EXISTENCE AND UNIQUENESS OF COEXISTENCE STATES FOR THE PREDATOR-PREY MODEL WITH DIFFUSION: THE SCALAR CASE

J. López-Gómez and R. Pardo
Departamento Matemática Aplicada, Universidad Complutense, 28040-Madrid, Spain

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Abstract. In this paper we solve the problem of the existence and uniqueness of coexistence states for the classical one-dimensional Lotka-Volterra predator-prey model with diffusion.

1. Introduction. In this paper, we shall show the existence and uniqueness of positive solutions in both components (the so called coexistence states) for the model

\[-U'' = \lambda U - AU^2 - BUV, \quad x \in (0,1),\]
\[-V'' = \mu V + CUV - DV^2, \quad x \in (0,1),\]

\[U(0) = U(1) = V(0) = V(1) = 0,\] (1.1)

where \(A, B, C, D, \lambda, \mu\) are real numbers such that \(A > 0, D > 0, C \geq 0\) and \(B \geq 0\).

Problem (1.1) usually arises in biology and chemistry in modeling the behavior of two interacting species on \((0,1)\). From a biological point of view the real parameters \(\lambda\) and \(\mu\) describe, if positive, the net birth rates of the species and, if negative, the net death rates. We are assuming logistic growth for both species and that \(V\) preys on \(U\).

Under these assumptions the change of variables \(u = AU, v = DV\) changes (1.1) into

\[-u'' = \lambda u - u^2 - buv, \quad x \in (0,1),\]
\[-v'' = \mu v + cv^2 - v^2, \quad x \in (0,1),\]

\[u(0) = u(1) = v(0) = v(1) = 0,\] (1.2b)

where \(b = \frac{B}{D}\) and \(c = \frac{C}{A}\). Throughout this paper we shall restrict our attention to (1.2).

In references [1–3], [5–6] and [10–17] were obtained some existence and uniqueness results for (1.2) in general bounded domains \(\Omega\) of \(\mathbb{R}^N\) with smooth enough boundary.

The characterization of the set of values of \((\lambda, \mu)\) for which (1.2) has some co-existence state is well known (see [1–2], [5–6] and [17]). Such a characterization

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was accomplished by an adequate use of fixed point index. Moreover, some partial answers to the problem of the uniqueness were given in [5], [10–12] and [14–15]. The uniqueness result in [5] is of local nature being valid when dealing with the scalar prototype, assuming in addition one of the diffusion coefficients is small enough. For general domains is available the result in [15], obtained for the case when both diffusion coefficients are small enough; i.e., for large enough domains, as already was stated there. A priori, in both cases, the size of the diffusion coefficients for which uniqueness holds depends on the values of $\lambda$, $\mu$, $b$ and $c$. In [11] was shown that the techniques to obtain uniqueness introduced in [4] work as well when dealing with predator-prey interactions. These techniques were used to build up some set of values of $(\lambda, \mu)$ for which (1.2) has exactly one coexistence state. We point out that the region built in [11] where uniqueness occurs is a proper subset of the set of values of $(\lambda, \mu)$ for which the existence of some coexistence state of (1.2) is available. In [10], [12] some monotone schemes were used giving rise to some partial answers to the problem of the existence and uniqueness of coexistence states of (1.2). The results there are very restrictive because, for instance, they do not allow $\mu$ to be negative, this being one of the most interesting cases to consider from a biological point of view.

Roughly speaking the main result here says that the uniqueness and the existence occur simultaneously. We conjecture the restriction on the spatial dimension here is of a technical nature. Such a restriction is only needed to prove Lemma 3.1 (non degeneration of coexistence states).

An outline of this paper is as follows. In Section 2 are introduced some notations and stated the main result. In Section 3 the main result is proven in several steps. The basic ingredient in the proofs is the continuation technique furnished by the implicit function theorem, after showing all coexistence states of (1.2) are not degenerate.

With the techniques introduced here, besides getting the uniqueness, the set of values of $(\lambda, \mu)$ for which (1.2) exhibits coexistence is characterized, without using global topological techniques as in the proofs of most results in the quoted papers.

2. The main result. We first introduce some notation. Fix $\nu > 0$; $U$ will be the Banach space

$$U = \{u \in C^{2+\nu}([0, 1]; \mathbb{R}) : u(0) = u(1) = 0\}.$$ 

Given $q \in C^\nu([0, 1]; \mathbb{R})$, $\lambda_1(q)$ will stand for the first eigenvalue of $-\frac{d^2}{dx^2} + q(x)$, subject to homogeneous Dirichlet boundary conditions. The following variational characterization is well known:

$$\lambda_1(q) = \inf \left\{ \int_0^1 (u')^2 + \int_0^1 qu^2 : u \in U, \int_0^1 u^2 = 1 \right\}; \quad (2.1)$$

$\lambda_1(0)$ will be denoted by $\lambda_1$. Given $\gamma > \lambda_1$, we shall denote by $\theta_\gamma$ the unique positive function satisfying

$$-\theta''_\gamma = \gamma \theta_\gamma - \theta^2_\gamma \quad \text{in } (0, 1), \quad \theta_\gamma(0) = \theta_\gamma(1) = 0. \quad (2.2)$$

If $\gamma < \lambda_1$, we set $\theta_\gamma \equiv 0$.

The main result is the following.
Theorem 2.1. The problem (1.2) has a coexistence state if and only if the following relations hold:
\[ \lambda > \lambda_1(b \theta_u), \quad \mu > \lambda_1(-c \theta_v). \] (2.3)
Moreover, if (2.3) is satisfied then (1.2) has exactly one coexistence state, and this state is linearly stable, provided \( b \) (or \( c \)) is small enough.

3. Proof. The proof will be accomplished in several steps. The basic ingredients are continuation in the parameter \( b \) and nondegeneration of coexistence states.

Lemma 3.1. Let \((u_0, v_0)\) be an arbitrary coexistence state of (1.2). Then the linearization of (1.2) at \((u_0, v_0)\), which is given by
\[
-u'' = \lambda u - 2u_0 u - bv_0 u - bu_0 v \quad \text{in } (0, 1), \\
-v'' = \mu u + cu_0 v + cv_0 u - 2v_0 v \quad \text{in } (0, 1), \\
u(0) = u(1) = v(0) = v(1) = 0,
\] (3.1)
only has the trivial solution \((u, v) = (0, 0)\). In other words, all the coexistence states are nondegenerate.

Proof. The Banach space \( U \) will be considered as ordered by the usual cone of positive functions
\[ P = \{ u \in U : u(x) \geq 0, \quad x \in (0, 1) \}. \]
From the Hopf maximum principle, \([7], [8]\), it follows that each coexistence state of (1.2) lies in the interior of \( P \times P \), say \( C^+ \). In other words, \( u_0 > 0, v_0 > 0 \) in \((0, 1)\) and \( u_0'(0) > 0, v_0'(0) > 0, u_0'(1) < 0, v_0'(1) < 0 \).

Since \((u_0, v_0)\) solves (1.2),
\[
-u'' + (u_0 + bv_0 - \lambda)u = 0, \quad -v'' + (-cu_0 + v_0 - \mu)v = 0,
\]
\[
u_0(0) = u_0(1) = v_0(0) = v_0(1) = 0.
\]
Hence
\[ \lambda_1(u_0 + bv_0 - \lambda) = \lambda_1(-cu_0 + v_0 - \mu) = 0. \]
Moreover, the linearized problem (3.1) can be written as
\[
-u'' + (2u_0 + bv_0 - \lambda)u = -bu_0 v \quad \text{in } (0, 1), \\
-v'' + (-cu_0 + 2v_0 - \mu)v = cv_0 u \quad \text{in } (0, 1), \\
u(0) = u(1) = v(0) = v(1) = 0.
\] (3.2)
From the monotonicity of \( \lambda_1(q) \) as a function of \( q \) it follows that
\[
\lambda_1(2u_0 + bv_0 - \lambda) > \lambda_1(u_0 + bv_0 - \lambda) = 0, \\
\lambda_1(-cu_0 + 2v_0 - \mu) > \lambda_1(-cu_0 + v_0 - \mu) = 0.
\]
Thus, the operators \( L_1 \) and \( L_2 \) defined by
\[ L_1 u = -u'' + (2u_0 + bv_0 - \lambda)u, \quad L_2 u = -u'' + (-cu_0 + 2v_0 - \mu)u, \quad u \in U, \]
have inverses, say $L_1^{-1}, L_2^{-1}$, which are compact and order preserving. In fact, $L_i^{-1}(P - \{0\}) \subset \text{int } P$ for $i = 1, 2$. Using these operators, (3.2) can be written as

$$L_1u = -bu_0v, \quad L_2v = cu_0u, \quad u, v \in U. \tag{3.3}$$

Now we shall show that the only solution of (3.3) is $u = v = 0$. To this end we argue by contradiction, assuming that there exists a solution couple $(u, v) \neq (0, 0)$ of (3.3). Both $u$ and $v$ must change sign in $(0, 1)$, because of the positivity of $L_1^{-1}$ and $L_2^{-1}$. Moreover, $u$ and $v$ can not vanish on an interval of positive length by the maximum principle ($u' = 0$ at the boundary of such an interval where $u > 0$ or $u < 0$, contradicting the maximum principle). Thus we can choose $u$ and a partition of $(0, 1)$, say

$$Q = \{0 = x_0 < x_1 < x_2 < \cdots < x_{m-1} < x_m = 1\},$$

such that

$$u(x) > 0, \; x \in (x_{2j}, x_{2j+1}), \quad j \geq 0, \; 2j + 1 \leq m,$$

$$u(x) < 0, \; x \in (x_{2j-1}, x_{2j}), \quad j \geq 1, \; 2j \leq m,$$

$$u(x_j) = 0, \; 0 \leq j \leq m. \tag{3.4}$$

Now arguing recursively the following relationships will be shown:

$$v(x_{2j}) > 0, \quad v(x_{2j+1}) < 0, \quad x_{2j}, x_{2j+1} \in Q - \{0, 1\}. \tag{3.5}$$

For this the following result will be used [9].

**Lemma 3.2.** Let $a, b \in \mathbb{R}$ such that $a < b$. Consider $q \in C^\nu([a, b]; \mathbb{R})$ and the operator $L$ defined by

$$Lu = -u'' + q(x)u, \quad u \in C^{2+\nu}([a, b]; \mathbb{R}), \quad u(a) = u(b) = 0.$$  

Assume that the principal eigenvalue of $L$ is strictly positive and consider $v \in C^{2+\nu}([a, b]; \mathbb{R})$ such that $Lv \geq 0$ in $(a, b)$, $v(a) \geq 0$ and $v(b) \geq 0$. Then $v > 0$ in $(a, b)$.

**Proof.** Since the principal eigenvalue of $L$ is strictly positive, there exists $w \in C^{2+\nu}([a, b]; \mathbb{R})$ such that $Lw = 0$ and $w > 0$ on $[a, b]$ (by considering an adequate extension of $q$, for example). The "generalized maximum principle" in [18, p. 8] (or the "weak maximum principle" in [8]) can be applied to get $u(x) = \frac{v}{w}(x) > 0$, $x \in (a, b)$. Thus $v > 0$ in $(a, b)$, and the lemma is proven.

Since the principal eigenvalues of $L_1$ and $L_2$ on $(0, 1)$ are positive, the principal eigenvalues of $L_1$ and $L_2$ on any subinterval of $(0, 1)$ are also positive (a consequence of (2.1), for example). In particular, Lemma 3.2 can be applied to the restrictions of $L_1$ and $L_2$ to every subinterval appearing in (3.4).

By hypothesis $u(x) > 0$, $x \in (x_0, x_1)$, and $u(x_0) = u(x_1) = 0$. Thus $(L_2v)(x) = cu_0(x)u(x) > 0$, $x \in (x_0, x_1)$. We claim that $v(x_1) < 0$. To show this claim we shall argue by contradiction, assuming that $v(x_1) \geq 0$. In this case, from Lemma 3.2 it follows that $v(x) > 0$, $x \in (x_0, x_1)$. Thus $(L_1u)(x) = -bu_0(x)u(x) < 0$, $x \in (x_0, x_1)$. Therefore $u(x) < 0$, $x \in (x_0, x_1)$, contradicting (3.4). So $v(x_1) < 0$. 

Again by hypothesis \( u(x) < 0, \ x \in (x_1, x_2) \) and \( u(x_1) = u(x_2) = 0 \). Thus \((L_2 v)(x) = c v_0(x) u(x) < 0, \ x \in (x_1, x_2)\). We claim that \( v(x_2) > 0 \). If \( v(x_2) \leq 0, \) since \( v(x_1) < 0 \), we could apply Lemma 3.2 showing that \( v(x) < 0 \) for \( x \in (x_1, x_2) \). Thus \((L_2 u)(x) = -b u_0(x) v(x) > 0, \ x \in (x_0, x_1)\). So \( u(x) > 0 \) for \( x \in (x_1, x_2) \), which would contradict (3.4). This contradiction shows the above claim.

Arguing recursively, (3.5) is shown. According to the parity of \( m \), either
\[
\begin{align*}
\text{(3.6)} \\
&u(x) > 0, \ x \in (x_{2k}, 1), \ v(x_{2k}) > 0,
\end{align*}
\]
or
\[
\begin{align*}
\text{(3.7)} \\
&u(x) < 0, \ x \in (x_{2k+1}, 1), \ v(x_{2k+1}) < 0,
\end{align*}
\]
is satisfied. Assume (3.6) holds. Then
\[
(L_2 v)(x) = c v_0(x) u(x) > 0, \ x \in (x_{2k}, 1).
\]
Since \( v(x_{2k}) > 0 \) and \( v(1) = 0 \), from Lemma 3.2 it follows that \( v(x) > 0 \) for every \( x \in (x_{2k}, 1) \). Thus
\[
(L_1 u)(x) = -b u_0(x) v(x) < 0, \ x \in (x_{2k}, 1).
\]
Therefore \( u < 0 \) in \((x_{2k}, 1) \), contradicting (3.6). If instead of (3.6), (3.7) holds, we get a contradiction arguing as above. This finishes the proof of Lemma 3.1.

**Lemma 3.3.** Assume (2.3) is satisfied and (1.2b) has exactly one coexistence state, say \((u_0, v_0)\), which is not degenerate. Then there exists \( \epsilon_0 = \epsilon(b, c, \lambda, \mu) > 0 \) such that for every \( \epsilon \in (0, \epsilon_0) \) the problem (1.2b+\( \epsilon \)) has exactly one coexistence state, say \((u(\epsilon), v(\epsilon))\). Moreover \((u(0), v(0)) = (u_0, v_0)\) and the mapping \( \epsilon \to (u(\epsilon), v(\epsilon))\), from a neighborhood of \( \epsilon = 0 \) in \( R \) to \( U^2 \), belongs at least to the class \( C^1 \).

**Proof.** Consider the operator \( K : U^2 \times R \to U^2 \), defined by
\[
K(u, v, \epsilon) = \left(-\frac{d^2}{dx^2}\right)^{-1}(\lambda - u - (b + \epsilon)v)u, \ [\mu + cu - v]v.
\]
Then \( K \) is a compact Fréchet differentiable operator whose component-wise positive fixed points in \((u, v)\) for a fixed \( \epsilon \) are the component-wise positive function pairs solving (1.2b+\( \epsilon \)). Define \( N : U^2 \times R \to U^2 \) by \( N(u, v, \epsilon) = (u, v) - K(u, v, \epsilon) \). Then the problem of the search for coexistence states of (1.2b) becomes the problem of the search for zeros of \( N(\cdot, \cdot, 0) \) in \( C^+ \). We already know that \( N(u_0, v_0, 0) = 0 \). Moreover, since \((u_0, v_0)\) does not degenerate, the operator \( D(u, v)N(u_0, v_0, 0) \) is an endomorphism of \( U^2 \) and thus the implicit function theorem provides us with a regular curve \( \epsilon \to (u(\epsilon), v(\epsilon)) = (u_0, v_0) + O(\epsilon), \ \epsilon \to 0, \) such that \( N(u(\epsilon), v(\epsilon), \epsilon) = 0, \ \epsilon \approx 0 \). Moreover, since \((u_0, v_0) \in C^+ \), \((u(\epsilon), v(\epsilon)) \in C^+ \) for \( \epsilon \) small enough. Furthermore, because of the uniqueness obtained as an application of the implicit function theorem, there exists a neighborhood of \((u_0, v_0, 0)\) in \( U^2 \times R \), say \( B \), such that if \((u, v, \epsilon) \in B \) satisfies \( N(u, v, \epsilon) = 0 \), then \((u, v) = (u(\epsilon), v(\epsilon))\).

In the sequel we shall show the existence of \( \epsilon_0 \); i.e., the global uniqueness of a coexistence state for \( \epsilon \in (-\epsilon_0, \epsilon_0) \). To this end we argue by contradiction, assuming that there exist two sequences, one of numbers \( \epsilon_n, n \geq 1, \epsilon_n \to 0, \) as \( n \to \infty, \) and
the other of coexistence states, say \((u_n, v_n) \in C^+, n \geq 1\), such that \((u_n, v_n, \epsilon_n) \notin B\) and

\[
N(u_n, v_n, \epsilon_n) = 0, \quad n \geq 1.
\]

(3.9)

It is well known that the set \(\{(u_n, v_n, \epsilon_n) : n \geq 1\}\) is bounded in \(U^2 \times \mathbb{R}\). Thus, since \(K\) is a compact operator and (3.9) can be written as

\[
K(u_n, v_n, \epsilon_n) = (u_n, v_n), \quad n \geq 1,
\]

there exists a subsequence, again called \((u_n, v_n, \epsilon_n), n \geq 1\), such that

\[
\lim_{n \to \infty} (u_n, v_n, \epsilon_n) = (u_\infty, v_\infty, 0),
\]

for some \((u_\infty, v_\infty) \in P \times P, (u_\infty, v_\infty) \neq (u_0, v_0)\). Therefore, \(u_\infty = 0\) or \(v_\infty = 0\), because otherwise we would contradict the uniqueness of a coexistence state of (1.2b). Assume \(u_\infty = 0\) and consider \(U_n = \frac{u_n}{\|u_n\|}, n \geq 1\). Then

\[
-u''_n = \lambda u_n - u_n U_n - (b + \epsilon_n) v_n U_n \quad \text{in } (0, 1),
\]

\[
-v''_n = \mu v_n + c u_n v_n - v^2_n \quad \text{in } (0, 1),
\]

\[
u_n(0) = U_n(0) = v_n(0) = u_n(1) = U_n(1) = v_n(1) = 0.
\]

So, since \(u_n \to 0\) as \(n \to \infty\), arguing as above there exists a subsequence, again called \(U_n\), such that \(U_n \to w\) as \(n \to \infty\), for some \(w \in P, \|w\| = 1\), and

\[
-w'' = \lambda w - bwv_\infty, \quad -v''_\infty = \mu v_\infty - v^2_\infty \quad \text{in } (0, 1),
\]

\[w(0) = v_\infty(0) = w(1) = v_\infty(1) = 0.
\]

Thus \(v_\infty = \theta_\mu\) and \(\lambda = \lambda_1(b\theta_\mu), \) which contradicts (2.3). If \(\mu \leq \lambda_1\) (i.e., if \(v_\infty \equiv 0\)) then \(\lambda = \lambda_1\) and since \(\lambda > \lambda_1(b\theta_\mu) \geq \lambda_1\), we get the same contradiction.

Similarly, if \(u_\infty \neq 0\) and \(v_\infty \equiv 0\), we can contradict (2.3). This finishes the proof of Lemma 3.3.

**Proof of Theorem 2.1.** Let \(\lambda, \mu, b, c\) be such that

\[
\lambda > \lambda_1(b\theta_\mu), \quad \mu > \lambda_1(-c\theta_\lambda).
\]

Consider the set

\[
B := \{\hat{b} \in [0, b] : (1.2b) \text{ has a unique coex. state, } \forall \beta \in [0, \hat{b}]\}.
\]

Since \(0 \in B, B\) is not empty. From Lemma 3.3 it follows that \(B\) is open in \([0, b]\). We claim that \(B\) is closed in \([0, b]\). Hence \(B = [0, b]\). To show this, let \(\{b_n\}_{n \geq 1}\) be a sequence in \(B\) converging to some real number \(b_\infty\). Since the mapping \(b \mapsto \lambda_1(b\theta_\mu)\) is increasing in \(b\) (but not necessarily strictly increasing, because \(\theta_\mu \equiv 0\) for \(\mu < \lambda_1\)), condition (3.10) is satisfied for \(b = b_\infty, b_n, n \geq 1\). Let \((u_n, v_n)\) be the unique coexistence state of (1.2b_n). Arguing as in the proof of Lemma 3.3 it follows that for some subsequence of \((u_n, v_n)\), again called \((u_n, v_n)\),

\[
\lim_{n \to \infty} (u_n, v_n) = (u_\infty, v_\infty).
\]
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for some \((u_\infty, v_\infty) \in P \times P\). Since condition (3.10) is satisfied for \(b = b_\infty\), we can argue again as in the proof of Lemma 3.3 to show that \((u_\infty, v_\infty)\) is a coexistence state of \((1.2b_\infty)\). The problem \((1.2b_\infty)\) has exactly one coexistence state, because otherwise from Lemma 3.1, using in addition the implicit function theorem as in the proof of Lemma 3.3, we would obtain that \((1.2b_\infty)\) has at least two coexistence states, for large enough \(n\), contradicting the fact that \(b_\infty \in B\). Thus \(b_\infty \in B\) and \(B = [0, b]\).

Since the coexistence solution for \(b = 0\) is linearly stable, remaining nondegenerate along the continuation \(0 \to b\), it is also linearly stable for every \(b\) small enough.

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