Applicable Analysis, Vol. 44, pp. 191–207
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Dynamics of the Lotka-Volterra Systems with Diffusion

Communicated by W. Walter

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AMS: 35K55, 35J60

Abstract We prove some new results on the steady states and the long term behavior for the Lotka-Volterra systems with diffusion, particularly for the cooperating species case, which is less studied than predator-prey and competing species cases.

KEY WORDS: Lotka-Volterra systems, long term behavior, steady states.
(Received for Publication 23 October 1990)

INTRODUCTION

We study the steady states and the long term behavior for the following system describing interaction of two species in the Lotka-Volterra model with diffusion,

$$u_t = \Delta u + u(a - bu + cv) \text{ in } \Omega, \quad u = 0 \text{ on } \delta\Omega$$
$$\qquad\qquad\qquad\qquad\qquad\qquad (1.1)$$
$$v_t = \Delta v + v(d + eu - fv) \text{ in } \Omega, \quad v = 0 \text{ on } \delta\Omega.$$

Here a, d, b and f are positive constants; the constants c and e can be of either sign, and those signs determine the type of interaction. Throughout the paper Ω denotes a smooth domain in R^n, and we are looking for the classical solutions $u(x,t)$ and $v(x,t)$, $x \in \Omega$ and $t > 0$. Also, we shall always assume that $b = f = 1$, which can be achieved by rescaling. The problem (1.1), particularly its steady states, have been studied in a number of papers, see e.g., [3,4,7,8,11] and the references therein. Local existence and uniqueness for (1.1) follow from [1].

Systems of the type (1.1) arise in mathematical ecology and describe the evolution of population densities of two interacting species inhabiting the region Ω, and undergoing diffusion to avoid crowding. The boundary conditions in (1.1) can be interpreted as emigration of species. This interpretation suggests that the growth

*Supported in part by the Taft faculty grant at the University of Cincinnati.

rates a and d must be sufficiently large to sustain the populations, as turns out to be the case below.

Two things determine the global behavior of solutions of (1.1). One is existence or non-existence of steady states for (1.1). For example, in the cooperating species case (i.e. $c > 0$, $e > 0$), we show that condition $ec > 1$ implies blow up in finite time of any nontrivial non-negative solution of (1.1). This is because the corresponding steady state problem has no positive solution, as was shown in [8]. The other thing determining the global behavior is stability or instability of trivial solutions of the steady state problem for (1.1), i.e. of $(0,0)$, $(u_a,0)$ and $(0,u_d)$. Here and throughout we denote by u_a the positive in Ω solution of

$$\Delta u + u(a-u) = 0 \quad \text{in } \Omega, \; u = 0 \text{ on } \delta\Omega,$$

which exists for $a > \lambda_1$, where λ_1 and $\varphi_1(x) > 0$ denote the principal eigenpair of $-\Delta$ on Ω.

The importance of the steady states for global behavior can be seen even in the scalar case. Consider, for example

$$u_t = \Delta u + u^3 \text{ in } \Omega, \; u = 0 \text{ on } \delta\Omega. \tag{1.2}$$

If we define the "energy" $J(u) = \int_\Omega \left(\frac{1}{2}|\nabla u|^2 - \frac{1}{4}u^4\right)dx$, we easily see that for any nontrivial steady state $\bar{u}(x)$, $J(\bar{u}) > 0$. Also it is easy to check that $J(u(x,t)) \le J(u(x,0))$. Assume now that

$$J(u(x,0)) \le 0. \tag{1.3}$$

If the solution $u(x,t)$ was bounded, then by H. Matano [10] its ω-limit set in $C^1(\Omega)$ would be non-empty and consist of steady-state solutions. This would contradict the above considerations, so that $u(x,t)$ must become unbounded, and it is natural to expect that this would happen in finite time. Here is a rigorous proof that (1.3) implies non-existence of a global solution (see also [9]). Multiply (1.2) by u, and denote $F = \int_\Omega u^2 dx$. Then

$$\frac{1}{2}F' = -2J(u) + \frac{1}{4}\int_\Omega u^4 dx \ge c_1 F^2 \text{ for some } c_1 > 0.$$

Some remarks on notation. By $u(x,t;u_0,v_0)$ and $v(x,t;u_0 v_0)$ we denote the solution of (1.1) depending on the data $u(x,0) = u_0(x)$, $v(x,0) = v_0(x)$. For scalar equations (like (1.2)) the corresponding notation is $u(x,t;u_0)$. We abbreviate $\int u = \int_\Omega u(x)dx$. By $\lambda_1(\Delta+a(x))$ we denote the principal eigenvalue of the operator $\Delta + a(x)$.

DYNAMICS OF A LOGISTIC EQUATION WITH DIFFUSION

Before considering interactions of several species, we study dynamics of a single species with population density $u(x,t)$ satisfying

$$u_t = \Delta u + u(a(x)-u) \text{ in } \Omega, \ u = 0 \text{ on } \delta\Omega. \tag{2.1}$$
$$u(x,0) = u_0(x) \qquad (u_0(x) \in C^2(\Omega) \text{ and } u_0 = 0 \text{ on } \delta\Omega).$$

Here Ω is a smooth domain in R^n, $a(x) \in C^\alpha(\bar{\Omega})$ for some $0 < \alpha < 1$.

The lemma 2.1 and the theorem 2.1 below are basically known, however we could not find any references for their present versions. Notice that in the theorem 2.1 convergence is proved in $C^1(\bar{\Omega})$ rather than in $C^0(\bar{\Omega})$, and for any non-negative data.

<u>Lemma 2.1</u>. Assume that $u(x) > 0$ in Ω is a solution of

$$\Delta u + u(a(x) - u) = 0 \text{ in } \Omega, \ u = 0 \text{ on } \delta\Omega, \tag{2.2}$$

with $a(x) \geq 0$ and $a(x) \not\equiv 0$ in Ω. Then $u(x)$ is the only nontrivial non-negative solution of (2.2).

<u>Proof</u>. Since $\varphi = \max_{\bar{\Omega}} a(x)$ is a supersolution, and $\psi = 0$ a subsolution, it follows that (2.2) has a maximal solution. It has to be $u(x)$, since (2.2) cannot have more than one positive solution (the proof is standard). Let $v(x)$ be another nontrivial solution with $0 \leq v(x) \leq u(x)$. Since

$$\int_\Omega uv(u-v)dx = 0,$$

$u(x) = v(x)$ except possibly when $v(x) = 0$. Let $\bar{x} \in \Omega$ be such that $v(\bar{x}) = 0$ but $v(x_n) > 0$ for a sequence $\{x_n\} \to \bar{x}$. Then by the continuity of u and v

$$u(\bar{x}) = \lim_{n\to\infty} u(x_n) = \lim_{n\to\infty} v(x_n) = v(\bar{x}) = 0,$$

which contradicts $u > 0$.

The following lemma is standard.

Lemma 2.2. The problem (2.2) has a positive solution if and only if

$$\bar{\lambda} = \lambda_1(\Delta + a(x)) > 0. \tag{2.3}$$

We denote by u_a the positive solution of (2.2). By $u(x,t;u_0)$ we denote the solution of (2.1).

Theorem 2.1. Assume that (2.3) holds and $u_0 \geq 0$ in Ω, $u_0 \not\equiv 0$. Then

$$\lim_{t\to\infty} u(x,t;u_0) = u_a \quad \text{in } C^1(\bar{\Omega}). \tag{2.5}$$

If the condition (2.3) fails then $\lim\limits_{t\to\infty} u(x,t;u_0) = 0$.

Proof. Suppose (2.3) holds, and assume first that $\varepsilon\varphi_1(x) \leq u_0(x)$ for all $x \in \Omega$, if ε is small enough. By the maximum principle

$$u(x,t;\varepsilon\varphi_1) \leq u(x,t;u_0) \leq u(x,t;M). \tag{2.6}$$

By [12] it follows that $u(x,t;\varepsilon\varphi_1)$ and $u(x,t;M)$ tend respectively the the minimal and maximal solutions of (2.2). In view of lemma 2.1 they both tend to u_a, and the theorem follows by (2.6).

For the general u_0 the theorem 2.8 in Matano [10] implies that the ω-limit set of u_0 in $C^1(\bar{\Omega})$ is non-empty, and consists of non-negative solutions of (2.2), which by lemma 2.1 are zero and u_a. If $u_a \in \omega(u_0)$ then at some T, $u(x,T) > \varepsilon\varphi_1(x)$ for some small ε, and then taking T as a new initial time we conclude (2.5).

It remains to exclude the possibility that $\omega(u_0) = \{0\}$ in $C^1(\bar{\Omega})$. If that was the case then $u(x,t) \to 0$ uniformly in x, i.e. $u(x,t) < \varepsilon$ for $t \geq T$. Setting $H = \int_\Omega u(x,t)\bar{u}(x)dx$ ($\bar{u}$ as defined by (2.4)) we obtain from (2.1) for $t \geq T$

$$H' \geq \bar{\lambda}H - \varepsilon H \geq cH \quad (\text{for some } c > 0)$$

with $H(T) > 0$. This shows that $H(t)$ cannot tend to zero as $t \to \infty$, a contradiction. ($H(t)$ cannot become zero at a finite time T, for otherwise step back a little, and repeat the above argument).

If (2.3) fails, then in view of lemma 2.2, $u(x,t;M)$ must tend to zero, and so does $u(x,t;u_0)$, which finishes the proof.

Assuming (2.3), denote by $u_{a+\varepsilon}$, $\varepsilon > 0$, the positive solution of

$$\Delta u + u(a(x)+\varepsilon - u) = 0 \text{ in } \Omega, \; u = 0 \text{ on } \delta\Omega. \tag{2.7}$$

Then $u_{a+\varepsilon} > u_a$ in Ω (notice that u_a is a subsolution of (2.7), and then the inequality follows as in [11]).

We shall need the following lemmas.

Lemma 2.3. $\lim_{\varepsilon\to 0} \|u_{a+\varepsilon}-u_a\|_{L^\infty(\bar\Omega)} = 0$.

Proof. Let $\varepsilon \le 1$. By the maximum principle

$$\|u_{a+\varepsilon}\|_{L^\infty(\bar\Omega)} \le \max_{\bar\Omega} a(x) + 1.$$

By the usual boot-strap (for any $0 < \alpha < 1$)

$$\|u_{a+\varepsilon}\|_{C^{2+\alpha}(\bar\Omega)} \le c \quad \text{independent of } \varepsilon \le 1.$$

Let $\{\varepsilon_k\}$ be an arbitrary sequence such that $\varepsilon_1 > \varepsilon_2 > \dots \to 0$. Then

$$u_{a+\varepsilon_1} > u_{a+\varepsilon_2} > \dots > u_a > 0 \quad \text{in } \Omega.$$

Since $C^{2+\alpha}(\Omega)$ imbeds compactly into $C^2(\bar\Omega)$, a subsequence $u_{a+\varepsilon_{k_j}}$ converges in $C^2(\Omega)$ to some $w(x) > 0$, which is then a solution of (2.2). By uniqueness $w = u_a$, and by monotonicity the entire sequence $\{u_{a+\varepsilon_k}\}$ converges to u_a.

Lemma 2.4. For the problem

$$v_t = \Delta v + a(x,t)v \text{ in } \Omega, \quad v = 0 \text{ on } \delta\Omega,$$

assume that $v(x,0) \ge 0$, $v(x,0) \not\equiv 0$, and $|a(x,t)| \le c$ uniformly in $x \in \Omega$ and $t > 0$. Then $v(x,t)$ cannot go to zero in finite time.

Proof. Set $H = \int_\Omega v(x,t)\varphi_1(x)dx$. Then $H(0) > 0$ and $H(t) \ge H(0)e^{-(\lambda_1+c)t}$.

STEADY STATES AND BLOW-UP FOR COOPERATING SPECIES

We consider a system (Ω a smooth domain in R^n)

$$\begin{aligned} &u_t = \Delta u + u(a - u + cv) \quad \text{in } \Omega,\ u = 0 \text{ on } \delta\Omega \\ &v_t = \Delta v + v(d + eu - v) \quad \text{in } \Omega,\ v = 0 \text{ on } \delta\Omega \\ &u(x,0) = u_0(x),\ v(x,0) = v_0(x), \end{aligned} \tag{3.1}$$

describing cooperative interaction of two species with population densities $u(x,t)$ and $v(x,t)$. We assume that a, c, d, e are positive constants, although we can admit for a and d to be functions of x. Corresponding steady state system

$$\Delta u + u(a - u + cv) = 0 \quad \text{in } \Omega, \; u = 0 \text{ on } \delta\Omega$$
$$\tag{3.2}$$
$$\Delta v + v(d + eu - v) = 0 \quad \text{in } \Omega, \; v = 0 \text{ on } \delta\Omega,$$

was analyzed in Korman-Leung [8], where the following theorem was proved.

Theorem 3.1. Assume that $a > \lambda_1, d > \lambda_1$. Then (3.2) has a positive solution (i.e. $u > 0$ and $v > 0$ in Ω) if and only if $ec < 1$.

If $ec > 1$ then it is easy to see that both $u(x,t)$ and $v(x,t)$ become unbounded as t increases, if

$$u_0 \geq 0, \; v_0 \geq 0 \text{ with } u_0 \not\equiv 0, \; v_0 \not\equiv 0 \text{ in } \Omega. \tag{3.3}$$

The following theorem shows more.

Theorem 3.2. Assume that $a > \lambda_1, d > \lambda_1$ and the initial data satisfies (3.3). If $ec > 1$, then solution of (3.1) blows up in finite time. If $ec = 1$ then solution of (3.1) exists for all time, and as $t \to +\infty$,

$$\|u(x,t)\|_{L^\infty(\Omega)} \to \infty, \quad \|v(x,t)\|_{L^\infty(\Omega)} \to \infty. \tag{3.4}$$

If $ec < 1$ then solution exists for all time and is bounded in $L^\infty(\Omega)$.

We prove this theorem at the end of this section after presenting some results on which it depends, which are also of independent interest. We start with a corresponding ODE.

Theorem 3.3. Let $u(t)$ and $v(t)$ be solutions of

$$\dot{u} = u(a - u + cv), \quad u(0) = u_0 > 0$$
$$\tag{3.5}$$
$$\dot{v} = v(d + eu - v), \quad v(0) = v_0 > 0.$$

Here a, c, d, e are positive constants.

(i). If $ec < 1$ then

$$\lim_{t\to\infty} u(t) = \frac{a+cd}{1-ec}, \quad \lim_{t\to\infty} v(t) = \frac{ae+d}{1-ec}.$$

(ii). If $ec = 1$ then solution exists for all $t > 0$, and $\lim_{t\to+\infty} u(t) = +\infty$,

$$\lim_{t\to+\infty} v(t) = +\infty.$$

(iii). If $ec > 1$ then both $u(t)$ and $v(t)$ go to $+\infty$ in finite time.

Proof. The claim (i) is standard. The limits in (i) are coordinates of the point of intersection of the lines ℓ_1: $a - u + cv = 0$ and ℓ_2: $d + eu - v = 0$ in the (u,v) plane. In cases (ii) and (iii) the lines ℓ_1 and ℓ_2 do not intersect and hence all solutions must tend to ∞. This is because all trajectories eventually enter and stay in the region $A = \{(u,v) \in R^2_+ | 0 < v < d+eu$ for $0 < u \le a$, $\frac{1}{c}u - \frac{1}{c}a < v < d+eu$ for $u > a\}$. Next we prove (iii), assuming for definiteness that $a \ge d$. Let x_1 be such that $u_0 > x_1$, $v_0 > px_1$, with p specified below. Compare (3.5) with the system

$$\dot{x} = x(d - x + cy), \quad x(0) = x_1$$

$$\dot{y} = y(d + ex - y), \quad y(0) = px_1.$$

Then clearly $u(t) \ge x(t)$, $v(t) \ge y(t)$ for all $t \ge 0$. Solution of the last system can be explicitly found in the form $y = px$ with $p = \frac{e+1}{c+1}$, and it blows up in finite time. Turning to the final case (ii), set $\mu_1(t) = e^{-at}$, $\mu_2(t) = e^{-dt}$. Rewrite (3.5) as $(e = \frac{1}{c})$

$$\begin{aligned} \frac{d}{dt}(\mu_1 u) &= \mu_1 u(-u + cv) \\ \frac{d}{dt}(\mu_2 v) &= \mu_2 v(\tfrac{1}{c}u - v). \end{aligned} \tag{3.6}$$

Denoting further $U = \mu_1 u$, $V = \mu_2 v$ and dividing the first equation in (3.6) by the second one,

$$\frac{dU}{dV} = -c\frac{U}{V}.$$

Integrating and returning to the original u and v,

$$\mu_1 u = \frac{c_1}{\mu_2^c v^c} \qquad (c_1 \text{ is a constant of integration}).$$

This implies that v cannot go to ∞ in finite time, since otherwise u would have to go to 0 in finite time. Since we already know that $u(t)$ and $v(t)$ tend to ∞ as $t \to \infty$, the theorem is proved.

Lemma 3.1. For the problem (3.1) assume that $u_0 \ge 0$, $u_0 \not\equiv 0$, $v_0 \ge 0$, $v_0 \not\equiv 0$ in Ω, and

$$-\Delta u_0 \le u_0(a - u_0 + cv_0) \text{ in } \Omega, \; u_0 = 0 \text{ on } \delta\Omega \tag{3.7}$$

$$-\Delta v_0 \le v_0(d + eu_0 - v_0) \text{ in } \Omega, \; v_0 = 0 \text{ on } \delta\Omega.$$

Let (u^0, v^0) satisfy inequalities like (3.7) but with the signs reversed and $u^0 \ge 0$ and $v^0 \ge 0$ on $\delta\Omega$. Assume moreover that $u^0 \ge u_0$ and $v^0 \ge v_0$ in Ω. Then

$$u_0 \le u(x,t;u_0,v_0) \le u^0$$
$$v_0 \le v(x,t;u_0,v_0) \le v^0 \quad \text{in } \Omega \times R_+, \tag{3.8}$$

and

$$u_t(x,t;u_0,v_0) \ge 0, \quad v_t(x,t;u_0,v_0) \ge 0 \text{ in } \Omega \times R_+. \tag{3.9}$$

<u>Proof</u>. Set $w_1 = u-u_0$, $w_2 = v-v_0$. Then

$$w_{1t} - \Delta w_1 \ge w_1(a - u + cv - u_0) + cu_0w_2$$
$$w_{2t} - \Delta w_2 \ge ev_0w_1 + w_2(d + eu - v + v_0)$$
$$w_i(x,0) = 0 \text{ on } \delta\Omega, \; w_i = 0 \text{ on } \delta\Omega, \; i = 1,2.$$

By the maximum principle for weakly coupled systems, $u \ge u_0$ and $v \ge v_0$ in $\Omega \times R_+$. To prove the other side of (3.8), define $w_1 = u^0-u$, $w_2 = v^0-v$. Then

$$w_{1t} - \Delta w_1 \ge w_1(a - u^0 - u + cv^0) + cuw_2$$
$$w_{2t} - \Delta w_2 \ge evw_1 + w_2(d + eu^0 - v + v^0)$$
$$w_i(x,0) \ge 0, \; i = 1,2.$$

Notice that by the previous part $u \ge 0$, $v \ge 0$ in Ω. Applying the maximum principle again, we conclude (3.8).

Next, define $u_h = \dfrac{u(x,t+h;u_0,v_0) - u(x,t;u_0,v_0)}{h}$, $v_h = \dfrac{v(x,t+h;u_0,v_0) - v(x,t;u_0,v_0)}{h}$. Since by (3.8) $u_h(x,0) \ge 0$ and $v_h(x,0) \ge 0$, an argument similar to the one above shows that $u_h(x,t) \ge 0$ and $v_h(x,t) \ge 0$ for all $x \in \Omega$, $t > 0$. Letting $h \to 0$, we conclude (3.9).

<u>Remark</u>. By a similar argument one sees that $u(x,t;u^0,v^0)$ and $v(x,t;u^0,v^0)$ satisfy (3.8), and $u_t(x,t;u^0,v^0) \le 0$, $v_t(x,t;u^0,v^0) \le 0$ in $\Omega \times R_+$.

Theorem 3.4. For the problem (3.1) assume existence of two pairs of functions (u_0, v_0) and (u^0, v^0) as in lemma 3.1. Then the following limits exist for all $x \in \Omega$: $\lim_{t\to\infty} u(x,t;u_0,v_0) = u(x)$, $\lim_{t\to\infty} v(x,t;u_0,v_0) = v(x)$, $\lim_{t\to\infty} u(x,t;u^0,v^0) = U(x)$, $\lim_{t\to\infty} v(x,t;u^0,v^0) = V(x)$, where (u,v) and (U,V) are positive solutions of (3.2). The ω-limit set of (3.1) (with respect to data in $[u_0,u^0] \times [v_0,v^0]$ is then contained in the order rectangle $[u,U] \times [v,V]$.

Proof. For $h > 0$ define $u_m(x,t) = u(x,t+mh;u^0,v^0)$, $v_m(x,t) = v(x,t+mh;u^0,v^0)$, m a positive integer. By lemma 3.1 both sequences are decreasing in m and the limits $\lim_{m\to\infty} u_m(x,t) = U(x,t)$ and $\lim_{t\to\infty} V_m(x,t) = V(x,t)$ exist, and $U(x,t) = V(x,t) = 0$ for $x \in \delta\Omega$. By the interior Schauder's estimates (see e.g., [10])

$$|u_m|_{2+\gamma,[\delta_1,\delta_2],K} + |v_m|_{2+\gamma,[\delta_1,\delta_2],K} \le c$$

for any $0 < \gamma < 1$, $\delta_2 > \delta_1 > 0$ and $K \subset\subset \Omega$. Since $C^{2+\gamma,1+\gamma/2}(K \times [\delta_1,\delta_2])$ is compactly imbedded in $C^{2,1}(K \times [\delta_1,\delta_2])$ it follows that for a subsequence

$$u_{m_k} \to U(x,t), \quad v_{m_k} \to V(x,t) \text{ in } C^{2,1}(K \times [\delta_1,\delta_2]).$$

By monotonicity the entire sequences $\{u_m\}$ and $\{v_m\}$ converge in $C^{2,1}(K \times [\delta_1,\delta_2])$. Since (u_m,v_m) are solutions of (3.1), we can pass to the limit in the equations and conclude that $(U(x,t),V(x,t))$ is a solution of (3.1) for $x \in \Omega$, $t > 0$.

Finally, we claim that $U_t = V_t = 0$ on $\Omega \times R_+$. Let $K \subset\subset \Omega$, and k = integer > 1. Consider $\bar{u}_m(x,t) = u(x,t + m\frac{h}{k};u^0,v^0)$, $\bar{v}_m(x,t) = v(x,t + m\frac{h}{k};u^0,v^0)$. The new sequences $\{\bar{u}_m\}$ and $\{\bar{v}_m\}$ have the old ones as subsequences. Since as above $\bar{u}_m$ and $\bar{v}_m$ converge, their limits are again $U(x,t)$ and $V(x,t)$ respectively, i.e.

$$\bar{u}_m \to U(x,t), \quad \bar{v}_m \to V(x,t) \text{ in } C^{2,1}(K \times [\delta_1,\delta_2]).$$

Set $\tau = \frac{h}{k}$, and assume τ is small (i.e. k is large). Let $x_0 \in K$, $t_0 \in (\delta_1+\tau, \delta_2-\tau)$, with τ so small that $\delta_2-\tau > \delta_1+\tau$. Then

$$U(x_0,t_0+\tau) - U(x_0,t_0) = \lim_{m\to\infty} u(x_0,t_0+\tau + m\tau;\ u^0,v^0) - \lim_{m\to\infty} u(x_0,t_0+m\tau) = 0.$$

Since U is differentiable it follows that

$$U_t(x_0,t_0) = \lim_{k\to\infty} \frac{U(x_0,t_0+\frac{h}{k}) - U(x_0,t_0)}{h/k} = 0.$$

Since $x_0, t_0, \delta_1, \delta_2$ and K were arbitrary, the claim follows, and the theorem is proved (the final statement follows easily by the maximum principle).

Corollary 1. Assume that $a > \lambda_1, d > \lambda_1$, $ec < 1$. Then the problem (3.2) has minimal and maximal positive solutions $(\underline{u},\underline{v})$ and $(\bar{u},\bar{v})$ respectively, and the ω-limit set of (3.1) with respect to data satisfying (3.3) is contained in the order rectangle $[\underline{u},\bar{u}] \times [\underline{v},\bar{v}]$.

Proof: Existence of the steady states was proved in [7]. In that work subsolutions were $u_0 = \varepsilon\varphi_1, v_0 = \varepsilon\varphi_2$ with sufficiently small ε. It remains to notice that in view of the theorem 2.1 we may assume without loss of generality that the initial data is above $\varepsilon\varphi_1$ for ε small (just shift the original time if necessary).

Corollary 2. Assume that $a \ge d > \lambda_1$, $ec < \delta^2$, where $\delta = \inf\limits_{\Omega} \frac{u_d}{u_a}$. Then (3.2) has a unique positive solution, which attracts all solutions of (3.1), with data satisfying (3.3).

Proof. Uniqueness of the steady state was proved in [8], the rest is as above.

For cooperating species conditions $a > \lambda_1$, $d > \lambda_1$ are not necessary for existence of positive steady states as the following result shows.

Theorem 3.5. Assume that $a > \lambda_1$, $ec < 1$ and $\lambda_1(\Delta + d + eu_a) > 0$. Then the problem (3.2) has a positive solution.

Proof. Fix constants $M,N > 0$ such that

$$a - M + cN < 0, \quad d + eM - N < 0.$$

By lemma 3.1, $u(x,t) \equiv u(x,t;M,N)$ and $v(x,t) \equiv v(x,t;M,N)$ are monotone decreasing in t, and by the argument of the theorem 3.4 they converge to a non-negative solution $(u(x),v(x))$ of (3.2). Clearly $u(x) \ge u_a(x) > 0$, since $u(x,t)$ lies above the solution $u(x,t;M)$ of (2.1), which tends to the $u_a > 0$ from above. Since $\lambda_1(\Delta + d + eu(x,t)) \ge \lambda_1(\Delta + d + eu_a) > 0$, it follows by lemma 2.2 that the second equation in (3.2) has a positive solution, and then by lemma 2.1, $v(x)$ is either that positive solution or zero. It remains to exclude the latter possibility. Indeed if $v \equiv 0$ then by the Vitali's theorem $v(x,t) \to 0$ as $t \to \infty$ uniformly in $x \in \bar{\Omega}$. We claim that then $u(x,t) \to u_a$ as $t \to \infty$ uniformly in $x \in \bar{\Omega}$. Indeed for any $\varepsilon > 0$ one can find $T > 0$, such that $cv(x,t) < \varepsilon$ for $t > T$ and $x \in \Omega$. Hence for $t > T$

$$u_a \le u(x,t) \le u_{a+\varepsilon},$$

and the claim follows by lemma 2.3.

Rewrite the second equation in (3.1)

$$v_t = \Delta v + v(d+eu_a) - v^2 + v(eu-eu_a). \tag{3.10}$$

Denote by $\bar{v} > 0$ the principal eigenfunction of $\Delta + d + eu_a$ corresponding to $\bar{\lambda} \equiv \lambda_1(\Delta+d+eu_a)$. Multiply both sides of (3.10) by $\bar{v}$ and integrate, setting $H = \int_\Omega v\bar{v}dx$. Then for $t > T$, with T large enough (using lemma 2.4)

$$H' \ge \frac{\bar{\lambda}}{2}H, \quad H(T) > 0. \tag{3.11}$$

But $H(t) \to 0$ as $t \to \infty$, which contradicts (3.11).

We need two more comparison results whose proofs easily follow from the maximum principle for weakly coupled systems.

Lemma 3.2. Let $\bar{u}(t)$, $\bar{v}(t)$ be solutions of

$$\bar{u}' = \bar{u}(a-\bar{u}+c\bar{v}), \quad \bar{u}(0) = \max_\Omega u_0(x),$$

$$\bar{v}' = \bar{v}(d+e\bar{u}-\bar{v}), \quad \bar{v}(0) = \max_\Omega v_0(x).$$

Then for all $x \in \Omega$ and $t > 0$,

$$u(x,t;u_0,v_0) \le \bar{u}(t), \quad v(x,t;u_0,v_0) \le \bar{v}(t).$$

Lemma 3.3. Let $U(x,t)$ and $V(x,t)$ be solutions of

$$U_t = \Delta U + U(A-U+cV) \text{ in } \Omega, \quad U = 0 \text{ on } \delta\Omega,$$

$$V_t = \Delta V + V(D+eU-V) \text{ in } \Omega, \quad V = 0 \text{ on } \delta\Omega,$$

$$U(x,0) = U_0(x), \quad V(x,0) = V_0(x),$$

with $A \ge a$, $D \ge d$, $U_0(x) \ge u_0(x) \ge 0$ and $V_0(x) \ge v_0(x) \ge 0$ for all $x \in \Omega$. Then $u(x,t) \le U(x,t)$, $v(x,t) \le V(x,t)$ for all $x \in \Omega$, $t > 0$.

Proof of the theorem 3.2.

(i) Case $ce > 1$. Assume first that $d = a$, and $u_0(x) = pv_0(x)$, where $p = \frac{c+1}{e+1}$. Then solution of (3.1) can be found in the form $u = pv$, with

$$v_t = \Delta v + v(a+\alpha v), \tag{3.12}$$

where $\alpha = c-p > 0$ (by [1] the solution is unique). Any solution of (3.12) with data satisfying (3.3) blows up in finite time. Indeed if $H(t) = \int_\Omega v(x,t)\varphi_1(x)dx$, then $H(0) > 0$ and (assuming $\int_\Omega \varphi_1(x)dx = 1$)

$$H' \geq -\lambda_1 H + aH + \alpha H^2 \geq \alpha H^2.$$

For the general case with say $a \geq d$, we can assume in view of the theorem 2.1 that $v_0(x) \geq g(x)$, $u_0(x) \geq pg(x)$ for some $g(x) > 0$ in Ω. Then by lemma 3.3, the solution of (3.1) lies above the solution of the same system with d in place of a, and $pg(x)$ and $g(x)$ in place of $u_0(x)$ and $v_0(x)$ respectively. By the above this implies the blow up.

(ii) Case $ce = 1$. By the theorem 2.1 we may assume that $u_0(x) \geq \varepsilon\varphi_1$, $v_0(x) \geq \varepsilon\varphi_1$ for some $\varepsilon > 0$. By taking ε sufficiently small we may assume that $\bar{u}_0 \equiv \varepsilon\varphi_1$ and $\bar{v}_0 \equiv \varepsilon\varphi_1$ satisfy (3.7), and hence by lemma 3.1,

$$u_t(x,t;\bar{u}_0,\bar{v}_0) \geq 0, \quad v_t(x,t;\bar{u}_0,\bar{v}_0) \geq 0 \quad \text{in } \Omega \times R_+. \tag{3.13}$$

Notice that either both $u(x,t;\bar{u}_0,\bar{v}_0)$ and $v(x,t;\bar{u}_0,\bar{v}_0)$ are bounded in $L^\infty(\Omega)$ or both are unbounded in $L^\infty(\Omega)$ (if one quantity is bounded then an easy comparison argument for (3.1) shows that the other one is bounded too). If both of the above quantities were bounded, then (3.13) would imply that $u(x,t;\bar{u}_0,\bar{v}_0)$ and $v(x,t;\bar{u}_0,\bar{v}_0)$ converge, and by the theorem 3.4 the limiting functions would give a positive solution of (3.2). But by the theorem 2.1 in [8], the problem (3.2) has no positive solutions if $ce = 1$. Hence in view of lemma 2.3 as time increases

$$\|u(x,t;u_0,v_0)\|_{L^\infty(\Omega)} \to \infty, \quad \|v(x,t;u_0,v_0)\|_{L^\infty(\Omega)} \to \infty.$$

Finally, using the lemma 3.2 and the theorem 3.2, we conclude that blow up cannot occur in finite time.

COMPETING SPECIES

The results of this section are similar to those of the preceding one, and so we omit the proofs.

We consider a system (Ω a smooth domain in R^n)

$$
\begin{aligned}
&u_t = \Delta u + u(a-u-cv) \text{ in } \Omega, \quad u = 0 \text{ on } \delta\Omega \\
&v_t = \Delta v + v(d-eu-v) \text{ in } \Omega, \quad v = 0 \text{ on } \delta\Omega \qquad (4.1)\\
&u(x,0) = \bar{u}_0(x), \quad v(x,0) = \bar{v}_0(x) \quad (a,c,d,e \text{ - positive constants}),
\end{aligned}
$$

and the corresponding steady state system

$$
\begin{aligned}
&\Delta u + u(a-u-cv) = 0 \text{ in } \Omega, \quad u = 0 \text{ on } \delta\Omega \\
&\Delta v + v(d-eu-v) = 0 \text{ in } \Omega, \quad v = 0 \text{ on } \delta\Omega.
\end{aligned} \qquad (4.2)
$$

Lemma 4.1. Assume there are two pairs of positive in Ω functions (u_0, v^0) and (u^0, v_0), with $u_0 = v_0 = 0$ on $\delta\Omega$ and $u^0 \geq 0$, $v^0 \geq 0$ on $\delta\Omega$, which satisfy

$$
\begin{aligned}
&-\Delta u_0 \leq u_0(a-u_0-cv^0) \\
&-\Delta v^0 \geq v^0(d-eu_0-v^0) \qquad \text{in } \Omega,
\end{aligned} \qquad (4.3)
$$

and similar inequalities for (u^0, v_0). Moreover, assume that $u_0 \leq u^0$ and $v_0 \leq v^0$ in Ω. Then

$$
\begin{aligned}
&u_0 \leq u(x,t;u_0,v^0) \leq u^0 \\
&v_0 \leq v(x,t;u_0,v^0) \leq v^0 \quad \text{in } \Omega \times R_+,
\end{aligned} \qquad (4.4)
$$

and

$$
u_t(x,t;u_0,v^0) \geq 0, \quad v_t(x,t;u_0,v^0) \leq 0 \quad \text{in } \Omega \times R_+, \qquad (4.5)
$$

and similar inequalities hold for $u(x,t;u^0,v_0)$ and $v(x,t;u^0,v_0)$.

Theorem 4.1. Assume existence of (u_0,v^0) and (u^0,v_0) as above. Then the following limits exist for all $x \in \Omega$: $\lim_{t\to\infty} u(x,t;u_0,v^0) = u(x)$, $\lim_{t\to\infty} v(x,t;u_0,v^0) = V(x)$, $\lim_{t\to\infty} u(x,t;u^0,v_0) = U(x)$, $\lim_{t\to\infty} v(x,t;u^0,v_0) = v(x)$. The pairs $(u(x),V(x))$ and $(U(x),v(x))$ are positive solutions of (4.2).

The ω-limit set of (4.2) with respect to data in $[u_0,u^0] \times [v_0,v^0]$ is contained in $[u,U] \times [v,V]$.

Corollary. Assume that

$$
\lambda_1(\Delta+a-cu_d) > 0; \quad \lambda_1(\Delta+d-eu_a) > 0.
$$

Then the problem (4.2) has positive solutions $(u(x),V(x))$ and $(U(x),v(x))$, and the ω-limit set of (4.1) with respect to the strictly positive data (i.e. satisfying (4.6) below) is $[u,U] \times [v,V]$.

Proof. Let $\bar{u}(x)$ and $\bar{v}(x)$ be the principal eigenfunctions of $\Delta + a - cu_d$ and $\Delta + d - eu_a$ respectively. Then we can take $u^0 = u_a$, $v^0 = u_d$, $u_0 = \varepsilon\bar{u}, v_0 = \varepsilon\bar{v}$ with ε sufficiently small. Hence we can apply the preceding theorem if the data satisfies

$$\bar{u}_0(x) \geq \varepsilon\bar{u},\ \bar{v}_0(x) \geq \varepsilon\bar{v} \text{ for } \varepsilon \text{ sufficiently small.} \tag{4.6}$$

Finally we mention that in [4] E.N. Dancer proved that (4.1) can have multiple positive solutions.

PREDATOR-PREY INTERACTION

We study the system

$$\begin{aligned} &u_t = \Delta u + u(a-u-cv) \quad \text{in } \Omega,\ u = 0 \text{ on } \delta\Omega \\ &v_t = \Delta v + v(-d+eu-v) \quad \text{in } \Omega,\ v = 0 \text{ on } \delta\Omega \\ &u(x,0) = u_0(x), \quad v(x,0) = v_0(x). \end{aligned} \tag{5.1}$$

Here $u(x,t)$ denotes the population density of a prey, and $v(x,t)$ that of a predator; a,c,d,e, are positive constants. We assume that the data satisfies (3.3), which implies by the maximum principle that $u(x,t)$ and $v(x,t)$ are non-negative for all x and t.

Unlike the previous cases the system (5.1) has no monotonicity properties. Its behavior is determined by stability of the trivial solutions $(0,0)$ and $(u_a,0)$. If the solution approaches $(u_a,0)$ then $v(x,t)$ tends to 0. However the lack of monotonicity does not allow us to use the Vitali's theorem as in the previous sections to conclude that $v(x,t)$ tends to zero uniformly in x. In case $n = 1$ we are able to conclude the uniform convergence, by using the following global a priori bound.

Lemma 5.1. Consider the problem $(\Omega \subset R^n, n \geq 1)$

$$\begin{aligned} &u_t = \Delta u + f(x,t) \text{ in } \Omega,\ u = 0 \text{ on } \delta\Omega \\ &u(x,0) = u_0(x). \end{aligned} \tag{5.2}$$

Assume that

(i) $\|f\|_{L^2(\Omega)} \le c_1$,

(ii) $\|u(x,t)\|_{L^2} \le c_2$,

with constants c_1, c_2 independent of t. Then

$$\|u\|_1 \le c, \ \text{c is independent of t.} \tag{5.3}$$

Here $\|\cdot\|_1$ denotes the norm in the Sobolev's space $H^1(\Omega)$; c depends on c_1, c_2 and $\|u_0\|_1$.

Proof. Our proof follows Babin and Vishik [2], and consists of several steps.

Step 1. Multiply (5.2) by u and integrate over Ω, and then in t from 0 to T. Obtain

$$\int_0^T \|u(x,\tau)\|_1^2 d\tau \le c(c_1, c_2, T, \|u_0\|_0). \tag{5.4}$$

Step 2. Multiply (5.2) by Δu and integrate over Ω. After the usual manipulations,

$$\|u(x,t)\|_1^2 \le \|u_0(x)\|_1^2 + c_1^2 T. \tag{5.5}$$

Step 3. Multiply (5.2) by $t\Delta u$ and integrate,

$$\begin{aligned} D_t(\tfrac{1}{2}t\|u\|_1^2) + t\int(\Delta u)^2 &= \tfrac{1}{2}\|u\|_1^2 - t\int f\Delta u \\ &\le \tfrac{1}{2}\|u\|_1^2 + \tfrac{t}{2}\int(\Delta u)^2 + \tfrac{t}{2}\int f^2. \end{aligned} \tag{5.6}$$

Integrating from 0 to t and using (5.4),

$$\frac{1}{2}t\|u\|_1^2 \le \frac{1}{2}\int_0^t \|u\|_1^2 d\tau + c_1^2 \frac{t^2}{4} \le c.$$

Let now $0 < \delta \le t \le T$. Then

$$\|u\|_1 \le c(c_1, c_2, T, \delta). \tag{5.7}$$

Step 4. Fix say $\delta = 1$ and $T = 10$. Then for $0 < t \le 1$ the estimate (5.3) follows from (5.5), while for $1 \le t \le 10$ it follows from (5.7). Take $t = 1$ as the new initial time. Then $\|u\|_1$ is bounded by the same quantity as in (5.7) for $2 \le t \le 11$, and so on.

Lemma 5.2. Assume that $\lim_{t\to\infty} v(x,t) = 0$ for each $x \in \bar{\Omega} \subset R^1$, and

$$\|v\|_1 \le c, \quad \text{uniformly in t.}$$

Then $v(x,t)$ tends to zero uniformly in $x \in \Omega$.

Proof. Take an arbitrary sequence $\{t_m\} \to \infty$. Suffices to show that $u_m(x) \equiv v(x,t_m)$ tends to zero uniformly in x, as $m \to \infty$. Since $n = 1$, $\|u_m\|_{C^\alpha} \le c\|u\|_1 \le c$, uniformly in t, for any $0 < \alpha < \frac{1}{2}$. Since $C^\alpha(\Omega)$ is compactly imbedded in $C^0(\Omega)$, it follows that a subsequence of $u_m(x)$ converges to zero uniformly in x. Remove this subsequence, and repeat the procedure until the entire sequence is exhausted.

Definition. We say that a species $u(x,t)$ dies out, if $\lim_{t\to\infty} u(x,t) = 0$, otherwise we say that $u(x,t)$ persists.

The following result shows that if the predator can survive with the maximal possible population of prey (i.e., the population of prey in the absence of the predator), then it will survive.

Theorem 5.1. For the problem (5.1) assume that $n = 1$ and the data satisfies (3.3). Then the conditions

(i) $a > \lambda_1$

(ii) $\lambda_1(\Delta + eu_a - d) > 0$

are necessary and sufficient for the persistence of both species.

Proof. Necessity follows by the theorem 2.1. Sufficiency. If $v(x,t) \to 0$ as $t \to \infty$, then by lemma 5.2 the convergence is uniform in x (notice that both u and v are bounded in $L^\infty(\Omega)$). Then as in the proof of the theorem 3.5, $u \to u_a$ as $t \to \infty$ uniformly in $x \in \Omega$. If we now denote by $\bar{v}$ the principal eigenfunction of $\Delta + eu_a - d$, and by $H = \int_\Omega v\bar{v}dx$, then from the second equation in (5.1) we obtain a contradiction as before. If $u(x,t) \to 0$ as $t \to \infty$, then again the convergence is uniform in x. From the second equation in (5.1) it follows that $v(x,t) \to 0$ as $t \to \infty$ uniformly in x (compare $v(x,t)$ with the solution of $V'(t) = -\frac{d}{2}V(t)$, for t large). But then from the first equation in (5.1), $u(x,t) \to u_a$, a contradiction.

In [3] under conditions similar to ours, E.N. Dancer has proved existence of positive steady state for (5.1).

Remark. After this paper was written, it came to our attention that the theorem 6.1 can be extended to general $n > 1$, using global a priori estimates in R. Redlinger, J. Diff. Eqns., 133-153(1986).

Acknowledgements. This research was carried out during a visit to the Institute of Mathematics and Applications which I wish to thank for the stimulating and friendly environment and partial support. I wish to thank E.N. Dancer for many useful discussions at the IMA and his kind patience. I also wish to thank A.V. Babin, P. Polačik and S. Stojanovic for useful discussions and Anne Feldman for the efficient typing.

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