtains.

THEOREM (3.3) *Suppose* $e < 1$ *and* $c > 2/e - 1$. *Then* $\lambda'(0) < 0$.

PROOF. $\lambda'(0) = \int_\Omega v_0^2[v_0 - ce\phi_0] \leqslant \int_\Omega v_0^2[(2 - e - ce)]\phi_0 < 0.$

4. Conclusions. As we noted in Section 1, if c and e are fixed positive constants, the region in a - d parameter space bounded by the curves $\Gamma_e = \{(a, \lambda_1(e\theta_a)): a \geqslant \lambda_1(0)\}$ and $\Gamma_c = \{(\lambda_1(c\theta_d), d): d \geqslant \lambda_1(0)\}$ is a region in which coexistence states for (1.4) exist. The estimates of Section 2 serve several purposes. First, they provide a computational estimate on this region of existence. For instance, if $c > 1$ and $e > 1$, Theorem 2.2 shows that region bounded by Γ_c and Γ_e is contained in the wedge in D (see Proposition 1.3) given by the lines $a = dc + (1 - c)\lambda_1(0)$ and $d = ae + (1 - e)\lambda_1(0)$. Theorem 2.2 also demonstrates that the region bounded by Γ_e and Γ_c does include, as should be expected, the regions of existence found in previous investigations. In the case $c < 1$ and $e < 1$, the region includes the region $\{(a,d): a = d, a > \lambda_1(0)\}$ found in [5] and the region $\{(a,d): a > \lambda_1(0) + dc, d > \lambda_1(0) + ae\}$ found in [11], [8]. If $c > 1$ and $e > 1$, the region of existence includes the diagonal again, as is also shown in [5].

Sharper necessary conditions for existence are provided by Theorem 2.3 in case $c < 1$ and $e < 1$. We may state this result as

THEOREM 4.1. *If* $c < 1$ *and* $e < 1$, *and* $a > \lambda_1(0)$ *and* $d > \lambda_1(0)$ *are such that* (1.4) *has a solution* (u,v) *with* $u > 0$ *and* $v > 0$ *on* Ω, *then*

$$d \geqslant [ae(1 - c) + \lambda_1(0)(1 - e)]/(1 - ce)$$

and

$$a \geqslant [dc(1 - e) + \lambda_1(0)(1 - c)]/(1 - ce).$$

Theorem 2.2 also shows that if the growth rates a and d are chosen so that $a > \lambda_1(0)$ and $d > \lambda_1(0)$, it is possible to c and e sufficiently small so that a coexistence state exists for (a,d).

If $c > 1$ and $e < 1$ or $c < 1$ and $e > 1$, the curves Γ_c and Γ_e both lie entirely on one side of the diagonal in the a - d plane. This result is consistent with Theorem 3.1 of [5]. The physical interpretation is that if one of the species affects the other sufficiently more strongly than it is itself affected, then the second species will be driven to extinction unless it compensates via a higher rate of reproduction.

In both [2] and [5], it is demonstrated in case $a = d$ and $c = e = 1$ that coexistence states are not unique. We use our information on the location of secondary bifurcation (in a - d space) to extend this biologically significant result. We first need the following lemma.

LEMMA 4.2. *Let* $c > 0$ *and* $e > 0$ *be fixed. Suppose* (a_n, d_n, u_n, v_n) *is a sequence of solutions to* (1.4) *with* $u_n > 0$ *and* $v_n > 0$ *such that* (a_n, d_n, u_n, v_n) *converges to* $(a, d, \theta_a, 0)$. *Then* $d = \lambda_1(e\theta_a)$.

PROOF. By (1.4),

$$\text{(4.1)} \quad \begin{aligned} -\Delta u_n &= a_n u_n - u_n^2 - c u_n v_n \\ -\Delta v_n &= d_n v_n - e u_n v_n - v_n^2. \end{aligned}$$

The second equation of (4.1) can be written as

$$\text{(4.2)} \quad (-\Delta + e u_n) v_n = d v_n - v_n^2.$$

Since $v_n > 0$, $\|v_n\|_{C_0^{1,\alpha}(\bar{\Omega})} > 0$. Hence

$$(-\Delta + e u_n) w_n = d_u w_n - w_n v_n,$$

where $w_n = v_n / \|v_n\|$. We have $(-\Delta + e u_n)^{-1}$ compact on $C_0^{1,\alpha}(\bar{\Omega})$ and

$$\text{(4.3)} \quad w_n = (-\Delta + e u_n)^{-1} [d_n w_n - w_n v_n].$$

Consider (4.3). Since $u_n \to \theta_a$ in $C_0^{1,\alpha}(\bar{\Omega})$ as $n \to \infty$, $(-\Delta + e u_n)^{-1} \to (-\Delta + e\theta_a)^{-1}$ as compact operators on $C_0^{1,\alpha}(\bar{\Omega})$. Standard compactness arguments now imply the existence of a $w \geqslant 0$, $\|w\|_{C_0^{1,\alpha}(\bar{\Omega})} = 1$ such that

$$\text{(4.4)} \quad w = d(-\Delta + e\theta_a)^{-1} w.$$

Equivalently,

$$-\Delta w = dw - e\theta_a w.$$

Hence $d = \lambda_1(e\theta_a)$.

THEOREM 4.3. *Suppose* $a_0 > \lambda_1(0)$ *and* $e_0 > 1$ *are fixed. Then there exists* $c_0 \in (0,1)$ *such that if* $\epsilon > 0$ *is given, there exists* $d^* \in (\lambda_1(e_0\theta_{a_0}) - \epsilon, \lambda_1(e_0\theta_{a_0}) + \epsilon)$ *such that* (1.4) *has at least two solutions with* $u > 0$ *and* $v > 0$ *in* Ω *for* $(a,d,c,e) = (a_0,d^*,c_0,e_0)$.

PROOF. Since $e_0 > 1$, we have that $\lambda_1(e_0\theta_{a_0}) > a_0$ and the point $(a_0,\lambda_1(e_0\theta_{a_0}))$ lies on the curve where bifurcation from the extinction states $(a,d,\theta_a,0)$ occurs. In fact, it is the only such point of the line $a = a_0$. Let $d_0 = \lambda_1(e_0\theta_{a_0})$. Then $\lambda_1(0) < a_0 < d_0$. Consider now the function $g(c) = \lambda_1(c\theta_{d_0})$, for $c \in [0,1]$. Then g is continuous on $[0,1]$ by Lemma 1.2(iv) and Theorem 2.2(i). Moreover, $g(0) = \lambda_1(0)$ and $g(1) = d_0$. Hence there exists $c_0 \in (0,1)$ such that $a_0 = \lambda_1(c_0\theta_{d_0})$. Since the function $d \to \lambda_1(c_0\theta_d)$ is strictly increasing in d for $d > \lambda_1(0)$, d_0 is the unique value of d for which $\lambda_1(c_0\theta_d) = a_0$. Consider (1.4) with $c = c_0$ and $e = e_0$. Thus results of [2] and Lemma 4.2 guarantee that if $a = a_0$ is held fixed, the continuum of positive solutions to (1.4) which emanate from the extinction states $(a_0,d,\theta_a,0)$ at $(a_0,\lambda_1(e_0\theta_{a_0}))$, which we denote by C, must meet the extinction states $(a_0,d,0,\theta_d)$ at a point $(\lambda_1(c_0\theta_d),d)$. By the choice of c_0, $d = d_0$. Hence $(a_0,d_0) = (a_0,\lambda_1(e_0\theta_{a_0})) = (\lambda_1(c_0\theta_{d_0}),d_0)$.

It is now easy to obtain the result. If there are distinct (u',v') and (u'',v'') with $u' > 0$, $u'' > 0$, $v' > 0$, $v'' > 0$ and (a_0,d_0,u',v'), $(a_0,d_0,u'',v'') \in C$, there is nothing to show. Assume then that there is at most one such solution to (1.4). There exists $\epsilon' \in (0,\epsilon)$ such that $C_1 = B((a_0,d_0,\theta_{a_0},0);\epsilon') \cap C$ and $C_2 = B((a_0,d_0,0,\theta_{d_0}):\epsilon') \cap C$ are disjoint, and, moreover, C_1 is an arc in $\{a_0\} \times R \times [C_0^{1,\alpha}(\bar{\Omega})]^2$ (here $B((a_0,d,u,v);\delta) = \{(a_0,d',u',v'): |d - d'| + \|u - u'\|_{C_0^{1,\alpha}(\bar{\Omega})} + \|v - v'\|_{C_0^{1,\alpha}(\bar{\Omega})} < \delta\}$). If the projections of C_1 and C_2 into R either both intersect $[d_0 - \epsilon', d_0)$ or $(d_0, d_0 + \epsilon']$, the result is established. Suppose with no loss of generality then that C_1 projects into $[d_0, d_0 + \epsilon']$ and C_2 projects into $[d_0 - \epsilon', d_0]$. Let $\bar{d} \in (d_0, d_0 + \epsilon']$ be such that $(a,\bar{d},\bar{u},\bar{v}) \in C_1$ for some $\bar{u} > 0$ and $\bar{v} > 0$. Since C_1 is an arc, there exists at least one solution to (1.4) in C_1 for each $d \in (d_0,\bar{d})$. However, since C is connected, $C_1 \cap C_2 = \emptyset$, and the projection of C_2 is contained in $[d_0 - \epsilon', d_0]$, there must also be a solution to (1.4) in $C \backslash C_1$ for each $d \in (d_0,\bar{d})$, which establishes the result.

Finally, we note that the results on the direction of bifurcation in Section 3 refine the analysis obtained in [2] by giving a more detailed picture near the bifurcation curves.

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University of Miami
Coral Gables, Florida 33124

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