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Bifurcation of steady-state solutions in predator-prey and competition systems

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Synopsis

We discuss steady-state solutions of systems of semilinear reaction-diffusion equations which model situations in which two interacting species u and v inhabit the same bounded region. It is easy to find solutions to the systems such that either u or v is identically zero; such solutions correspond to the case where one of the species is extinct. By using decoupling and global bifurcation theory techniques, we prove the existence of solutions which are positive in both u and v corresponding to the case where the populations can co-exist.

1. Introduction

The system of reaction-diffusion equations

$$\begin{aligned} u_t(x,t)-d_1\,\Delta u(x,t)&=a_1u-b_1u^2\pm c_1uv,\\ v_t(x,t)-d_2\,\Delta v(x,t)&=a_2v-b_2v^2\pm c_2uv, \end{aligned} \tag{1.1}$$

for $x\in D$ and $t\geqq 0$, where D denotes a bounded region in $\mathbb{R}^n$ $(n=1,2,3)$ and Δ denotes the Laplacian, models the situation where two species co-exist in D; $u(x,t)$ and $v(x,t)$ represent the population densities of the species at the time t and at a point $x\in D$. The constants $d_1, d_2>0$ give the rates at which the species diffuse. The constants a_1 and a_2 give, if positive, the net birth rates of the species and, if negative, the net death rates of the species. We shall assume throughout that the constants $b_1, b_2>0$; this assumption ensures that the species are self-limiting, i.e. u and v must remain bounded as $t\to\infty$. The signs of the constants c_1 and c_2 are determined by the nature of the interaction between the species; in the paper, we shall consider both the case where v preys on u and the case where u and v are competing species.

We discuss steady-state solutions of (1.1) satisfying homogeneous Dirichlet boundary conditions. We give a partial description of the structure of the non-negative solutions of

$$\begin{aligned} -d_1\,\Delta u&=a_1u-b_1u^2\pm c_1uv, \quad \text{for} \quad x\in D,\\ -d_2\,\Delta v&=a_2v-b_2v^2\pm c_2uv, \end{aligned} \tag{1.2}$$

$$u(x)=v(x)=0, \quad \text{for} \quad x\in\partial D. \tag{1.3}$$

Sub and supersolution techniques have recently been used by Leung [7], Zhou and Pao [11], Schiaffino and Tesei [10] to prove the existence of solutions to equations like (1.2)–(1.3). The above system has also been studied by Conway, Gardner and Smoller [4] in the case of a single space dimension. Our approach here produces similar but more unified results. We use a decoupling technique introduced by Brown [2] and discuss (1.2)–(1.3) by using bifurcation techniques. We regard all of the constants in the problem as fixed except for either a_1 or a_2 and we describe how the set of steady-state solutions changes as a_1 or a_2 changes.

Roughly speaking, our decoupling technique consists of fixing one of the functions, u say, solving with this fixed u the second equation in (1.2) for v to obtain a solution $v(u)$ and then substituting $v(u)$ for v in the first equation which can then be regarded as a single equation in u. This technique was used in [2] for the case of inhomogeneous boundary conditions; the technique is harder to apply here as the homogeneous boundary condition leads to the possibility that $v(u)$ might be the zero function and so a more careful analysis of solutions of a single equation is required. Section 2 is used to collect all the results we require about the solutions of a single equation. In Sections 3 and 4, we discuss cases where v preys on u regarding first a_2 and then a_1 as the bifurcation parameter. In Section 5, we discuss the case where u and v are competing species. Finally, in Section 6, we show how simple analogues of our results hold in the case of Neumann boundary conditions.

For simplicity, we work throughout with equations of the form (1.2) and Dirichlet boundary conditions. Our results, however, generalize to equations of the form

$$-d_1\,\Delta u = f(u, v); \quad -d_2\,\Delta v = g(u, v),$$

where f and g satisfy suitable hypotheses, and to mixed boundary conditions of the form $u + \alpha(\partial u/\partial n) = 0$ where $\alpha > 0$.

2. Non-negative solutions of single elliptic equations

In this section, we collect together some known results about single equations which are required later.

It is well known that the linear eigenvalue problem

$$-\Delta\phi = \lambda\phi \quad \text{on} \quad D; \quad \phi = 0 \quad \text{on} \quad \partial D,$$

has an infinite sequence of eigenvalues $\{\lambda_n\}$ such that $0 < \lambda_1 < \lambda_2 \leqq \lambda_3 \ldots$ with corresponding eigenfunctions $\phi_1, \phi_2, \phi_3, \ldots$ where $\phi_1(x) > 0$ for $x \in D$. Suppose that $q: D \to \mathbb{R}$ is smooth and that d is a positive real number. Then the linear eigenvalue problem

$$-d\,\Delta u + qu = \lambda u \text{ on } D; \quad u = 0 \text{ on } \partial D, \tag{2.1}$$

also has an infinite sequence of eigenvalues which are bounded below. We denote the lowest eigenvalue of (2.1) by $\lambda_1(d, q)$. It is known that $\lambda_1(d, q)$ is a simple eigenvalue and that the corresponding eigenfunctions do not change sign on D. Clearly, $\lambda_1(d, 0) = \lambda_1 d$ and $\lambda_1(d, q)$ is an increasing function of q.

Consider now the non-linear boundary value problem

$$-d\,\Delta u + qu = au - bu^2 \text{ on } D; \quad u = 0 \text{ on } \partial D, \tag{2.2}$$

where d and q are as above and a and b are real numbers with $b > 0$. It is known that, if $a \leqq \lambda_1(d, q)$, then $u = 0$ is the only non-negative solution of (2.2) whereas, if $a > \lambda_1(d, q)$, then (2.2) has a solution u which is positive on D. In the (a, u) plane, these positive solutions lie on a curve of solutions bifuracting from the zero solution at $(\lambda_1(d, q), 0)$. The existence of this positive solution can also be established by sub and supersolution techniques; a supersolution u is given by the constant function $u \equiv b^{-1}(|a| + \sup\{|q(x)|: x \in D\})$ and a subsolution is given by a sufficiently small multiple of the positive eigenfunction of (2.1) corresponding to $\lambda_1(d, q)$ (see Sattinger [9]). Since $u \to (au - bu^2)/u$ is a decreasing function, it follows that (see Cohen and Laetsch [3]), for each fixed $a > \lambda_1(d, q)$, there is a unique solution of (2.2) which is positive on D.

3. Predator-prey systems with a_2 as bifurcation parameter

Consider the system

$$\begin{aligned} -d_1 \Delta u &= a_1 u - b_1 u^2 - c_1 uv \text{ in } D, \\ -d_2 \Delta v &= a_2 v - b_2 v^2 + c_2 uv, \\ u &= v = 0 \text{ on } \partial D, \end{aligned} \tag{3.1}$$

where the constants $b_1, b_2, c_1, c_2 > 0$. Equation (3.1) arises from the situation in which the v population preys on the u population. We shall regard all the parameters to be fixed apart from a_2, the birth rate of the predator species, which we shall treat as a bifurcation parameter.

Our approach involves decoupling the two equations in (3.1) in the way in which we now describe. Let $v \in C^1(D)$ and consider the following equation for u:

$$-d_1 \Delta u = a_1 u - b_1 u^2 - c_1 uv \text{ in } D; \quad u = 0 \text{ on } \partial D. \tag{3.2}$$

We can write this as

$$-d_1 \Delta u + c_1 vu = a_1 u - b_1 u^2; \quad u = 0 \text{ on } \partial D, \tag{3.3}$$

which we can regard as a special case of (2.2) with $q = c_1 v$. Thus, if $a_1 \leqq \lambda_1(d_1, c_1 v)$, then (3.3) has no positive solution whereas, if $a_1 > \lambda_1(d_1, c_1 v)$, then (3.3) has a unique positive solution. We define a map from $C^1(D)$ to $C^1(D)$ by

$$\begin{aligned} u(v) &= 0 \quad \text{if} \quad a_1 \leqq \lambda_1(d_1, c_1 v) \\ &= \text{unique positive solution of (3.2) if } a_1 > \lambda_1(d_1, c_1 v). \end{aligned}$$

Clearly, $(u(v), v)$ will be a solution of the system (3.1) if v satisfies the single equation

$$-d_2 \Delta v = a_2 v - b_2 v^2 + c_2 u(v) v \text{ in } D; \quad v = 0 \text{ on } \partial D. \tag{3.4}$$

In order to investigate the solution of (3.4), we require the properties of $v \to u(v)$ given by the following lemma.

LEMMA 3.1. (i) *$v \to u(v)$ is a continuous function from $C^1(D)$ to $C^1(D)$;* (ii) *if $v_1 \geqq v_2$, then $u(v_1) \leqq u(v_2)$.*

Proof. (i) Let $v_n \to v$ in $C^1(D)$. In order to prove that $v \to u(v)$ is continuous, it suffices to prove that $u(v_n) \to u(v)$ in $C^1(D)$.

Since

$$\lambda_1(d_1, c_1 v) = \inf\left\{\int_D (|\text{grad } u|^2 + c_1 v u^2)\, dx \colon u \in H_1^0(D), \|u\|_{L_2} = 1\right\}$$

and

$$\lambda_1(d_1, c_1 v_n) = \inf\left\{\int_D (|\text{grad } u|^2 + c_1 v_n u^2)\, dx \colon u \in H_1^0(D), \|u\|_{L_2} = 1\right\}$$

and v_n converges uniformly to v on D, it follows that $\{\lambda_1(d_1, c_1 v_n)\}$ converges to $\lambda_1(d_1, c_1 v)$ as $n \to \infty$.

Firstly, suppose that $u(v)$ is non-zero. Then we must have that $a_1 > \lambda_1(d_1, c_1 v)$. Hence, when n is sufficiently large, $a_1 > \lambda_1(d_1, c_1 v_n)$ and so $u(v_n)$ is non-zero. Let ψ_n denote the positive eigenfunction of $-d_1 \Delta + c_1 v_n$ corresponding to the eigenvalue $\lambda_1(d_1, c_1 v_n)$ such that $\sup\{\psi(x)\colon x \in D\} = 1$. Then,

$$-d_1 \Delta u + c_1 v_n u = a_1 u - b_1 u^2 \text{ on } D; \quad u = 0 \text{ on } \partial D,$$

has a subsolution $b_1^{-1}(a_1 - \lambda_1(d_1, c_1 v_n))\psi_n$ and a supersolution given by any sufficiently large positive constant. Thus, $u(v_n)$ must be between these sub and supersolutions and so there must exist $\varepsilon > 0$ such that, for all sufficiently large n, $u(v_n) > \varepsilon b_1^{-1} \psi_n$. Therefore there exists, for sufficiently large n, an $x_n \in D$ such that $u(v_n)(x_n) > \varepsilon b_1^{-1}$. Hence, no subsequence of $\{u(v_n)\}$ can converge to the zero function.

Assume that $u(v_n)$ does not converge to $u(v)$ in $C^1(D)$; we shall obtain a contradiction. Then we can find a subsequence of $\{u(v_n)\}$, which we again denote by $\{u(v_n)\}$, lying outside a certain C^1 neighbourhood of $u(v)$. Since $\{v_n\}$ is uniformly bounded, there exists $k > 0$ such that $a_1 k - b_1 k^2 - c_1 k v_n(x) < 0$ for all n and all $x \in D$. Let $U = \{x \in D\colon u(v_n)(x) > k\}$. Since we have

$$-d_1 \Delta u(v_n) = a_1 u(v_n) - b_1[u(v_n)]^2 - c_1 u(v_n) v_n,$$

it follows that $-\Delta u(v_n)(x) < 0$ for $x \in U$. Hence, $u(v_n)$ must attain its maximum on $\bar{U}$ at a point on ∂U. However, $u(v_n)(x) = k$ on ∂U and so $u(v_n)(x) \leqq k$ for all $x \in D$. Thus, $\{u(v_n)\}$ is uniformly bounded. Hence, $a_1 u(v_n) - b_1[u(v_n)]^2 - c_1 u(v_n) v_n$ is uniformly bounded in $L_p(D)$ for any $p \geqq 1$. Thus, standard bootstrapping arguments applied to equation (3.2) show that $\{u(v_n)\}$ is uniformly bounded in $C^{2+\alpha}(D)$ and so possesses a subsequence, again denoted by $\{u(v_n)\}$, which converges in $C^2(D)$ to w say. Now $w \neq u(v)$ and w is not equal to the zero function but this is impossible as, letting $n \to \infty$ in (3.2), we can see that w must be a non-negative solution of

$$-d_1 \Delta w = a_1 w - b_1 w^2 - c_1 w v \text{ in } D; \quad w = 0 \text{ on } \partial D.$$

Hence, $\{u(v_n)\}$ must converge to $u(v)$ in $C^1(D)$ and so the proof is complete for the case where $u(v)$ is non-zero.

Now suppose that $u(v)$ is the zero function. Then the zero function is the unique non-negative solution of (3.2). Assume that $\{u(v_n)\}$ does not converge to the zero function in $C^1(D)$. Then there is a subsequence of $\{u(v_n)\}$, again denoted by $\{u(v_n)\}$, lying outside a certain C^1 neighbourhood of the zero function. Compactness and bootstrapping arguments like those used above show that

$\{u(v_n)\}$ possesses a subsequence which converges in $C^2(D)$ to w say. Now w cannot equal the zero function but must be a non-negative solution of (3.2), which is impossible. Hence, $\{u(v_n)\}$ must converge to the zero function in $C^1(D)$.

Thus the proof of (i) is complete.

(ii) Suppose $v_1 \geqq v_2$. There exists a constant $k > 0$ such that $a_1 - b_1 k - c_1 v_i(x) < 0$ for $x \in D$ and $i = 1, 2$. Then, for $i = 1, 2$, $u \equiv k$ is a supersolution of

$$-d_1 \Delta u = a_1 u - b_1 u^2 - c_1 u v_i \text{ in } D; \quad u = 0 \text{ on } \partial D.$$

If we choose $M > 0$ such that $u \to a_1 u - b_1 u^2 - c_1 v_i(x) u + Mu$ are increasing functions for $i = 1, 2$ and all $x \in D$, it is well known (see, e.g. Amann [**1**]) that $u(v_i)$ is the limit of the decreasing sequence $u_n^{(i)}$ which is defined inductively by $u_0^{(i)} \equiv k$ and

$$-d_1 \Delta u_{n+1}^{(i)} + M u_{n+1}^{(i)} = [a_1 - b_1 u_n^{(i)} - c_1 v^{(i)} + M] u_n^{(i)} \text{ in } D,\ u_{n+1}^{(i)} = 0 \text{ on } \partial D.$$

Since $v_1 \geqq v_2$, it follows from the maximum principle that $u_1^{(1)} \leqq u_1^{(2)}$ and, by induction, that $u_n^{(1)} \leqq u_n^{(2)}$ for all n. Thus, $u(v_1) \leqq u(v_2)$.

We now return to the study of (3.1). First we consider the case when a_1, the birth-rate of the prey, is small.

THEOREM 3.2. *Suppose $a_1 \leqq \lambda_1(d_1, 0)$ and (u, v) is a non-negative solution of* (3.1). *Then,*

(i) *u is the zero function,*

(ii) *if $a_2 \leqq \lambda_1(d_2, 0)$, v is also the zero function; if $a_2 > \lambda_1(d_2, 0)$, v is either the zero function or the unique positive solution of*

$$-d_2 \Delta v = a_2 v - b_2 v^2 \text{ in } D; \quad v = 0 \text{ on } \partial D. \tag{3.5}$$

Proof. On multiplying the first equation in (3.1) by u and integrating over D, we obtain

$$-d_1 \int_D \Delta u(x) u(x)\, dx \leqq a_1 \int_D u^2(x)\, dx - b_1 \int_D u^3(x)\, dx.$$

But, by the spectral theorem,

$$-d_1 \int_D \Delta u(x) u(x)\, dx \geqq \lambda_1(d_1, 0) \int_D u^2(x)\, dx$$

and so we must have that u is the zero function.

Since u is the zero function, v must satisfy (3.5) and so statement (ii) follows from the discussion in Section 2 about the solutions of a single equation.

Now suppose that $a_1 > \lambda_1(d_1, 0)$. Then, (3.1) has solutions $(0, 0)$ and $(u(0), 0)$ for all values of a_2. We shall seek values of a_2 which correspond to bifurcation points from the line of solutions $(u(0), 0)$. It is straightforward to carry out a bifurcation analysis directly on (3.1) but this yields only local results. We shall instead discuss the decoupled equations as we are then able to apply results from global bifurcation theory to equation (3.4).

Let L be the differential expression defined by

$$Lv = -d_2 \Delta v - c_2 u(0) v.$$

We assume without loss of generality that L is invertible, i.e. that

$\lambda_1(d_2, -c_2u(0)) \neq 0$. (Otherwise, we replace L by $L+k$ so that $L+k$ is invertible and write (3.4) as

$$(L+k)v = av - b_2v^2 + c_2[u(v) - u(0)]v,$$

where $a = a_2 + k$, and then argue as below.) Then it is well known that the equation

$$Lu = f \text{ on } D; \quad u = 0 \text{ on } \partial D,$$

has a unique solution for all $f \in L^2(D)$; if we denote this unique solution by Kf, then $K: L^2(D) \to L^2(D)$ (and $K: C^1(D) \to C^1(D)$) is a compact linear operator.

Let $F: C^1(D) \to C^1(D)$ be defined by

$$F(v) = -b_2v^2 + c_2[u(v) - u(0)]v.$$

Then F is continuous and, by Lemma 3.1(i), we see that $\|F(v)\| = o(\|v\|)$ as $v \to 0$ in $C^1(D)$ where $\| \ \|$ denotes the norm in $C^1(D)$.

We may write (3.4) as

$$v = a_2Kv + KFv. \tag{3.6}$$

Since $\|KFv\| = o(\|v\|)$ as $v \to 0$ in $C^1(D)$, the well known bifurcation results of Crandall and Rabinowitz [**5**] and Rabinowitz [**8**] can be applied to (3.6). Since $a_2 = \lambda_1(d_2, -c_2u(0))$ is a simple characteristic value of K, bifurcation occurs at this value of a_2 and in a neighbourhood of the bifurcation point all non-trivial solutions (a, v) of (3.6) lie on a curve in $\mathbb{R} \times C^1(D)$ of the form $\{(a(\alpha), \psi(\alpha)): -\varepsilon \leqq \alpha \leqq \varepsilon\}$ where $a(0) = \lambda_1(d_2, -c_2u(0))$ and $\psi(\alpha) = \alpha\psi_1 +$ terms of higher order in α where ψ_1 is a positive eigenfunction of L corresponding to $\lambda_1(d_2, -c_2u(0))$. Thus, for α sufficiently small and positive, the corresponding non-trivial solutions v lie in the cone

$$P = \left\{v \in C^1(D): v(x) > 0 \text{ for } x \in D; \frac{\partial u}{\partial n}(x) < 0 \text{ for } x \in \partial D\right\}.$$

Moreover, there exists a connected set of non-trivial solutions of (3.6) denoted by S such that either S joins $(\lambda_1(d_2, -c_2u(0)), 0)$ to ∞ in $\mathbb{R} \times C^1(D)$ or S joins $(\lambda_1(d_2, -c_2u(0)), 0)$ to $(b, 0)$, where b is some other characteristic value of K. In addition, S has a connected subset $S^+ \subset S - \{(a(\alpha), \psi(\alpha)): -\varepsilon \leqq \alpha \leqq 0\}$ such that S^+ also satisfies one of the above alternatives. Clearly, solutions (a_2, v) in S^+ sufficiently close to the bifurcation point lie in the cone $\mathbb{R} \times P$. In fact, more can be proved.

THEOREM 3.3. (i) *The connected family of solutions S^+ is contained in $\mathbb{R} \times P$.* (ii) $\{\lambda \in \mathbb{R}: (\lambda, v) \in S^+\} = (\lambda_1(d_2, -c_2u(0)), \infty)$.

Proof. (i) Suppose that S^+ is not contained in $\mathbb{R} \times P$. Then there exists $(\lambda_0, v_0) \in S^+ \cap (\mathbb{R} \times \partial P)$ such that $(\lambda_0, v_0) \neq (\lambda_1(d_2, -c_2u(0)), 0)$ and (λ_0, v_0) is the limit of a sequence $\{(\lambda_n, v_n)\}$ contained in $S^+ \cap (\mathbb{R} \times P)$. Choose $M > 0$ such that $\lambda_0 - b_2v_0 + c_2(u(v_0) - u(0)) + M > 0$ and $M - c_2u(0) > 0$ for all $x \in D$. Then, as v_0 satisfies

$$(L+M)v_0 = (\lambda_0 - b_2v_0 + c_2(u(v_0) - u(0)) + M)v_0, \quad \text{for} \quad x \in D,$$

we have that

$$(L+M)v_0(x) \geqq 0, \quad \text{for} \quad x \in D. \tag{3.7}$$

Since $v_0 \in \partial P$, either v_0 has an interior zero in D or $\partial v_0/\partial n$ has a zero on ∂D. Hence, it follows from (3.7) and the strong maximum principle that $v_0 \equiv 0$. Thus, $(\lambda_0, 0)$ is a bifurcation point of (3.6). Hence, λ_0 must be an eigenvalue of $-d_2\,\Delta u - c_2 u(0)$; but, since close to a bifurcation point all bifurcating solutions have the same nodal behaviour as the corresponding eigenfunctions and $v_n \geqq 0$ for all n, it follows that $\lambda_0 = \lambda_1(d_2, -c_2 u(0))$, which is a contradiction. Hence, S^+ is contained in $\mathbb{R} \times P$.

(ii) Let $(\lambda, v) \in S^+$. We have that

$$Lv = \lambda v - b_2 v^2 + c_2[u(v) - u(0)]v \text{ in } D. \tag{3.8}$$

Since $v \geqq 0$, $u(v) \leqq u(0)$. Thus, multiplying both sides of (3.8) by v and integrating over D and using the spectral theorem as in the proof of Theorem 3.2 shows that $\lambda \geqq$ least eigenvalue of L, i.e. $\lambda \geqq \lambda_1(d_2, -c_2 u(0))$.

It remains to prove that S^+ cannot approach ∞ for any finite value of λ; we achieve this by obtaining an *a priori* bound for the solutions of (3.6). Suppose (a_2, v) lies on S^+. Choose $M(a_2)$ such that $a_2 v - b_2 v^2 + c_2 u(0)v < 0$ whenever $v > M(a_2)$. Let $U = \{x \in D: v(x) > M(a_2)\}$. Then,

$$-d_2\,\Delta v = a_2 v - b_2 v^2 + c_2 u(v)v \leqq a_2 v - b_2 v^2 + c_2 u(0)v \leqq 0, \quad \text{for} \quad x \in U.$$

Since $v(x) = M(a_2)$ for $x \in \partial U$, it follows from the maximum principle that $v(x) \leqq M(a_2)$ for $x \in U$. Hence, $v(x) \leqq M(a_2)$ for all $x \in D$. Thus, the right hand side of equation (3.4) is bounded in $C(D)$, the constant being dependent on a_2, and so standard bootstrapping argument show that there exists $K(a_2) > 0$ such that $\|v\| < K(a_2)$ where $\|\ \|$ denotes the $C^1(D)$ norm.

Thus, if $\{\lambda: (\lambda, v) \in S^+\}$ were bounded, S^+ would be bounded in $\mathbb{R} \times C^1(D)$, which is impossible. Hence, $\{\lambda: (\lambda, v) \in S^+\}$ is unbounded and so, since this set is also connected, it must equal $(\lambda_1(d_2, -c_2 u(0)), \infty)$. This completes the proof.

Theorem 3.3 shows the existence of S^+, an unbounded continuum of non-trivial solutions of equation (3.6). Close to the bifurcation point $(\lambda_1(d_2, -c_2 u(0)), 0)$, v is small and positive so that $u(v)$ is also positive. As a_2 increases, v may increase and so $u(v)$ may become equal to the zero function, i.e. a non-trivial solution v of equation (3.6) may correspond to a solution (u, v) of the system (3.1) with $u = 0$. The next theorem shows that, for sufficiently large a_2, the non-trivial solution of (3.6) must correspond to a trivial solution of (3.1).

THEOREM 3.4. *For every fixed value of a_1, there exists $K > 0$ such that, whenever $a_2 > K$, there are no solutions (u, v) of* (3.1) *with u and v both positive.*

Proof. Let (u, v) be any non-negative solution of (3.1). Suppose that $v \neq 0$. Then, v is the unique positive solution of the equation

$$-d_2\,\Delta v - c_2 uv = a_2 v - b_2 v^2 \text{ in } D; \quad v = 0 \text{ on } \partial D. \tag{3.9}$$

Let λ_1 denote the least eigenvalue and let ϕ_1 denote the corresponding eigenfunction of $-\Delta$ with Dirichlet boundary conditions such that $\max\{\phi_1(x): x \in D\} = 1$. It is easy to check that $b_2^{-1}(a_2 - d_2\lambda_1)\phi_1$ is a subsolution for (3.9) provided $a_2 > d_2\lambda_1$

and that any sufficiently large positive constant is a supersolution. Hence, if $a_2 > d_2\lambda_1$, we must have that $v \geqq b_2^{-1}(a_2 - d_2\lambda_1)\phi_1 = k(a_2)\phi_1$ where $k(a_2) \to \infty$ as $a_2 \to \infty$.

Now consider the linear eigenvalue problem

$$-d_1\,\Delta u + c_1 k(a_2)\phi_1 u = \lambda u \text{ in } D; \quad u = 0 \text{ on } \partial D. \tag{3.10}$$

Let $\mu_1(a_2)$ denote the least eigenvalue of (3.10). Then,

$$\mu_1(a_2) = \inf\left\{\int_D (d_1|\text{grad } u|^2 + c_1 k(a_2)\phi_1 u^2)\,dx : u \in H_1^0(D), \|u\|_{L_2} = 1\right\}.$$

We now show that $\mu_1(a_2) \to \infty$ as $a_2 \to \infty$. Suppose otherwise. Then there exists a sequence $\{u_n\} \subseteq H_1^0(D)$ such that $\int u_n^2\,dx = 1$, $\int_D |\text{grad } u_n|^2\,dx$ is uniformly bounded and $\int_D \phi_1 u_n^2\,dx \to 0$ as $n \to \infty$. Since $\{u_n\}$ is a bounded sequence in $H_1^0(D)$ and $H_1^0(D)$ can be embedded compactly in $L_2(D)$, there exists a subsequence which we again denote by $\{u_n\}$ such that $\{u_n\}$ converges to u_0 in $L_2(D)$. Thus, $\int_D \phi_1 u_0^2\,dx = 0$ and so u_0 must be the zero function; since we must also have $\int u_0^2\,dx = 1$, this is impossible and so $\mu_1(a_2) \to \infty$ as $a_2 \to \infty$.

Suppose a_2 is chosen sufficiently large so that $\mu(a_2) > a_1$. Then the smallest eigenvalue of

$$-d_1\,\Delta\phi + cv\phi = \lambda\phi \text{ in } D; \quad \phi = 0 \text{ on } \partial D$$

is greater than a_1 and so the only non-negative solution of

$$-d_1\,\Delta u + cvu = a_1 u - b_1 u^2 \text{ in } D; \quad u = 0 \text{ on } \partial D$$

is the zero function, i.e. if a_2 is chosen sufficiently large and $v \not\equiv 0$, we must have that $u \equiv 0$ and so the proof is complete.

We can now give a reasonable description of the bifurcation diagram in the $a_2-(u, v)$ plane. The only way in which the continuum of solutions S^+ for equation (3.6) can join the bifurcation point $(\lambda_1(d_2, -c_2 u(0)), 0)$ to ∞ is by $u(v)$ becoming equal to zero for a_2 sufficiently large. If, however, $u(v) \equiv 0$, then v must be a solution of

$$-d_2\,\Delta v = a_2 v - b_2 v^2 \text{ in } D; \quad v = 0 \text{ on } \partial D.$$

Thus, the continuum of solutions of system (3.1) $\{(a_2, u(v), v) : (a_2, v) \in S^+\}$ must join up with the continuum of solutions $\{(a_2, 0, v) : (a_2, v)$ is a solution of (3.5)$\}$ discussed in Theorem 3.2(ii).

It is not clear that there is a unique solution which is positive in both components and so kinks may be possible in the continuum of solutions positive in both components. The above discussion on global bifurcation, however, does lead to the following result.

THEOREM 3.5 (i) *There exists* $\lambda^* > \lambda_1(d_2, 0)$ *such that, for all* $a_2 \in (\lambda_1(d_2, -c_2 u(0)), \lambda^*)$, *system* (3.1) *has at least one solution* (u, v) *which is positive in both components.*
(ii) *There exists* $\hat{\lambda} \geqq \lambda^*$ *such that, for all* $a_2 > \hat{\lambda}$, *every non-negative solution* (u, v) *of system* (3.1) *has at least one component identically equal to zero.*

The above results are natural from the ecological point of view. If the birth-rate of the predator is too low ($<\lambda_1(d_2, -c_2u(0))$), then it is impossible for the predator to survive. Note, however, that the above birth-rate is lower than that required for the predator to survive in the absence of prey (i.e. $\lambda_1(d_2, 0)$). If the birth-rate of the predator is too high ($>\hat{\lambda}$), then the prey cannot survive in the presence of the predator. Theorem 3.5 guarantees the existence of a range of predator birth-rates for which prey and predator can co-exist.

4. Predator-prey systems with a_1 as bifurcation parameter

We again study system (3.1) but this time we fix all the parameters except for a_1, the birth-rate of the prey, which we treat as a bifurcation parameter. We now decouple the equations by fixing u and solving for v. Let $u \in C^1(D)$ and consider the following equation for v:

$$-d_2\,\Delta v = a_2v - b_2v^2 + c_2uv \text{ in } D; \quad v = 0 \text{ on } \partial D,$$

which can be rewritten as

$$-d_2\,\Delta v - c_2uv = a_2v - b_2v^2 \text{ in } D; \quad v = 0 \text{ on } \partial D. \tag{4.1}$$

The above equation has a unique positive solution if $a_2 > \lambda_1(d_2, -c_2u)$ but otherwise the only non-negative solution of (4.1) is the zero function. We define a map from $C^1(D)$ to $C^1(D)$ by

$$\begin{aligned} v(u) &= 0 \quad \text{if} \quad a_2 \leqq \lambda_1(d_2, -c_2u) \\ &= \text{unique positive solution of (4.1) if } a_2 > \lambda_1(d_2, -c_2u). \end{aligned}$$

By using the same methods as used on $v \to u(v)$ in Lemma 3.1, it can be proved that $u \to v(u)$ is a continuous function from $C^1(D)$ to $C^1(D)$ and that $u \to v(u)$ is an increasing function.

Consider a_2 to be fixed. For all values of a_1, system (3.1) has the solution $u = 0$, $v = 0$. When $a_1 = \lambda_1(d_1, 0)$, there bifurcates from this zero solution a continuum of solutions (a_1, u, v) with $v = 0$ and $u = u(0)$ where $u(0)$ is the solution of (3.2) when $v = 0$; note that $u(0)$ depends on a_1. The discussion in Section 2 shows that bifurcation is to the right of $\lambda_1(d_1, 0)$ and the continuum of solutions extends from $a_1 = \lambda_1(d_1, 0)$ to $a_1 = \infty$.

Now suppose $a_2 > \lambda_1(d_2, 0)$. Then system (3.1) also has a solution $(a_1, 0, v(0))$ where $v(0)$ is the solution of (4.1) when $u = 0$. Arguments similar to those of Section 3 show that, when $a_1 = \lambda_1(d_1, c_1v(0))$, there bifurcates from this branch of solutions a continuum of solutions of the form (a_1, u, v) where $v = v(u)$ and u satisfies

$$-d_1\,\Delta u = a_1u - b_1u^2 - c_1v(u)u \text{ in } D; \quad u = 0 \text{ on } \partial D. \tag{4.2}$$

As before, it can be shown that there exists a continuum of solutions S^+ of (4.2), that S^+ is contained in $\mathbb{R} \times P$, i.e. $u \geqq 0$ whenever $(a_1, u) \in S^+$ and that $\{a_1: (a_1, u) \in S^+\} = (\lambda_1(d_1, c_1v(0)), \infty)$. If $(a_1, u) \in S^+$, then $u \geqq 0$ and so $v(u) \geqq v(0)$, i.e. $v(u)$ is not identically zero. Hence, the continuum of solutions of the system (3.1) $\{(a_1, u, v(u)): (a_1, u) \in S^+\}$ cannot meet the continuum of solutions $\{(a_1, u(0), 0): a_1 > \lambda_1(d_1, 0\}$. Thus, consideration of the bifurcation diagram leads to the following result.

THEOREM 4.1. *Suppose* $a_2 > \lambda_1(d_2, 0)$. *The system* (3.1) *has a solution which is positive in both components provided that* $a_1 > \lambda_1(d_1, c_1 v(0))$.

Now suppose that we fix $a_2 \leqq \lambda_1(d_2, 0)$. We cannot obtain existence results on non-trivial solutions directly by using bifurcation theory but we can proceed indirectly by using our previous results.

THEOREM 4.2. *Suppose* $a_2 \leqq \lambda_1(d_2, 0)$. *Then, provided* a_1 *is sufficiently large, system* (3.1) *has a solution which is positive in both components.*

Proof. We have that $u(0)$ satisfies the equation

$$-d_1 \Delta u = a_1 u - b_1 u^2 \text{ in } D; \quad u = 0 \text{ on } \partial D.$$

Since the constant function a_1/b_1 is a supersolution and $b_1^{-1}(a_1 - \lambda_1 d_1)\phi_1$, where λ_1 is the least eigenvalue and ϕ_1 is the principal eigenfunction of $-\Delta$ with $\max \phi_1(x) = 1$, is a subsolution of the above equation, it follows that $b_1^{-1}(a_1 - \lambda_1 d_1)\phi_1 \leqq u(0) \leqq a_1 b_1^{-1}$.

It follows from an argument similar to that used in the proof of Theorem 3.4 that $\lambda_1(d_2, -c_2 u(0)) \to -\infty$ as $a_1 \to \infty$. Hence, for a_1 sufficiently large, we have that $\lambda_1(d_2, -c_2 u(0)) < a_2 \leqq \lambda_1(d_2, 0)$ and so it follows from our previous results (see Theorem 3.5(i)) that system (3.1) has a solution which is positive in both components.

Since $u(0)$ is a non-straightforward function of a_1, there seems to be no direct way of carrying out a bifurcation analysis of the branch of trivial solutions $\{(a_1, u(0), 0): a_1 > \lambda_1(d_1, 0)\}$. However, the next theorem indicates that the non-trivial solutions whose existence is established in Theorem 4.2 bifurcate from this branch.

THEOREM 4.3. *Suppose* $a_2 < \lambda_1(d_2, 0)$. *Then* $(u(0), 0)$ *is a stable solution of* (3.1) *when* a_1 *is sufficiently close to* $\lambda_1(d_1, 0)$ *but* $(u(0), 0)$ *is an unstable solution of* (3.1) *when* a_1 *is sufficiently large.*

Proof. The principle of linearized stability holds for (3.1) (see Henry **[6]**). Thus, if we define the linear operator $L: C_0^{2+\alpha}(D) \times C_0^{2+\alpha}(D) \to C^\alpha(D) \times C^\alpha(D)$ by

$$L\begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} -d_1 \Delta u - a_1 u + 2b_1 u(0) u + c_1 u(0) v \\ -d_2 \Delta v - a_2 v - c_2 u(0) v \end{pmatrix},$$

where $C_0^{2+\alpha}(D) = \{u \in C^{2+\alpha}(D): u(x) = 0 \text{ for } x \in \partial D\}$, we have that $(u(0), 0)$ is stable if the spectrum of L lies entirely in the right half-plane and $(u(0), 0)$ is unstable if L has negative eigenvalues.

First we examine the linear operator $L_1: C_0^{2+\alpha}(D) \to C^\alpha(D)$ defined by $L_1(u) = -d_1 \Delta u - a_1 u + 2b_1 u(0) u$. It is well known that the spectrum of L_1 consists entirely of eigenvalues. Since

$$-d_1 \Delta u(0) - a_1 u(0) + b_1 [u(0)]^2 = 0,$$

we have

$$-d_1 \Delta u(0) - [a_1 - b_1 u(0)] u(0) = 0. \tag{4.3}$$

Since $u(0)$ is positive, (4.3) shows that 0 is the principal eigenvalue of $-d_1 \Delta - a_1 + b_1 u(0)$ and so all the eigenvalues of $-d_1 \Delta - a_1 + 2b_1 u(0)$ are positive. Thus, the spectrum of L_1 lies entirely in the right half-plane.

Suppose that λ is an eigenvalue of L. Then

$$-d_1\,\Delta u - a_1 u + 2b_1 u(0)u + c_1 u(0)v = \lambda u,$$
$$-d_2\,\Delta v - a_2 v - c_2 u(0)v = \lambda v, \tag{4.4}$$

for u, v not both identically zero.

Suppose $\lambda \leqq 0$. We shall show that, when a_1 is sufficiently close to $\lambda_1(d_1, 0)$, this leads to a contradiction. Since the solution $u(0)$ bifurcates from zero solution when $a_1 = \lambda_1(d_1, 0)$, we can make the sup norm of $u(0)$ as small as we please by making a_1 sufficiently close to $\lambda_1(d_1, 0)$. Since $a_2 < \lambda_1(d_2, 0)$, all the eigenvalues of $-d_2\,\Delta - a_2$ are positive. Hence, when a_1 is sufficiently close to $\lambda_1(d_1, 0)$, all the eigenvalues of $-d_2\,\Delta - a_2 - c_2 u(0)$ are positive. Thus, for a_1 close to $\lambda_1(d_1, 0)$, the second equation in (4.4) implies that $v = 0$. Then, since all eigenvalues of $-d_1\,\Delta - a_1 + 2b_1 u(0)$ are positive, the first equation in (4.4) implies that $u = 0$ which is a contradiction. Hence for a_1 sufficiently close to $\lambda_1(d_1, 0)$, all eigenvalues of (4.4) are positive and so $(u(0), 0)$ is stable.

Since $b_1^{-1}(a_1 - \lambda_1 d_1)\phi_1 \leqq u(0) \leqq b_1^{-1} a_1$, it follows as in the proof of Theorem 3.4 that the least eigenvalue of $-d_2\,\Delta - a_2 - c_2 u(0)$ goes to $-\infty$ as $a_1 \to \infty$. Hence, for a_1 sufficiently large, the least eigenvalue λ_0 (say) of $-d_2\,\Delta - a_2 - c_2 u(0)$ is negative; let v_0 denote the corresponding eigenfunction. Then, since the spectrum of $-d_1\,\Delta - a_1 + 2b_1 u(0)$ lies in the right half-plane, the equation

$$-d_1\,\Delta u - a_1 u + 2b_1 u(0)u - \lambda_0 u = -c_1 u(0)v_0$$

has a solution. Hence, λ_0 is an eigenvalue of (4.4), and, since $\lambda_0 < 0$, $(u(0), 0)$ is an unstable solution of (3.1).

The fact demonstrated in Theorems 4.1, 4.2 and 4.3 that prey and predator can co-exist provided the prey birth-rate is sufficiently high agrees with what is suggested by the ecological considerations that the high birth-rate enables the prey and hence the predator to survive.

5. Systems of competing species

We now consider the system which arises when u and v correspond to competing species, viz,

$$\begin{aligned} -d_1\,\Delta u &= a_1 u - b_1 u^2 - c_1 uv \text{ in } D; \quad u = 0 \text{ on } \partial D,\\ -d_2\,\Delta v &= a_2 v - b_2 v^2 - c_2 uv \text{ in } D; \quad v = 0 \text{ on } \partial D, \end{aligned} \tag{5.1}$$

where $b_1, c_1, b_2, c_2 > 0$. As in the previous section, the equations can be decoupled; this leads to the functions $u(v)$, respectively $v(u)$, the maximal non-negative solutions of the first and second equations of (5.1) for fixed v, respectively fixed u. We shall fix a_1 and treat a_2 as a bifurcation parameter. Arguments similar to those used in the proof of Theorem 3.2 lead to the following result which describes the situation where a_1 is small.

THEOREM 5.1. *Suppose* $a_1 \leqq \lambda_1(d_1, 0)$. Then,
(i) $(0, 0)$ *is the only non-negative solution of* (5.1) *if* $a_2 \leqq \lambda_1(d_2, 0)$.
(ii) $(0, 0)$ *and* $(0, v(0))$ *are the only non-negative solutions of* (5.1) *if* $a_2 > \lambda_1(d_2, 0)$.

In fact, the curve of solutions S of the form $(a_2, 0, v(0))$ bifurcates from the curve corresponding to the zero solution at $a_2 = \lambda_1(d_2, 0)$; bifurcation is to the right and $\{a: (a, 0, v(0)) \in S\} = [\lambda_1(d_2, 0), \infty)$.

Now suppose that $a_1 > \lambda_1(d_1, 0)$. Then, for all values of a_2, we have the solution $(u(0), 0)$ of (5.1) and we can investigate bifurcation from this branch by considering the equation

$$-d_2\,\Delta v = a_2 v - b_2 v^2 - c_2 u(v) v \text{ in } D; \quad v = 0 \text{ on } \partial D. \tag{5.2}$$

Bifurcation occurs when $a_2 = \lambda_1(d_2, c_2 u(0))$. As in Section 3, it can be shown that there exists a continuum S^+ of solutions (a_2, v) of (5.2) such that $v > 0$ for all $v \in S^+$ and S^+ intersects with the curve corresponding to the zero solution only when $a_2 = \lambda_1(d_2, c_2 u(0))$.

On multiplying (5.2) by v and integrating by parts, we obtain that $a_2 > \lambda_1(d_2, 0)$ for all a_2 such that $(a_2, v) \in S^+$. Also, a maximum principle argument similar to that used in the proof of Theorem 3.3 (ii) shows that $v < a_2/b_2$ for all such v such that $(a_2, v) \in S^+$ and so, by bootstrapping arguments, for all a_2, there exists $M(a_2) > 0$ such that $\|v\| \leqq M(a_2)$ whenever $(a_2, v) \in S^+$ where $\| \ \|$ denotes the norm in $C^1(D)$. Since S^+ connects $(\lambda_1(d_2, c_2 u(0)), 0)$ with ∞ in $C^1(D)$, it follows that $\{a_2: (a_2, v) \in S^+\} \supseteq (\lambda_1(d_2, c_2 u(0)), \infty)$.

A theorem analogous to Theorem 3.4 again holds for this case, i.e. there exists $K > 0$ such that, if $a_2 > K$, then all solutions (u, v) of (5.1) have at least one component identically equal to zero. The only change required in the proof is that λ_1 and ϕ_1, the least eigenvalue and principal eigenfunction of the Laplacian, must be replaced by the least eigenvalue and principal eigenfunction of

$$-d_2\,\Delta\phi + c_2 u(0)\phi = \lambda\phi \text{ in } D; \quad \phi = 0 \text{ on } \partial D,$$

in order to obtain a subsolution which gives a lower bound for v in terms of a_2. Thus, as in the predator-prey case, the continuum of solutions $\{(a_2, u(v), v): v \in S^+\}$ which emanates from the continuum of trivial solutions of the form $(a_2, u(0), 0)$ must join up with the continuum of trivial solutions of the form $(a_2, 0, v(0))$.

The above results can be summarized as follows.

THEOREM 5.2. *Suppose $a_1 > \lambda_1(d_1, 0)$. There exist numbers μ_1, μ_2, μ_3 such that $\lambda_1(d_2, 0) < \mu_1 \leqq \mu_2 < \mu_3$ and*
(i) *whenever $\mu_1 \leqq a_2 \leqq \mu_2$, system* (5.1) *has at least one solution (u, v) which is positive in both components;*
(ii) *whenever $a_2 > \mu_3$, every non-negative solution (u, v) of system* (5.1) *has at least one component identically equal to zero.*

We do not know the direction of the bifurcation of the branch of non-trivial solutions from the trivial branches where at least one component is identically zero. This direction will depend in general on the relative sizes of b_1, b_2, c_1 and c_2. However, we have obtained the ecologically reasonable result that in order for the competing species to co-exist then the birth-rates must satisfy $a_1 > \lambda_1(d_1, 0)$ and $a_2 > \lambda_1(d_2, 0)$, i.e. the birth-rates of the species must be greater than the birth-rates required for the existence of either species in the absence of the other but, if the birth-rate of one species is too big relative to the birth-rate of the other species, then co-existence is impossible.

Finally, in this section, we discuss an example where it is possible to give a reasonably precise description of the continuum of solutions where neither component is identically zero. Consider the following special system

$$\begin{aligned} -\Delta u &= (a_1 - bu - cv)u \text{ in } D; \quad u = 0 \text{ on } \partial D, \\ -\Delta v &= (a_2 - cv - bu)v \text{ in } D; \quad v = 0 \text{ on } \partial D. \end{aligned} \tag{5.3}$$

If $a_1 = a_2 = a$, then system (5.3) has a solution of the form $v = \alpha u$ provided that u satisfies the single equation

$$-\Delta u = (a - (b + \alpha c)u)u \text{ in } D; \quad u = 0 \text{ on } \partial D. \tag{5.4}$$

For any fixed $\alpha, 0 < \alpha < \infty$, equation (5.4) has a unique positive solution $u(\alpha)$ provided that $a > \lambda_1$ where λ_1 denotes the least eigenvalue of $-\Delta$ with zero boundary conditions on D. When $\alpha = 0$, we obtain the solution $u(0)$ (using the same notation as earlier in the section). Since $u(\alpha) \leqq a/(b + \alpha c)$, it follows that $\lim_{\alpha \to \infty} u(\alpha) = 0$. Arguments similar to those used in Lemma 3.1 show that $\alpha \to u(\alpha)$ is a continuous mapping from $\mathbb{R}$ to $C^1(D)$.

Now suppose that (u, v) is any solution of (5.3) such that u and v are positive on D. Then u satisfies

$$[-\Delta + q(x)]u = a_1 u \text{ on } D; \quad u = 0 \text{ on } \partial D$$

and v satisfies

$$[-\Delta + q(x)]v = a_2 v \text{ on } D; \quad v = 0 \text{ on } \partial D,$$

where $q(x) = bu(x) + cv(x)$. Since u and v are eigenfunctions of $-\Delta + q(x)$ which do not change sign on D, they must both be eigenfunctions which correspond to the least eigenvalue of $-\Delta + q(x)$ and so $a_1 = a_2$. Moreover, as the least eigenvalue of $-\Delta + q(x)$ is simple, it follows that $v = \alpha u$ for some number $\alpha > 0$.

Now fix $a_1 > \lambda_1$ and consider the bifurcation diagram in the $a_2 - (u, v)$ plane. Solutions which are not identially zero in either component can exist only when $a_2 = a_1$ and so the continuum of non-trivial solutions joining the branch of trivial solutions of the form $(a_2, u(0), 0)$ with the branch of trivial solutions of the form $(a_2, 0, v(0))$ is $\{(a_1, u(\alpha), \alpha u(\alpha)) : \alpha > 0\}$.

6. Neumann boundary conditions

Finally, we show that the results of the previous section are very easy to establish when the Dirichlet boundary condition is replaced by a Neumann boundary condition as it is then possible to discuss positive spatially homogeneous solutions by very elementary methods.

First consider the case where u and v are competing species, i.e. the following system of equations is satisfied:

$$\begin{aligned} -d_1 \Delta u &= a_1 u - b_1 u^2 - c_1 uv \text{ in } D; \quad \frac{\partial u}{\partial n} = 0 \text{ on } \partial D, \\ -d_2 \Delta v &= a_2 v - b_2 v^2 - c_2 uv \text{ in } D; \quad \frac{\partial v}{\partial n} = 0 \text{ on } \partial D. \end{aligned} \tag{6.1}$$

Spatially homogeneous solutions of (6.1) are given by solutions of the algebraic equations

$$\begin{aligned}(a_1 - b_1 u - c_1 v)u &= 0,\\ (a_2 - b_2 v - c_2 u)v &= 0.\end{aligned} \tag{6.2}$$

Note that the least eigenvalue of the linear problem

$$-d_1\,\Delta\phi = \lambda\phi \text{ in } D;\quad \frac{\partial\phi}{\partial n} = 0 \text{ on } \partial D$$

is 0; thus we would expect bifurcations at $\lambda_1(d_1, 0)$ and $\lambda_1(d_2, 0)$ for the Dirichlet problem to be replaced by bifurcations at 0 for the Neumann problem.

Consider $a_1 > 0$ as fixed and let a_2 increase from $-\infty$ to ∞. If $a_2 < 0$, then (6.2) has only the non-negative solutions $(0, 0)$ and $(a_1/b_1, 0)$. If $a_2 > 0$, we also have the solution $(0, a_2/c_2)$ and a solution (u^*, v^*) given by the intersection of the lines $b_1 u + c_1 v = a_1$ and $b_2 v + c_2 u = a_2$. It is easy to show algebraically or graphically that $u^* > 0$ and $v^* > 0$ if and only if a_2 lies between $a_1 b_2/c_1$ and $a_1 c_2/b_1$. Thus we obtain a bifurcation diagram like that suggested by Theorem 5.2.

Similar considerations for the predator-prey case give rise to bifurcation diagrams like those suggested by the theorems in Sections 3 and 4.

Note. After this paper was submitted for publication, there came to our attention two interesting preprints containing results intersecting those above but obtained by completely different methods, *viz.* C. Cosner and A. Lazer "Stable co-existence states in the Volterra–Lotka competition model with diffusion" and E. N. Dancer "On positive solutions of some pairs of differential equations".

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