TAIWANESE JOURNAL OF MATHEMATICS
Vol. 8, No. 2, pp. 155-182, June 2004
This paper is available online at http://www.math.nthu.edu.tw/tjm/

SPATIAL PATTERNS FOR POPULATION MODELS IN A HETEROGENEOUS ENVIRONMENT

Yihong Du

Abstract. In this paper, we review some recent results on the effects of heterogeneous spatial environment on various population models. By making use of the observation that the population models make deep changes of behavior when certain coefficient functions vanish in the underlying domain, it is shown that sharp stable patterns can be obtained if the heterogeneous environment is designed suitably. The one species logistic model, two species competition and predator-prey models are discussed.

1. Introduction

It has now become well accepted that ecology and evolution are fundamentally influenced by the spatial characterization of the environment. Moreover, it is generally believed that the innumerable patterns which we witness are mainly the effects of environmental changes, with spatial heterogeneity playing a pivotal role for creating patterns. To capture the spatial influence, diffusion has been included in population models; for example, the classical Lotka-Volterra competition model

$$\begin{cases} u' = a_1 u - b_1 u^2 - c_1 uv, \\ v' = a_2 v - b_2 v^2 - c_2 uv, \end{cases}$$

becomes

$$(1.1)\qquad \begin{cases} u_t - d_2 \Delta u = a_1 u - b_1 u^2 - c_1 uv, & (x,t) \in \Omega \times (0,\infty), \\ v_t - d_2 \Delta v = a_2 v - b_2 v^2 - c_2 uv, & (x,t) \in \Omega \times (0,\infty), \\ u_\nu = v_\nu = 0, & (x,t) \in \partial\Omega \times (0,\infty), \end{cases}$$

Received April 23, 2003.
Communicated by S. B. Hsu.
2000 *Mathematics Subject Classification*: 35J25, 35J85, 49A29.
Key words and phrases: Logistic equation, Competition model, Predator-prey, Pattern, Heterogeneous environment.
Part of this paper was written during my visit to the National Center of Theoretical Sciences, Taiwan, in the period Nov. 2002 - Jan. 2003. I would like to thank NCTS for the warm hospitality and for providing a superb research environment.

where the coefficients a_i, b_i, c_i, d_i, $i = 1, 2$, are positive constants, Ω is a bounded smooth domain in R^N $(N \geq 1)$, and ν denotes the outward unit normal to $\partial\Omega$. In order to understand the effects of spatial heterogeneity, one naturally replaces the constant coefficients in (1.1) by positive functions of the space variable x.

Population models like (1.1) with constant coefficients have received extensive studies in the past three decades. It is known that the long-time dynamical behavior of these models is usually determined by the nonnegative steady-state solutions, i.e., the nonnegative solutions of the corresponding elliptic system. The problem of existence and uniqueness of the positive steady-state solutions has been a central focus of extensive research, via the method of monotone iterations and order preserving operators (e.g., [50], [39], [28]), the method of bifurcation theory (e.g., [2], [53]), and the method of degree theory [e.g., [6], [7]), or a combination of these (e.g., [3],[8], [12], [24], [25],[27], [51]). Interestingly, all these approaches extend easily to the case that the constant coefficients are replaced by positive functions. Therefore, similar existence and uniqueness results can be easily obtained for the variable coefficients case. In order to observe important changes that population models may undergo as the spatial environment changes from homogeneous to heterogeneous, one is naturally led to look at the spatial properties of the solutions. Coincidentally, the understanding of the spatial properties of solutions is becoming more and more important due to the urge to understand the mechanism of pattern formation.

In this paper, we report some recent results along this line of thinking. We will show how patterned solutions in various population models can be obtained by suitably design a spatially heterogeneous environment. The population models to be discussed will include the one species logistic model, the two species competition model and the two species predator-prey model. One basic observation used in this study is that when some of the coefficient functions vanish on part of the underlying domain, the behavior of the model undergoes some deep qualitative changes.

The rest of this paper is organized as follows. In section 2, we consider the logistic model which will play an important role in the discussions of the later sections. Section 3 is concerned with the competition model, where we first consider the degenerate case and then use perturbation to see how solutions with prescribed patterns can be constructed. In section 4, we discuss the Leslie-Gower predator-prey model and examine the change of its behavior as the spatial environment changes from homogeneous to heterogeneous; we also compare it with the classical Lotka-Volterra model and show that these models may behave very differently in heterogeneous environment.

This paper is based on our recent results in [13], [17], [20], [21] and [19]. It is my pleasure to thank my co-authors E.N. Dancer, Sze-Bi Hsu, Qingguang Huang, and Shujie Li; without their help, many of the results in this paper would not exist.

Before ending this section, we would like to mention some related research.

The spatial behavior of positive solutions of the two species competition model has received extensive studies even in the constant coefficient case, i.e., when the spatial environment is homogeneous. (This might be more important from the point of view of understanding the mechanism of pattern formation.) In Kishimoto-Weinberger [38], it was shown that, if the spatial domain Ω is convex, then problem (1.1) with constant coefficients has no stable positive steady-state that depends on x, i.e., all its stable positive steady-states are constant solutions. On the other hand, in Matano-Mimura [46], spatially variable stable positive steady-state solutions were constructed for (1.1) for certain non-convex Ω (see also [37]). In Dancer-Du [12], it was proved that in the strong competition case, positive steady-states of (1.1) tend to segregate over Ω, i.e., uv is close to 0 with u close to $\max\{w, 0\}$ and v close to $\max\{-w, 0\}$, where w is a sign-changing solution of a scalar elliptic equation deduced from (1.1). In Lou-Ni [44], the competition model with self-diffusion and cross-diffusion was closely examined and the existence and asymptotic profile of space dependent positive steady-states were obtained when certain parameters are large. In Du-Lou [24], a predator-prey model was analyzed along a similar line of thinking, but without self-diffusion or cross-diffusion.

In a series of recent papers, Hutson-Lou-Mischaikow-Polacik studied various perturbations of the special competition model

$$\begin{cases} u_t - \mu\Delta u = \alpha(x)u - u^2 - uv, & (x,t) \in \Omega \times (0,\infty), \\ v_t - \mu\Delta v = \alpha(x)v - v^2 - uv, & (x,t) \in \Omega \times (0,\infty), \\ u_\nu = v_\nu = 0, & (x,t) \in \partial\Omega \times (0,\infty), \end{cases}$$

and obtained interesting results revealing some fundamental effects of heterogeneous environment on the competition model. We refer to [34], [35] and [36] for details. Further related results can be found in [1], [4], [5], [40], [42], [47] and [48].

2. The logistic Equation

In this section, we will examine the effects of heterogeneous spatial environment on the logistic model

$$\begin{cases} u_t - d(x)\Delta u = \lambda(x)u - b(x)u^2, & (x,t) \in \Omega \times (0,\infty), \\ u_\nu = 0, & (x,t) \in \partial\Omega \times (0,\infty). \end{cases}$$

Here we assume that the coefficient functions $d(x), \lambda(x)$ and $b(x)$ are positive and continuous over $\overline{\Omega}$.

It turns out that the behavior of this model is very sensitive to $b(x)$ being small in part of the domain Ω. In order to simplify our presentation, we will assume that $d(x)$ and $\lambda(x)$ are positive constants; moreover, by a rescaling of the variable x, we can reduce d to 1 (with Ω changed though). Thus our model can be reduced to the form

$$\text{(2.1)}\qquad \begin{cases} u_t - \Delta u = \lambda u - b(x)u^2, & (x,t) \in \Omega \times (0,\infty),\\ u|_{\partial\Omega} = 0, & (x,t) \in \partial\Omega \times (0,\infty). \end{cases}$$

The following result is well known.

Theorem 2.1.

(i) (2.1) *has no positive steady-state solution when* $\lambda \le 0$, *and it has a unique positive steady-state* u^* *when* $\lambda > 0$.

(ii) *Let* $u(x,t)$ *be an arbitrary positive solution of (2.1). Then* u *is defined for all* $t > 0$ *and it satisfies*

(a) $\lim_{t\to\infty} u(x,t) = 0$ *uniformly for* $x \in \overline{\Omega}$ *if* $\lambda \le 0$,

(b) $\lim_{t\to\infty} u(x,t) = u^*(x)$ *uniformly for* $x \in \overline{\Omega}$ *if* $\lambda > 0$.

To demonstrate the effects of heterogeneous environment on (2.1), we choose $b(x)$ of the form

$$b(x) = b_\epsilon(x) := b_0(x) + \epsilon,$$

where ϵ is a positive constant and $b_0(x)$ is a continuous function satisfying

$$b_0(x) > 0,\ \forall x \in \overline{\Omega} \setminus \overline{D};\ b_0(x) = 0,\ \forall x \in D := \cup_{j=1}^m D_j.$$

Here $D_1, \dots, D_m$ are smooth subdomains of Ω with the following properties

$$\overline{D}_j \subset \Omega,\ \overline{D}_j \cap \overline{D}_k = \emptyset,\ \forall j \ne k.$$

By Theorem 2.1, for each $\epsilon > 0$, (2.1) with $b = b_\epsilon$ has a unique positive steady-state u_ϵ if $\lambda > 0$, and it attracts all the positive solutions of (2.1) as $t \to \infty$. We will examine the behavior of u_ϵ as $\epsilon \to 0$ and reveal that u_ϵ develops a clear pattern for small ϵ. To this end, we need to study (2.1) with $b = b_0$ (known as the degenerate logistic model) and also a related boundary blow-up problem. Let us denote by $\lambda_1(D_j)$ the first eigenvalue of the Dirichlet problem

$$-\Delta u = \lambda u,\ u|_{\partial D_j} = 0.$$

Without loss of generality, we may assume that

$$\lambda_1(D_1) \le \lambda_1(D_2) \le \dots \le \lambda_1(D_m).$$

Theorem 2.2. *The problem*

$$\text{(2.2)}\qquad -\Delta u = \lambda u - b_0(x)u^2, \forall x \in \Omega,\ u|_{\partial\Omega} = 0, \forall x \in \partial\Omega,$$

has a unique positive solution u_0 *for* $\lambda \in (0, \lambda_1(D_1))$, *and it has no positive solution otherwise.*

Remark 2.3. Theorem 2.2 remains true if the term u^2 in (2.2) is replaced by u^p for any $p > 1$. This equation with $p = (N+2)/(N-2)$ for $N \geq 3$ arises in certain geometric problems, and Theorem 2.2 was first proved in that context. See [49].

For convenience of notation, we use the convention that $\lambda_1(D_{m+1}) = \infty$. The following result is taken from [21], which is a generalization of a result in [20].

Theorem 2.4. *For any* $\lambda \in (-\infty, \lambda_1(D_{k+1}))$, *the problem*

$$(2.3) \qquad -\Delta u = \lambda u - b_0(x)u^2 \text{ in } \Omega \setminus (\cup_{j=1}^k \overline{D}_j);\ u|_{\partial\Omega} = 0;\ u|_{\cup_{j=1}^k \partial D_j} = \infty$$

has a minimal positive solution $\underline{U}$ *and a maximal positive solution* $\overline{U}$ *in the sense that any positive solution of (2.3) satisfies* $\underline{U} \leq u \leq \overline{U}$. *(2.3) has no positive solution when* $\lambda \geq \lambda_1(D_{k+1})$.

Note that unless each D_j is simply connected, $\Omega \setminus (\cup_{j=1}^k \overline{D}_j)$ may have more than one (but finitely many, due to the smoothness of D_j) components. By a positive solution of (2.3), we mean a solution which is positive on each component of the underlying region.

We are now ready to state out main result of this section (see [21] for a proof).

Theorem 2.5. *Let* $\lambda > 0$ *be fixed and* u_ϵ *be the unique positive solution of* (2.1) *with* $b(x) = b_\epsilon(x)$. *Then the following holds.*

(i) *If* $0 < \lambda < \lambda_1(D_1)$, *then as* $\epsilon \to 0$, u_ϵ *converges uniformly to* u_0, *the unique positive solution of* (2.2).

(ii) *If* $\lambda_1(D_k) \leq \lambda < \lambda_1(D_{k+1})$ *for some* $1 \leq k \leq m$, *then*

   (a) $\lim_{\epsilon\to 0} u_\epsilon(x) = \infty$ *uniformly on* $\cup_{j=1}^k \overline{D}_j$,

   (b) $\lim_{\epsilon\to 0} u_\epsilon(x) = \underline{U}(x) < \infty$ *uniformly on any compact subset of* $\overline{\Omega} \setminus (\cup_{j=1}^k \overline{D}_j)$, *where* $\underline{U}(x)$ *is the minimal positive solution of* (2.3).

Theorem 2.5 shows that u_ϵ has a clear spatial pattern for small $\epsilon > 0$: its value over $\cup_{j=1}^k \overline{D}_j$ is much bigger than that over the rest of Ω. By choosing the D_j's suitably, one can realize a rather arbitrary pattern. Since u_ϵ is the global attractor of the parabolic problem, we find that the population distribution eventually develops a clear prescribed pattern.

It is interesting to look at the function $v_\epsilon := \epsilon u_\epsilon$. It is easily seen that v_ϵ is the global attractor of all the positive solutions of the following logistic model

$$v_t - \Delta v = \lambda v - [1 + \epsilon^{-1} b_0(x)]v^2 \text{ in } \Omega \times (0, \infty);\ v|_{\partial\Omega \times (0,\infty)} = 0.$$

The function v_ε also develops a clear pattern which is described in the following result (see [21] for a proof).

Theorem 2.6. *Let* $\lambda > 0$ *be fixed and* v_ε *be defined as above. Then the following holds.*

(i) *If* $0 < \lambda \leq \lambda_1(D_1)$, *then as* $\varepsilon \to 0$, v_ε *converges uniformly to* 0 *on* $\overline{\Omega}$.

(ii) *If* $\lambda_1(D_k) < \lambda \leq \lambda_1(D_{k+1})$ *for some* $1 \leq k \leq m$, *then*

(a) $\lim_{\varepsilon\to 0} v_\varepsilon(x) = \theta_j(x)$ *uniformly on* $\overline{D}_j$ *for* $j = 1, ..., k$, *where* θ_j *is the unique positive solution of*

$$-\Delta v = \lambda v - v^2 \text{ in } D_j;\ v|_{\partial D_j} = 0.$$

(b) $\lim_{\varepsilon\to 0} v_\varepsilon(x) = 0$ *uniformly on* $\overline{\Omega} \setminus (\cup_{j=1}^k D_j)$.

Note that if we define $\theta(x) = 0$ on $\overline{\Omega} \setminus (\cup_{j=1}^k \overline{D}_j)$, and $\theta(x) = \theta_j(x)$ on $\overline{D}_j$, then $\theta(x)$ is continuous on $\overline{\Omega}$, with support $\cup_{j=1}^k \overline{D}_j$. Theorem 2.6 shows that in case (ii) v_ε converges to θ uniformly on $\overline{\Omega}$.

A biological interpretation of Theorem 2.6 is the following: *If a heterogeneous environment is suitably designed, the population distribution* (*in the long time*) *will concentrate only on the desired part of the habitat.*

3. The Competition Model

Our method in this section covers competition models of the general form (1.1) with variable coefficients. However, to simplify our presentation, we consider a competition model of the following special form

$$(3.1)\qquad \begin{cases} u_t - \Delta u = \lambda u - b(x)u^2 - cuv, \\ v_t - \Delta v = \mu v - v^2 - duv, \\ u|_{\partial\Omega\times(0,\infty)} = v|_{\partial\Omega\times(0,\infty)} = 0. \end{cases}$$

In sharp contrast to the logistic model, even for the special case that $b(x) \equiv 1$, the existence and uniqueness problem for the positive steady-state solutions of (3.1) is not completely understood. The long-time dynamical behavior of (3.1) is, generally speaking, rather poorly understood. Nevertheless, a general picture about the set of the positive steady-state solutions of (3.1) is available, and there are partial results on its long-time dynamical behavior. These partial results reveal that the dynamics of (3.1) can be extremely complicated. Clearly, the understanding of the heterogeneous spatial effects on (3.1) will be a difficult one.

In the following, we first recall the existing results on the steady-state solutions of (3.1) and its dynamical behavior, we then follow the approaches used in [15-17] to demonstrate how patterned solutions can be constructed by suitably designing the heterogeneous environment, in the spirit of section 2 but with much more technical difficulties.

3.1. Steady-state Solutions and Dynamical Behavior

We recall in this subsection the known results on the steady-state solutions of (3.1) and its dynamical behavior described by these steady-state solutions. Throughout this subsection, we assume that $b(x)$ is continuous and positive over $\overline{\Omega}$. We are only interested in nonnegative solutions.

Clearly $(u, v) = (0, 0)$ is a steady-state of (3.1), and it is called the trivial steady-state. There are exactly two semitrival steady-states, namely nonnegative steady-states (u, v) with exactly one component identically zero. If $v = 0$, then u is a positive steady-state of (2.1), which exists if and only if $\lambda > 0$, and it is unique when exists. We denote this unique positive steady-state of (2.1) by ϕ_λ. If $u = 0$, then v satisfies

$$-\Delta v = \mu v - v^2 \text{ in } \Omega, \ v_\nu|_{\partial\Omega} = 0.$$

It is well known that this standard logistic problem has a unique positive solution $v = \theta_\mu$ when $\mu > 0$, and there is no positive solution when $\mu \leq 0$. Clearly $\phi_\lambda = \theta_\lambda$ when $b(x) \equiv 1$. Therefore, the two semitrivial steady-states of (3.1) are $(\phi_\lambda, 0)$ and $(0, \theta_\mu)$.

The positive steady-states of (3.1) are much more difficult to determine, and have been studied in many previous works. We choose to follow [3] where a bifurcation and monotonicity approach was taken. We would like to remark that in [3], the Dirichelt boundary conditions are used, but the method easily extends to the Neumann boundary conditions case as in (3.1). In this approach, one fixes $\lambda > 0$ and uses local and global bifurcation arguments as in [2], to conclude that there is a bounded global branch of positive steady-states of (3.1), $S = \{(\mu, u, v)\}$, that joins the semitrivial solutions at $(\mu_0, \phi_\lambda, 0)$ and $(\mu^0, 0, \theta_{\mu^0})$, respectively, where $\mu_0 = \lambda_1^\Omega(d\phi_\lambda)$ and $\mu^0 > 0$ is determined uniquely by

$$\lambda = \lambda_1^\Omega(c\theta_{\mu^0}).$$

Here and in what follows, we use $\lambda_1^\Omega(\psi)$ to denote the first eigenvalue of the Neumann problem

$$-\Delta u + \psi u = \lambda u \text{ in } \Omega, \ u_\nu|_{\partial\Omega} = 0.$$

More information about S can be obtained by making use of the monotonicity of the system. For example, if

$$\mu_* = \inf\{\mu : (\mu, u, v) \in S\}, \quad \mu^* = \sup\{\mu : (\mu, u, v) \in S\},$$

then there is no positive solution when $\mu \notin [\mu_*, \mu^*]$. This fact is not obvious as it is not clear that S contains all the possible positive solutions of the system. But it is a consequence of the monotonicity of the system which allows to show that all the maximal and minimal positive solutions must belong to S; this also gives rise to some multiplicity results.

The results obtained by this approach can be summarized as follows.

Theorem 3.1. *Let $\lambda > 0$ be fixed. Then*

(i) (Existence and nonexistence): *There exist μ_* and μ^* satisfying $0 < \mu_* \le \mu^* < \infty$ such that (3.1) has no positive steady-state for $\mu \notin [\mu_*, \mu^*]$, and has at least one positive steady-state for $\mu \in (\mu_*, \mu^*)$.*

(ii) (Location of μ_* and μ^*): $\mu_* \le \min\{\mu_0, \mu^0\}$, $\mu^* \ge \max\{\mu_0, \mu^0\}$.

(iii) (Continuum): *There is a continuum of positive steady-states of (3.1), $S = \{(\mu, u, v)\} \subset R \times C(\overline{\Omega}) \times C(\overline{\Omega})$, that connects the semi-trivial solutions $(\mu_0, \theta_{\mu_0}, 0)$ and $(\mu^0, 0, \theta_{\mu^0})$. Moreover,*

$$\mu_* = \inf\{\mu : (\mu, u, v) \in S\}, \quad \mu^* = \sup\{\mu : (\mu, u, v) \in S\}.$$

(iv) (Multiplicity): *If $\mu_* < \min\{\mu_0, \mu^0\}$, then (3.1) has at least two positive steady-states for $\mu \in (\mu_*, \min\{\mu_0, \mu^0\})$, and at least one positive steady-state for $\mu = \mu_*$. If $\mu^* > \max\{\mu_0, \mu^0\}$, then (3.1) has at least two positive steady-states for $\mu \in (\max\{\mu_0, \mu^0\}, \mu^*)$, and at least one positive solution for $\mu = \mu^*$. Moreover, all these solutions can be chosen from the continuum S.*

Next, we discuss the dynamical behavior of (3.1). The fact that (3.1) defines a monotone dynamical system will play an important role in the discussion here.

Denote $X = C(\overline{\Omega})$, $X^+ = \{u \in X : u(x) \ge 0, \text{ for all } x \in \Omega\}$. Then $P = (-X^+) \times X^+$ is a cone in $E = X \times X$, and P induces an order in E:

$$(u_1, v_1) \le_P (u_2, v_2) \text{ if } (u_2, v_2) - (u_1, v_1) = (u_2 - u_1, v_2 - v_1) \in P,$$

i.e., $u_2(x) \le u_1(x),\ v_2(x) \ge v_1(x),\ \forall x \in \Omega.$

A simple comparison of (3.1) with the decoupled system

$$(3.2) \qquad \begin{cases} u_t - \Delta u = \lambda u - b(x)u^2, & u_\nu|_{\partial\Omega\times(0,\infty)} = 0 \\ v_t - \Delta v = \mu v - v^2, & v_\nu|_{\partial\Omega\times(0,\infty)} = 0 \end{cases}$$

shows that, whenever the initial value (u_0, v_0) is in $X^+ \times X^+$, the solution of (3.1) remains in $X^+ \times X^+$, and is defined for all $t > 0$. Moreover, for any such solution (u, v),

$$\overline{\lim}_{t\to\infty} u(t) \le \phi_\lambda; \quad \overline{\lim}_{t\to\infty} v(t) \le \theta_\mu:$$

Here, and in what follows, $(u(t); v(t))$ denotes $(u(\cdot; t); v(\cdot; t))$. This shows that the order interval

$$[(\phi_\lambda; 0); (0; \theta_\mu)]_P = \{(u; v) \in E : (\phi_\lambda; 0) \le_P (u; v) \le_P (0; \theta_\mu)\}$$

is a global attractor for solutions of (3.1) with nonnegative initial values.

An application of the parabolic maximum principle shows that (3.1) is order-preserving for the order induced by P in E, namely,

$$(u_1(0); v_1(0)) \le_P (u_2(0); v_2(0)) \text{ implies } (u_1(t); v_1(t)) \le_P (u_2(t); v_2(t)) \text{ for all } t > 0;$$

where $(u_1; v_1)$ and $(u_2; v_2)$ are solutions of (3.1).

The following theorem covers the case that (3.1) has no positive steady-states, and it shows that the dynamics of (3.1) on $X^+ \times X^+$ can be completely described for this case.

Theorem 3.2. *Let $(u; v)$ be a solution of (3.1) with initial value $(u_0; v_0)$, $u_0; v_0 \in X^+ \setminus \{0\}$.*

(i) *If $\lambda \le 0$, then $(u; v) \to (0; 0)$ uniformly on Ω as $t \to \infty$ if $\mu \le 0$, and that limit is $(0; \theta_\mu)$ if $\mu > 0$.*

(ii) *If $\lambda > 0$, then $(u; v) \to (\phi_\lambda; 0)$ uniformly on Ω as $t \to \infty$ if $0 < \mu < \mu_*$, and that limit is $(0; \theta_\mu)$ if $\mu > \mu^*$, where μ_* and μ^* are as in Theorem 3.1.*

The biological interpretation of Theorem 3.2 is the following. When no coexistence can be reached, at least one of the two species will be wiped out in the long run, and the specific growth rates of the two species determine which species will die out.

The case left by Theorem 3.2 is basically the case when (3.1) has a positive steady-state:

$$\lambda > 0; \quad \mu_* < \mu < \mu^*:$$

The dynamics of (3.1) for this case is rather complicated, and we will divide this case into several subcases.

(i) $\mu_0 < \mu^0$, $\mu_0 < \mu < \mu^0$.

(ii) $\mu_* < \min\{\mu_0; \mu^0\}$, $\mu_* < \mu < \min\{\mu_0; \mu^0\}$.

(iii) $\mu^* > \max\{\mu_0; \mu^0\}$; $\max\{\mu_0; \mu^0\} < \mu < \mu^*$:

(iv) $\mu^0 < \mu_0$, $\mu^0 < \mu < \mu_0$.

Theorem 3.3. *In case (i), (3.1) has a minimal positive steady-state* $(\underline{u};\underline{v})$ *and a maximal positive steady-state* $(\overline{u};\overline{v})$ *in the sense that any positive steady-state* $(u;v)$ *of (3.1) satisfies* $(\underline{u};\underline{v}) \leq_P (u;v) \leq_P (\overline{u};\overline{v})$. *Moreover, the order interval*

$$[(\underline{u};\underline{v});(\overline{u};\overline{v})]_P = \{(u;v) \in E : (\underline{u};\underline{v}) \leq_P (u;v) \leq_P (\overline{u};\overline{v})\}$$

attracts all the solutions of $(3{:}1)$ *with nontrivial nonnegative initial values.*

Note that, if the maximal and minimal solutions coincide, then the order interval reduces to one point, and Theorem 3.3 gives a complete description for the dynamical behavior of (3.1). However, a counter-example in [8, section 3] can be easily modified to show that there are cases that these two solutions are different.

Theorem 3.4. *In case* (ii), $(3{:}1)$ *has a maximal positive steady-state* $(\overline{u};\overline{v})$ *and the order interval* $[(Á_{¸};0);(\overline{u};\overline{v})]_P$ *attracts all the solutions of* $(3{:}1)$ *with nontrivial nonnegative initial values.*

Note that in Theorem 3.4, there is at least one more positive steady-state of (3.1) in that order interval. Moreover, the bifurcation and analyticity argument of [18] and a result in [8] can be used to show that, generically, the maximal solution $(\overline{u};\overline{v})$ is asymptotically stable. (A more detailed discussion of this point will be given later.) The other end point of the order interval, $(µ_{¸};0)$, is also asymptotically stable, as it is easily checked to be linearly stable. Thus, inside this order interval, the so called global attractor, the long time behavior of the solution $(u;v)$ of (3.1) depends on its initial value $(u_0;v_0)$. If $(u_0;v_0)$ is close enough to $(Á_{¸};0)$, then $(u;v) \to (Á_{¸};0)$ as $t \to \infty$, while if the initial value is close enough to $(\overline{u};\overline{v})$, then, generically, $(u;v) \to (\overline{u};\overline{v})$ as $t \to \infty$. If the initial value is not close to either end points, and is not a steady-state solution, the long time behavior of $(u;v)$ is not fully known.

Theorem 3.5. *In case (iii),* $(3{:}1)$ *has a minimal positive steady-state* $(\underline{u};\underline{v})$, *and the order interval* $[(\underline{u};\underline{v});(0;µ_1)]_P$ *attracts all the solutions of* $(3{:}1)$ *with nontrivial nonnegative initial values.*

Remarks similar to that for case (ii) apply for the dynamics of (3.1) in the order interval $[(\underline{u};\underline{v});(0;µ_1)]_P$ here.

Finally let us consider case (iv). In this case, the two semitrival solutions $(Á_{¸};0)$ and $(0;µ_1)$ are linearly stable, and hence asymptotically stable. Theorem 3.1 guarantees at least one positive steady-state solution for (3.1), but we are unable to reduce the analysis of its dynamics to a global attractor smaller than $[(Á_{¸};0);(0;µ_1)]_P$ like in the previous cases. Note that, the behavior of the system on $[(Á_{¸};0);(0;µ_1)]_P$ is similar to that for cases (ii) and (iii) on their corresponding reduced order intervals.

The proofs of Theorems 3.2-3.5 are similar and can be found in [15] and [33]. Further results on monotone dynamical systems can be found in [14], [29], [45] and [52].

3.2. Stable Steady-states with Prescribed Patterns

As in section 2, in order to observe the effects of spatial heterogeneity, we now take $b(x) = b_\varepsilon(x) = b_0(x) + \varepsilon$ (where $b_0(x)$ is as defined in section 2), and consider (3.1) with $b = b_\varepsilon$. For any fixed $\varepsilon > 0$, Theorem 3.1 still applies, but the values μ_*, μ^* and μ_0 depend on ε, and will be denoted by $\mu_*(\varepsilon)$, $\mu^*(\varepsilon)$ and $\mu_0(\varepsilon)$, respectively. The semitrivial solution $(\phi_\lambda, 0)$ now becomes $(\phi_\lambda^\varepsilon, 0)$. But $(0, \theta_\mu)$ and μ^0 are independent of ε.

The behavior of $\mu_0(\varepsilon), \mu_*(\varepsilon)$ and $\mu^*(\varepsilon)$ as $\varepsilon \to 0$ will become crucial in our later analysis. We consider $\mu_0(\varepsilon) = \lambda_1^\Omega(d\phi_\lambda^\varepsilon)$ first. If $0 < \lambda < \lambda_1(D_1)$, then by part (i) of Theorem 2.5 and the continuous dependence of $\lambda_1^\Omega(\phi)$ on ϕ, we find

$$\mu_0^\varepsilon = \lambda_1^\Omega(d\phi_\lambda^\varepsilon) \to \lambda_1^\Omega(d\phi_0);$$

where ϕ_0 is the unique positive solution of (2.2).

Suppose next that $\lambda \geq \lambda_1^{D_1}(0)$. We will need the following result whose proof can be found in [17]. (In fact, the proof in [17] was for the Dirichlet boundary condition case; for Neumann boundary conditions, the proof is similar.)

Proposition 3.6. *Suppose* $\psi_n \in C(\overline{\Omega})$ *satisfies*

(i) $\psi_n \geq -M$ *for some constant* M *and all* $n \geq 1$,

(ii) $\psi_n \to \infty$ *uniformly on* $D^k := \cup_{j=1}^k D_j$ *for some* k *satisfying* $1 \leq k \leq m$,

(iii) *there exists* $\psi \in C(\overline{\Omega} \setminus D^k)$ *such that* $\psi_n \leq \psi$ *and* $\psi_n \to \psi$ *in* $L^p(\Omega')$ *for every* $p > 1$ *and any* $\Omega' \subset\subset \Omega \setminus D^k$.

Then

$$\lambda_1^\Omega(\psi_n) \to \lambda_1^{\Omega \setminus D^k}(\psi):$$

Here we need to explain the meaning of $\lambda_1^{\Omega\setminus D^k}(\psi)$. We may assume that $\Omega \setminus D^k$ has i components $\omega_1, \ldots, \omega_i$. (The number i must be finite due to the smoothness of the boundary of $\Omega \setminus D^k$.) For each $1 \leq s \leq i$, define $\lambda_1^{\omega_s}(\psi)$ by,

$$\lambda_1^{\omega_s}(\psi) = \lim_{n\to\infty} \lambda_1^{\omega_s}(\max\{\psi, n\}):$$

Then

$$\lambda_1^{\Omega\setminus D^k}(\psi) = \min_{1\leq s\leq i} \lambda_1^{\omega_s}(\psi):$$

Combining Theorem 2.5 and Proposition 3.6, and noticing that ϕ_ε increases as ε decreases, we obtain

Corollary 3.7. *If $\lambda_1(D_k) \le \lambda < \lambda_1(D_{k+1})$ for some $1 \le k \le m$, then*

$$\lim_{\epsilon \to 0} \lambda_1^{\Omega}(d\phi_\lambda^\epsilon) = \lambda_1^{\Omega \setminus \cup_{j=1}^{k} D_j}(d\underline{U}),$$

where $\underline{U}$ is the minimal positive solution of (2.3).

We now consider $\mu_*(\epsilon)$ and $\mu^*(\epsilon)$. As will become clear later, the behavior of these two functions of ϵ is much more difficult to understand, and it plays a crucial role in the study of this section. We need to first understand the degenerate competition model, i.e., (3.1) with $b = b_0$. An important step in this analysis is the following a priori estimate, whose proof can be found in [17].

Lemma 3.8. *Given real numbers λ and M, there exists $C = C(\lambda, M) > 0$ such that any positive steady-state (u, v) of (3.1) with $b = b_0$ and $\mu \le M$ satisfies*

$$\|u\|_\infty + \|v\|_\infty \le C.$$

Let us recall that $\|\cdot\|_\infty$ denotes the $L^\infty(\Omega)$ norm.

Using Lemma 3.8 and a bifurcation argument, we can prove the following result on the positive steady-states of (3.1) with $b = b_0$ (see [15] and [17]).

Theorem 3.9. *Suppose $\lambda \ge \lambda_1(D_1)$. Then*

(i) (Existence and nonexistence) *There exists $\hat{\mu}_* \le \mu^0$ such that (3.1) with $b = b_0$ has no positive steady-state for $\mu < \hat{\mu}_*$, and it has at least one positive steady-state for $\mu > \hat{\mu}_*$.*

(ii) (Multiplicity and stability) *If $\hat{\mu}_* < \mu^0$, then (3.1) with $b = b_0$ has at least two positive steady-states for $\mu \in (\hat{\mu}_*, \mu^0)$, and at least one positive steady-state for $\mu = \hat{\mu}_*$. Moreover, at least one positive steady-state is asymptotically stable for $\mu \in (\hat{\mu}_*, \mu^0)$.*

(iii) (Continuum) *All the positive steady-states stated in (i) and (ii) above can be chosen from an unbounded positive solution branch S which joins the semitrivial steady-state $(\mu^0, 0, \theta_{\mu^0})$ and ∞.*

Remark 3.10. If $0 < \lambda < \lambda_1(D_1)$, then the conclusions of Theorem 3.1 still hold when $b = b_0$ (which can be proved by slightly modifying the proof for Theorem 3.1). This reveals that the number $\lambda_1(D_1)$ is critical for the change of behavior of (3.1) with $b = b_0$.

Making use of Lemma 3.8 and Theorem 3.9, we can prove the following result (see [16] and [17] for details).

Proposition 3.11. *The functions $\epsilon \to \mu^*(\epsilon)$ and $\epsilon \to \mu_*(\epsilon)$ are both nonincreasing. Moreover,*

(i) *if* ¸ $\geq$ ¸$_1$(D$_1$), *then* $\lim_{² \to 0}$ ¹*(²) $= \infty$ *and* $\lim_{² \to 0}$ ¹$_*$(²) = ¹̂ $\leq$ ¹̂$_*$, *where* ¹̂$_*$ *is defined in Theorem 3.9;*

(ii) *if* 0 < ¸ < ¸$_1$(D$_1$), *then* $\lim_{² \to 0}$ ¹*(²) = ¹* *and* $\lim_{² \to 0}$ ¹$_*$(²) = ¹$_*$, *where* ¹* *and* ¹$_*$ *are as defined in Theorem 3.1* (*see Remark 3.10 above*).

We would like to roughly explain how the fact that ¹*(²) $\to \infty$ as ² $\to 0$ is proved in the case ¸ $\geq$ ¸$_1$(D$_1$). Here we regard (3.1) with b = b$_²$ as a smooth perturbation of (3.1) with b = b$_0$. Then a degree theoretic argument and the a priori estimate established in Lemma 3.8 can be used to show that any bounded part of the global bifurcation branch S of positive steady-states of (3.1) with b = b$_0$ is perturbed to give a part of the global bifurcation branch S$_²$ of (3.1) with b = b$_²$. Since S bifurcates from the semitrivial solution (¹^0; 0; µ$_{¹0}$) and continues to infinity through ¹ $\to \infty$, for small ² > 0, after bifurcating from the (same) semitrivial solution (¹^0; 0; µ$_{¹0}$), S$_²$ follows S until ¹ is very large (depending on ²) and then bends back at ¹ = ¹*(²), after that S$_²$ is continued for smaller ¹ until it joins the other semitrivial solution (¹$^²_0$; Á$^²_¸$; 0).

We are now in a position to describe how to find an asymptotically stable patterned positive steady-state (u$_²$; v$_²$) of (3.1) with b = b$_²$. We assume from now on that

$$(3{:}3) \qquad ¸ \geq ¸_1(D_1):$$

From the above discussions, we know that ¹$^²_0$ = ¸$^\Omega_1$(dÁ$^²_¸$) has a finite limit as ² $\to 0$, the value of which is determined by ¸ in a rather implicit manner.

By Proposition 3.11, we have ¹*(²) $\to \infty$ as ² $\to 0$. Therefore, for all small ², ¹*(²) > max{¹$^²_0$; ¹^0}, and by Theorem 3.9, (3.1) with b = b$_²$ has at least two positive steady-states for ¹ satisfying ¹*(²) > ¹ > max{¹$^²_0$; ¹^0} and at least one positive steady-state for ¹ = ¹*(²). What is more important for our purpose here is that the proof of Theorem 3.9 shows that for each ¹ satisfying ¹$^²_0$ < ¹ $\leq$ ¹*(²), there exists a minimal positive steady-state (u$_²$; v$_²$) in the sense that any possible positive steady-state (u; v) satisfies u $\leq$ u$_²$ and v $\geq$ v$_²$.

By Theorem 3.5, for ¹ $\in$ (¹$^²_0$; ¹*(²)), the order interval

$$[(u_²; v_²); (0; µ_¹)]_P := \{(u; v) \in E : (u_²; v_²) \leq_P (u; v) \leq_P (0; µ_¹)\}$$

attracts all the solutions of (3.1) with b = b$_²$ and with nontrivial nonnegative initial values in E. Moreover, the proof of this theorem shows that (u$_²$; v$_²$) is globally attractive from below in the sense that if (u(x; t); v(x; t)) is a nontrivial nonnegative solution with initial value (u(·; 0); v(·; 0)) $\leq_P$ (u$_²$; v$_²$), then (u(·; t); v(·; t)) $\to$ (u$_²$; v$_²$) in E as t $\to \infty$.

Let us recall that the proof of these facts is based on the observation that for ¹ in this range, (Á$_²$; 0) is linearly unstable and there exists a sequence of lower steady-state solutions $(u_n, v_n) \in [(\phi_\epsilon, 0), (0, \theta_\mu)]_P$ which converges to $(\phi_\epsilon, 0)$, and any solution of (3.1) with initial value (u_n, v_n) converges to (u_ϵ, v_ϵ) as $t \to \infty$.

It is important for us to know whether (u_ϵ, v_ϵ) is asymptotically stable as a steady-state of (3.1) with $b = b_\epsilon$, though we already know that it is globally attractive from below. As we will show later, this is generically the case; in the possible exceptional cases the definition of (u_ϵ, v_ϵ) needs to be changed in order to obtain asymptotical stability. We will give the detailed discussion of this point after we have found the spatial pattern of (u_ϵ, v_ϵ).

Our main result on the spatial behavior of (u_ϵ, v_ϵ) is the following (see Theorem 3.8 in [17]).

Theorem 3.12. *If* $\lambda_1(D_k) < \lambda < \lambda_1(D_{k+1})$ *and* $\mu > \lambda_1^{\Omega \setminus D^k}(dU^*)$ *for some* $1 \le k \le m$, *where* $D^k := \cup_{j=1}^k D_j$ *and* U^* *is the maximal positive solution of (2.3), then, as* $\epsilon \to 0$,

(a) $(u_\epsilon, v_\epsilon) \to (\infty, 0)$ *uniformly on* D^k,

(b) $\overline{U}_\infty \le \underline{\lim}_{\epsilon \to 0} u_\epsilon, \ \overline{\lim}_{\epsilon \to 0} u_\epsilon \le \underline{U}_\infty; \quad \underline{V}_\infty \le \underline{\lim}_{\epsilon \to 0} v_\epsilon, \ \overline{\lim}_{\epsilon \to 0} v_\epsilon \le \overline{V}_\infty$, *where the limits are uniform on any compact subset of* $\overline{\Omega} \setminus D^k$, $(\underline{U}_\infty, \underline{V}_\infty)$ *and* $(\overline{U}_\infty, \overline{V}_\infty)$ *are respectively the minimal and maximal positive solutions of the boundary blow-up problem*

$$(3.4) \qquad \begin{cases} -\Delta u = \lambda u - b(x)u^2 - cuv, \ x \in \Omega \setminus D^k, \\ -\Delta v = \mu v - v^2 - duv, \ x \in \Omega \setminus D^k, \\ u_\nu|_{\partial\Omega} = v_\nu|_{\partial\Omega} = 0, \ u|_{\partial D^k} = \infty, v|_{\partial D^k} = 0. \end{cases}$$

Moreover, for any positive sequence $\{\epsilon_n\}$ *that converges to 0,* $\{(u_{\epsilon_n}, v_{\epsilon_n})\}$ *has a subsequence that converges, uniformly on any compact subset of* $\overline{\Omega} \setminus D^k$, *to a positive solution of* (3.4).

Here, the maximal and minimal positive solutions of (3.4) are understood in the sense that any positive solution (u, v) of (3.4) satisfies

$$\underline{U}_\infty \ge u \ge \overline{U}_\infty, \ \underline{V}_\infty \le v \le \overline{V}_\infty.$$

Theorem 3.12 shows that (u_ϵ, v_ϵ) exhibits a clear pattern as $\epsilon \to 0$. We will demonstrate below that an intuitively clearer pattern is given by a rescaled version of (u_ϵ, v_ϵ), namely $(\tilde{u}_\epsilon, v_\epsilon) := (\epsilon u_\epsilon, v_\epsilon)$. It is easily checked that $(\tilde{u}_\epsilon, v_\epsilon)$ is a minimal positive solution of the following elliptic system

$$(3.5) \qquad \begin{cases} -\Delta u = \lambda u - [\epsilon^{-1} b(x) + 1]u^2 - cuv, \\ -\Delta v = \mu v - v^2 - \epsilon^{-1} duv, \\ u_\nu|_{\partial\Omega} = v_\nu|_{\partial\Omega} = 0. \end{cases}$$

Clearly $(\tilde u_\epsilon, v_\epsilon)$ has the same dynamical properties as (u_ϵ, v_ϵ) in (3.1) when regarded as a steady-state of the corresponding parabolic problem of (3.5).

We have the following result (see [17]) which improves several conclusions in Theorem 3.12.

Theorem 3.13. *If $\lambda_1(D_k) < \lambda < \lambda_1(D_{k+1})$ and $\mu > \lambda_1^{\Omega\setminus D^k}(dU^*)$ for some $1 \le k \le m$, where $D^k := \cup_{j=1}^k D_j$ and U^* is the maximal positive solution of (2.3), then, as $\epsilon \to 0$,*

(a) *$(\tilde u_\epsilon, v_\epsilon) \to (\tilde\theta_\lambda, 0)$ uniformly on D^k, where, for $j = 1, ..., k$, $\tilde\theta_\lambda|_{D_j}$ is the unique positive solution of*

$$(3.6)\qquad -\Delta u = \lambda u - u^2 \text{ in } D_j;\ u|_{\partial D_j} = 0;$$

(b) *for any positive sequence $\epsilon_n \to 0$, $\{(\tilde u_{\epsilon_n}, v_{\epsilon_n})\}$ has a subsequence that converges to $(0, V)$ uniformly on $\overline{\Omega\setminus D^k}$, where $V \in C(\overline{\Omega\setminus D^k})$ and is the second component of some positive solution (U, V) of (3.4).*

To understand the asymptotical stability of (u_ϵ, v_ϵ), we fix $\epsilon > 0$ small and consider its dependence on μ. It is convenient to write

$$(u_\epsilon, v_\epsilon) = (u_\epsilon(\mu), v_\epsilon(\mu)) = (u(\mu), v(\mu)).$$

By a simple comparison argument we find that $(u(\mu), v(\mu))$ increases with μ in the order $\le_P$ for $\mu \in (\mu_0^\epsilon, \mu^*(\epsilon)]$.

Denote

$$O = O_\epsilon := \{\mu \in (\mu_0^\epsilon, \mu^*(\epsilon)] : (u(\mu), v(\mu)) \text{ is linearly stable}\}.$$

We can use a result in [18] to show that (see [17] for details)

Proposition 3.14. *O is an open set in $(\mu_0^\epsilon, \mu^*(\epsilon)]$, and its complement $(\mu_0^\epsilon, \mu^*(\epsilon)] \setminus O$ has measure zero in R^1.*

Let $E^0 = E^0_\epsilon := (\mu_0^\epsilon, \mu^*(\epsilon)] \setminus O_\epsilon$. Then E^0 is the exceptional set where it is unclear whether $(u(\mu), v(\mu))$ is asymptotically stable. We need Dancer's theory (see [8, 9, 10, 11]) to understand this case. By this theory, the following result holds.

Proposition 3.15. *If $(u(\mu), v(\mu))$ is continuous at $\mu_0 \in E^0$, then $(u(\mu_0), v(\mu_0))$ is asymptotically stable; if $(u(\mu), v(\mu))$ is discontinuous at $\mu_0 \in E^0$, then $(u(\mu_0), v(\mu_0))$ is unstable, but in this case, the limit*

$$(u^*(\mu_0), v^*(\mu_0)) := \lim_{\mu\to\mu_0+0} (u(\mu), v(\mu))$$

exists, it is a positive steady-state of (3.1) with $b = b_\epsilon$*, and is asymptotically stable.*

Note that, by the implicit function theorem, at each $\mu_0 \in O$, the map $\mu \to (u(\mu); v(\mu))$ is continuously differentiable in μ.

We are now ready to explain the modification of $(u_\epsilon; v_\epsilon)$ so that it is always asymptotically stable but still has the spatial patterns as described in Theorem 3.12. We define, for each $\mu \in (\mu_0^\epsilon; \mu^*(\epsilon))$,

$$(u_\epsilon^*(\mu); v_\epsilon^*(\mu)) = \lim_{\mu' \to \mu+0} (u_\epsilon(\mu'); v_\epsilon(\mu')):$$

Then from the above discussion, we know that $(u_\epsilon^*(\mu); v_\epsilon^*(\mu))$ is always asymptotically stable. Moreover, if $\mu_0 \in [\mu_1; \mu_2] \subset (\mu_0^\epsilon; \mu^*(\epsilon))$, then

$$(u_\epsilon(\mu_1); v_\epsilon(\mu_1)) \le_P (u_\epsilon(\mu_0); v_\epsilon(\mu_0)) \le_P (u_\epsilon^*(\mu_0); v_\epsilon^*(\mu_0)) \le_P (u_\epsilon(\mu_2); v_\epsilon(\mu_2)):$$

From this, we easily see by Theorem 3.12 that if $\mu_1; \mu_2$ are close enough to μ_0, then $(u_\epsilon^*(\mu_0); v_\epsilon^*(\mu_0))$ exhibits the same pattern as $(u_\epsilon(\mu_i); v_\epsilon(\mu_i))$, $i = 0; 1; 2$, when $\epsilon \to 0$. Indeed, Theorem 3.12 remains valid when $(u_\epsilon(\mu); v_\epsilon(\mu))$ is replaced by $(u_\epsilon^*(\mu); v_\epsilon^*(\mu))$. Similarly, Theorem 3.13 remains true when $(\epsilon u_\epsilon(\mu); v_\epsilon(\mu))$ is replaced by $(\epsilon u_\epsilon^*(\mu); v_\epsilon^*(\mu))$.

4. A Predator-prey Model

In this section, we mainly consider the following diffusive predator-prey system

$$(4{:}1)\qquad \begin{cases} u_t - d_1 \Delta u = \lambda u - \alpha u^2 - \beta uv; & x \in \Omega; t > 0; \\ v_t - d_2 \Delta v = \mu v(1 - \delta \frac{v}{u}); & x \in \Omega; t > 0; \\ \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = 0; & x \in \partial\Omega; t > 0; \end{cases}$$

where Ω is a bounded domain in R^N with smooth boundary $\partial\Omega$, $d_1; d_2; \lambda; \mu; \alpha; \beta; \delta$ are continuous positive functions of $x \in \overline{\Omega}$. This system describes the interaction of a prey species u and a predator species v in a given spatial region Ω; the Neumann boundary condition means that no species can pass across the boundary of Ω.

The ODE case of this model is known as the Leslie-Gower model, and has been studied by many people; we refer to [31] and [32] for more details and related work. For our diffusive model (4.1), we want to know whether the strategy used in the previous sections can be adapted to show that it is possible to design a heterogeneous environment so that the populations concentrate on certain desired parts of a given spatial region Ω, i.e., the population distribution develops a prescribed pattern. As will become clear, this is not easy at all since the predator-prey model behaves very differently from the competition model. Moreover, we will compare (4.1) with the classical Lotka-Volterra predator-prey model and observe some essential differences between them.

4.1. The Homogeneous Case

In contrast to the competition model, if all the coefficient functions in (4.1) are positive constants, then simple dynamics is expected (though not completely proved). By replacing u by u/δ, and α by $\alpha\delta$, we readily see that (4.1) is reduced to

$$(4.2)\qquad \begin{cases} u_t - d_1\Delta u = u(\lambda - \alpha u - \beta v), & x \in \Omega, t > 0, \\ v_t - d_2\Delta v = \mu v(1 - \frac{v}{u}), & x \in \Omega, t > 0, \\ \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = 0, & x \in \partial\Omega, t > 0. \end{cases}$$

Clearly,

$$(u^*, v^*) = \left(\frac{\lambda}{\alpha + \beta}, \frac{\lambda}{\alpha + \beta}\right)$$

is the only constant positive steady-state of (4.2).

Let $(u(x,t), v(x,t))$ be a positive solution of (4.2). A simple comparison argument yields $0 < u(x,t) < U(x,t)$ for all $t > 0$ and $x \in \Omega$, where U is the unique solution of

$$U_t - d_1\Delta U = \lambda U - \alpha U^2 \text{ in } \Omega \times (0,\infty), \; U_\nu|_{\partial\Omega\times(0,\infty)} = 0, \; U(x,0) = u(x,0).$$

It is well known that $U(x,t) \to \lambda/\alpha$ as $t \to \infty$ uniformly in x. From these facts, it follows by standard comparison arguments that $u(x,t)$ and $v(x,t)$ exist and remain positive for all $t > 0$, and

$$\overline{\lim}_{t\to\infty} v(x,t) \le \lambda/\alpha.$$

Adapting the Lyapunov function in [31] by defining

$$V(u,v) = \int \frac{u - u^*}{u^2}du + c\int \frac{v - v^*}{v}dv,$$

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

where $c > 0$ is a suitable constant, and $(u(x,t), v(x,t))$ is an arbitrary positive solution of (2.1), we can easily establish the following result.

Proposition 4.1. *When* $\alpha > \beta$, (u^*, v^*) *attracts every positive solution of* (4.2).

The restriction $\alpha > \beta$ can be relaxed by using a different Lyapunov function where V is replaced by

$$V^*(u, v) = \int \frac{u^2 - (u^*)^2}{u^2} du + c \int \frac{v - v^*}{v} dv$$

for some suitable constant c. Let s_0 be the unique positive zero of

$$h(s) = 32s^3 + 16s^2 - s - 1.$$

Then it is easily seen that $s_0 \in (1/4, 1/5)$. We have the following improvement of Proposition 4.1.

Theorem 4.2. *Suppose* $\alpha/\beta > s_0$. *Then* (u^*, v^*) *attracts every positive solution of* (4.2).

Remark 4.3. We conjecture that the conclusion of Theorem 4.2 is valid for all positive constants α and β.

4.2. The Heterogeneous Case

We now consider the case that all the coefficients in (4.1) are continuous positive functions on $\overline{\Omega}$. Given any continuous positive function pair $(u_0(x), v_0(x))$ on $\overline{\Omega}$, let $(u(x,t), v(x,t))$ be the unique solution of (4.1) satisfying $(u(x,0), v(x,0)) = (u_0(x), v_0(x))$. Standard theory of parabolic equations implies that the solution exists as long as it is bounded (in the L^∞-norm, for example). A simple comparison argument shows that the solution remains positive and $0 < u(x,t) < U(x,t)$ for $t > 0$, $x \in \Omega$, where U is the unique solution to

$$U_t - d_2\Delta U = \lambda U - \alpha U^2 \text{ in } \Omega \times (0,\infty);\ U_\nu = 0 \text{ on } \partial\Omega \times (0,\infty);\ U(x,0) = u_0(x). \tag{4.3}$$

From well-known results on the logistic model, we know that

$$U(x,t) \to U^*(x) \text{ as } t \to \infty \text{ uniformly in } x, \tag{4.4}$$

where U^* is the unique positive steady-state of (4.3). By the maximum principle we have $U^*(x) > 0$ on $\overline{\Omega}$.

If we denote by $V(x,t)$ the unique solution of

$$V_t - d_2\Delta V = \mu V\left(1 - \delta\frac{V}{U}\right) \text{ in } \Omega \times (0,\infty);\ V_\nu = 0 \text{ on } \partial\Omega \times (0,\infty);\ V(x,0) = v_0(x),$$

we find from the comparison principle that $0 < v(x,t) < V(x,t)$ for $t > 0$ and $x \in \Omega$. Moreover, using (4.4), one easily shows that $V(x,t) \to V^*(x)$ as $t \to \infty$ uniformly in x, where V^* is the unique positive solution of

$$-d_2\Delta V = \mu V\left(1 - \delta\frac{V}{U^*}\right) \text{ in } \Omega,\ V|_{\partial\Omega} = 0.$$

Therefore, we have

$$\overline{\lim}_{t\to\infty} u(x,t) \le U^*(x),\quad \overline{\lim}_{t\to\infty} v(x,t) \le V^*(x). \tag{4.5}$$

Unfortunately, not much more can be proved beyond (4.5) about the long-time behavior of (4.1). From now on, we will mainly consider the positive steady-state of (4.1). We suspect that (4.1) has a unique positive steady-state which attracts every positive solution as $t \to \infty$. While a complete answer to this difficult question is still beyond our reach, we are nevertheless able to obtain existence and spatial properties for the positive steady-states under suitable assumptions of the coefficient functions. Our approach is based on various elliptic estimates, topological degree theory and the use of boundary blow-up solutions.

As in the previous sections, it turns out that the spatial behavior of the steady-states is very sensitive to $\alpha(x)$ being small. To simplify the mathematical presentation, we will from now on assume that all the coefficient functions are positive constants, except α, which is a nonconstant function of x. As we are concerned with steady-states only, we need only study the positive solutions of the elliptic system

$$\begin{cases} -d_1\Delta u = \lambda u - \alpha(x)u^2 - \beta uv, & x \in \Omega, \\ -d_2\Delta v = \mu v(1 - \delta\frac{v}{u}), & x \in \Omega, \\ u|_{\partial\Omega} = v|_{\partial\Omega} = 0, & x \in \partial\Omega. \end{cases} \tag{4.6}$$

By some simple change of scales, (4.6) can be reduced to the following simpler form:

$$\begin{cases} -\Delta u = \lambda u - \alpha(x)u^2 - \beta uv, & x \in \Omega, \\ -\Delta v = \mu v(1 - \frac{v}{u}), & x \in \Omega, \\ u|_{\partial\Omega} = v|_{\partial\Omega} = 0, & x \in \partial\Omega. \end{cases} \tag{4.7}$$

We would like to remark that our techniques work as well without these simplifications, but using the form (4.7) simplifies greatly the notations.

Let us recall that in (4.7), λ, μ, β are positive constants, and $\alpha(x)$ is a continuous positive function over $\overline{\Omega}$.

By an a priori estimate and degree argument, we can prove the following general existence result (see [19] for details).

Theorem 4.4. *Problem* (4.7) *always has a positive solution.*

We now consider a degenerate case where $\alpha = b_0$ and b_0 is defined in section 2.

Theorem 4.5. *Suppose that* $\lambda \in (0, \lambda_1(D_1))$. *Then* (4.7) *with* $\alpha = b_0$ *has a positive solution for every* $\lambda > 0$ *and* $\beta > 0$.

In terms of the existence of positive solutions of (4.7), in view of Theorem 4.4 where $\alpha(x)$ is positive on Ω, Theorem 4.5 suggests that the vanishing of $\alpha(x)$ on D does not cause essential changes to the behavior of (4.7) in the case $\lambda < \lambda_1(D_1)$; indeed, in either theorems, the existence of a positive solution is guaranteed for every $\mu > 0$ and $\beta > 0$.

In sharp contrast, we will show in the following that this is no longer the case once $\lambda > \lambda_1(D_1)$. In fact, for any fixed λ in this range, we will prove that for each $\mu \in (0, \lambda_1(D_1))$, there exists a $\beta_{\lambda,\mu} > 0$ so that (4.7) with $\alpha = b_0$ has no positive solution when $0 < \beta < \beta_{\lambda,\mu}$. This implies that the dynamics of the model undergoes some deep changes when the value of λ crosses $\lambda_1(D_1)$.

For convenience of notation, we continue to use the convention that $\lambda_1(D_{m+1}) = \infty$. Let us fix $\mu \in (0, \lambda_1(D_1))$ and suppose $\lambda \in (\lambda_1(D_k), \lambda_1(D_{k+1}))$ for some $1 \le k \le m$. By Theorem 2.4, for λ in this range, the boundary blow-up problem (2.3) has a minimal positive solution U_λ. Applying Lemma 2.3 in [21], we find that if (u, v) is a positive solution of (4.7), then

$$u(x) \le U_\lambda(x), \ \forall x \in \Omega \setminus (\cup_{j=1}^k \overline{D}_j).$$

Define

$$\alpha_\lambda(x) = \begin{cases} 0, & x \in \cup_{j=1}^k \overline{D}_j, \\ 1/U_\lambda(x), & x \in \Omega \setminus (\cup_{j=1}^k \overline{D}_j). \end{cases}$$

Clearly α_λ is continuous on $\overline{\Omega}$ and $\alpha_\lambda > 0$ on $\Omega \setminus (\cup_{j=1}^k \overline{D}_j)$. By our choice of μ and the main result of [Ou] (see also [FKLM]), the problem

$$(4.8) \qquad -\Delta V = \mu V(1 - \alpha_\lambda(x)V) \text{ in } \Omega, \ V|_{\partial\Omega} = 0$$

has a unique positive solution V_λ. Moreover, by a simple comparison argument, we find $v \le V_\lambda$ if (u, v) is a positive solution of (4.7) with $\alpha = b_0$.

Let us introduce some notations for our discussions to follow. We will use $\lambda_1^\omega(\phi)$ and $\lambda_1^{\omega,*}(\phi)$ to denote the first eigenvalues of the operator $-\Delta + \phi$ over ω under Neumann and Dirichlet boundary conditions, respectively. It is well known that

$$\lambda_1^\omega(\phi) < \lambda_1^{\omega,*}(\phi);$$

and both $\lambda_1^\omega(\phi)$ and $\lambda_1^{\omega,*}(\phi)$ are increasing with ϕ in the following sense:

$$\phi_1 \le \phi_2 \text{ and } \phi_1 \not\equiv \phi_2 \text{ imply } \lambda_1^{\omega,*}(\phi_1) < \lambda_1^{\omega,*}(\phi_2), \ \lambda_1^\omega(\phi_1) < \lambda_1^\omega(\phi_2).$$

Note that $\lambda_1^{D_j,*}(0) = \lambda_1(D_j)$.

If (u,v) is a positive solution of (4.7) with $\alpha = b_0$, then from the equation for u we obtain

$$\lambda = \lambda_1^{\Omega}(\alpha u + \beta v) < \lambda_1^{\Omega,*}(\alpha u + \beta v) < \lambda_1^{D_i,*}(\alpha u + \beta v) = \lambda_1^{D_i,*}(\beta v).$$

Since $v \le V_\lambda$, we obtain

$$(4.9) \qquad \lambda < \lambda_1^{D_i,*}(\beta V_\lambda),\ \ i = 1, \dots, m.$$

From well-known properties of principle eigenvalues, we see that $f_i(\beta) := \lambda_1^{D_i,*}(\beta V_\lambda)$ is a continuous, strictly increasing function of β, and $f_i(0) = \lambda_1(D_i)$, $f_i(\infty) = \infty$. Since $\lambda > \lambda_1(D_j)$ for $j = 1, \dots, k$, we can find a unique $\beta_j = \beta_j(\lambda) > 0$ such that $f_j(\beta_j) = \lambda$. Therefore,

$$(4.10) \qquad \lambda = \lambda_1^{D_j,*}(\beta_j V_\lambda);\ \lambda \ge \lambda_1^{D_j,*}(\beta V_\lambda);\ \forall \beta \le \beta_j;\ j = 1, \dots, k.$$

Comparing (4.9) with (4.10), we immediately obtain the following result.

Theorem 4.6. *Suppose* $\mu \in (0, \lambda_1(D_1))$ *and* $\lambda \in (\lambda_1(D_k), \lambda_1(D_{k+1}))$ *for some* $1 \le k \le m$. *Let* $\beta_1, \dots, \beta_k$ *be as in* (4.10). *Then* (4.7) *with* $\alpha = b_0$ *has no positive solution if* $0 < \beta \le \max\{\beta_1, \dots, \beta_k\}$.

Our next result shows that even if $\lambda > \lambda_1(D_k)$ for some $k \in \{1, \dots, m\}$, (4.7) with $\alpha = b_0$ can still have a positive solution for every $\beta > 0$ if μ is large enough; precisely, if $\mu > \max\{\lambda_1(D_m), \lambda\}$. Thus, existence of a positive solution is regained when μ becomes large.

Theorem 4.7. *Suppose that* $\mu > \lambda_1(D_m)$. *Then* (4.7) *with* $\alpha = b_0$ *has a positive solution for every* $\lambda \in (0, \mu)$ *and* $\beta > 0$.

The proof of Theorem 4.7 relies on an a priori estimate and a topological degree argument; see [19] for details.

The nonexistence result, Theorem 4.6, suggests a chance of constructing positive solutions of (4.7) with prescribed patterns. More precisely, if we perturb the degenerate $\alpha(x) = b_0(x)$ by $b_0(x) + \epsilon$ with small positive ϵ, then by Theorem 4.4 we know that the perturbed (4.7) has a positive solution (u_ϵ, v_ϵ); Theorem 4.6 suggests that if λ, μ and β are chosen suitably, then as $\epsilon \to 0$, the function pair (u_ϵ, v_ϵ) has no finite limit and hence may exhibit sharp spatial patterns. This is indeed the case but we are unable to determine the exact location of the pattern in the general case. To overcome this difficulty, we are led to the study of the behavior of $\beta_j(\lambda)$ as $\lambda \to \infty$. Let us recall that for $\mu \in (0, \lambda_1(D_1))$ and $\lambda > \lambda_1(D_m)$, $\beta = \beta_j(\lambda)$ is the unique solution to

$$\lambda = \lambda_1^{D_j,*}(\beta V_\lambda);\ \ j = 1, \dots, m;$$

where V_λ is given by (4.8).

The asymptotical behavior of $\beta_j(\lambda)$ for large λ is determined in the following result (see [19] for a proof).

Proposition 4.8. *Let $\tilde V$ be the unique positive solution of*

$$-\Delta V = \mu V(1-\alpha(x)V) \text{ in } \Omega,\ V|_{\partial\Omega} = 0. \tag{4.11}$$

Then

$$\lim_{\lambda\to\infty} \beta_j(\lambda) = \beta_j^\infty := (\min_{\overline{D}_j} \tilde V)^{-1}.$$

We now assume that $\alpha(x) = b_0(x) + \epsilon$. Moreover, we assume that

$$\mu \in (0, \lambda_1(D_1)),\ \beta \in (0, \min\{\beta_1^\infty, ..., \beta_m^\infty\}).$$

Therefore, in view of Proposition 4.8, there exists $\Lambda > 0$ such that

$$\beta < \beta_j(\lambda),\ \forall \lambda > \Lambda,\ j = 1, 2, ..., m.$$

We fix $\lambda > \Lambda$ and consider the following problem,

$$\begin{cases} -\Delta u = \lambda u - [b_0(x)+\epsilon]u^2 - \beta uv, & x\in\Omega,\\ -\Delta v = \mu v(1-\frac{v}{u}), & x\in\Omega,\\ u = v = 0, & x\in\partial\Omega, \end{cases} \tag{4.12}$$

where $\epsilon > 0$ is a positive constant. By Theorem 4.4, (4.12) always has a positive solution. Denote by (u_ϵ, v_ϵ) an arbitrary positive solution of (4.12); we want to show that as $\epsilon \to 0$, (u_ϵ, v_ϵ) exhibits a clear spatial pattern. To this end, let $\{\epsilon_n\}$ be an arbitrary sequence of positive numbers decreasing to 0 as $n\to\infty$, and denote $(u_n, v_n) = (u_{\epsilon_n}, v_{\epsilon_n})$. We have the following result (see [19]).

Theorem 4.9. *$\{(u_n, v_n)\}$ has a subsequence, still denoted by (u_n, v_n), such that*

$$u_n \to \tilde u \text{ in } C^1(\overline{\omega}) \text{ for any subdomain } \omega \text{ satisfying } \overline{\omega} \subset \overline{\Omega}\setminus\overline{D},$$

$$u_n \to \infty \text{ uniformly on } \overline{D},\ v_n \to \tilde v \text{ in } C^1(\overline{\Omega}),$$

where $\tilde u$ is a positive solution to

$$-\Delta \tilde u = \lambda \tilde u - \alpha(x)\tilde u^2 - \beta \tilde u \tilde v \text{ in } \Omega\setminus\overline{D},\ \tilde u|_{\partial D} = \infty,\ \tilde u|_{\partial\Omega} = 0, \tag{4.13}$$

and $\tilde v$ is a positive solution to

$$-\Delta \tilde v = \mu \tilde v(1-\alpha(x)\tilde v) \text{ in } \Omega,\ \tilde v|_{\partial\Omega} = 0, \tag{4.14}$$

where

$$\alpha(x) = \begin{cases} 0, & x \in \overline{D}, \\ 1/\tilde{u}(x), & x \in \overline{\Omega} \setminus \overline{D}. \end{cases}$$

Moreover,

$$\lambda_1^{D_j,*}(\beta\tilde{v}) = \lambda, \quad j = 1, 2, \dots, m. \tag{4.15}$$

Remark 4.10. Note that $(\tilde{u}, \tilde{v})$ is determined by (4.13), (4.14) and (4.15) altogether, and Theorem 4.9 implies that there is at least one positive solution $(\tilde{u}, \tilde{v})$ to (4.13)-(4.15), provided that $\mu \in (0, \lambda_1(D_1))$, $\beta \in (0, \min\{\beta_1^\infty, \dots, \beta_m^\infty\})$ and $\lambda > \Lambda$.

Theorem 4.9 shows that for all large n, (u_n, v_n) is close to a function (u^*, v^*) of the form $u^*(x) = \infty$ on $\overline{D}$, $u^*(x) = \tilde{u}(x)$ on $\overline{\Omega} \setminus \overline{D}$, $v^* = \tilde{v}$ in Ω, where $(\tilde{u}, \tilde{v})$ solves (4.13)-(4.15). Clearly u_n develops a sharp pattern over Ω: its value over D is much bigger than that over the rest of Ω. However, v_n does not develop into a sharp pattern. The following result (see [19]) further describes the profile of u_n for large n.

Theorem 4.11. *Suppose that (u_n, v_n) converges to $(\tilde{u}, \tilde{v})$ as in Theorem 4.9. Then $\epsilon_n u_n \to w$ in $C(\overline{\Omega})$, where $w = 0$ on $\overline{\Omega} \setminus D$, and on each D_j, $j = 1, \dots, m$, w is the unique positive solution of*

$$-\Delta w = \lambda w - w^2 - \beta\tilde{v}w \text{ in } D_j, \quad w|_{\partial D_j} = 0.$$

It is worthwhile to point out that if (u_ϵ, v_ϵ) is a positive solution to (4.12), then (z_ϵ, v_ϵ), with $z_\epsilon = \epsilon u_\epsilon$, is a positive solution to the predator-prey model

$$\begin{cases} -\Delta z = \lambda z - [\epsilon^{-1}\alpha(x) + 1]z^2 - \beta z v, & x \in \Omega, \\ -\Delta v = \mu v(1 - \epsilon \frac{v}{z}), & x \in \Omega, \\ z_\epsilon = v_\epsilon = 0, & x \in \partial\Omega. \end{cases}$$

Remark 4.12. Theorem 4.11 implies that for small $\epsilon > 0$, z_ϵ exhibits a sharp pattern over Ω: it is close to 0 over $\overline{\Omega} \setminus D$, and is close to a continuous positive function over D. Note that v_ϵ is close to a continuous positive function over the entire Ω. By choosing D suitably, we see that rather arbitrary patterns can be realized by z_ϵ.

4.3. Comparison with the Classical Lotka-Volterra Model

It is interesting to compare (4.7) with the following Lotka-Volterra model

$$(4.16) \qquad \begin{cases} -\Delta u = \lambda u - b(x)u^2 - cuv, & x \in \Omega, \\ -\Delta v = \mu v - v^2 + duv, & x \in \Omega, \\ u_\nu = v_\nu = 0, & x \in \partial\Omega, \end{cases}$$

Problem (4.16) with Dirichlet boundary conditions was studied in [DD2] but most of the techniques there easily carry over to (4.16).

Following [13] we assume that $b(x) = b_0(x)$ where b_0 is as defined in section 2 but with $D = D_1$, i.e., $m = 1$.

As in section 3, the semitrivial steady-states of (4.16) can be easily determined. They are $(u_\lambda, 0)$ and $(0, \theta_\mu)$, where θ_μ is defined as in section 3, and u_λ is the unique positive solution of

$$-\Delta u = \lambda u - b_0(x)u^2 \text{ in } \Omega, \; u_\nu|_{\partial\Omega} = 0,$$

which exists if and only if $0 < \lambda < \lambda_1(D)$.

To analyze the set of positive steady-states for (4.16) we will need the following a priori estimate (see [13]).

Lemma 4.13. *Given an arbitrary positive constant M we can find another positive constant C, depending only on M and b, c, d, Ω in (4.16), such that if (u, v) is a positive solution of (4.16) with $|\lambda| + |\mu| \le M$, then*

$$\|u\|_\infty + \|v\|_\infty \le C.$$

Let μ^0 be defined as in section 3.1, we have the following result.

Theorem 4.14. *When $0 < \lambda < \lambda_1(D)$, (4.16) has a positive solution if and only if*

$$(4.17) \qquad \lambda_1^\Omega(-du_\lambda) < \mu < \mu^0.$$

Moreover, there is a bounded connected set of positive solutions $\Gamma = \{(\mu, u, v)\}$ in the space E which joins the semitrivial solutions at $(\lambda_1^\Omega(-du_\lambda), u_\lambda, 0)$ and $(\mu^0, 0, \theta_{\mu^0})$.

If $\lambda \ge \lambda_1(D)$, then we no longer have a semitrivial solution of the form $(u, 0)$, and the behavior of (4.16) undergoes a deep change. We can use Lemma 4.13 and a bifurcation argument to prove the following result.

Theorem 4.15. *When $\lambda \ge \lambda_1(D)$, (4.16) has a positive solution if and only if $\mu < \mu^0$. Moreover, there is an unbounded connected set of positive solutions*

$\Gamma = \{(\lambda; u; v)\}$ *in* E *which joins the semitrivial solution branch at* $(\lambda^0; 0; \mu_{\lambda^0})$ *and satisfies*

$$\{\lambda : (\lambda; u; v) \in \Gamma\} = (-\infty; \lambda^0): \qquad (4:18)$$

Remark 4.16. We conjecture that (4.16) has at most one positive solution, and when such a solution exists, it attracts all the positive solutions of the corresponding parabolic system. The first half of this conjecture can be proved for the case Ω is a 1-dimensional domain, i.e., a bounded interval, by using the technique in [30] or [41].

We are now ready to observe some essential differences between (4.16) and (4.7). While our results in section 4.2 show that patterned positive solutions for (4.7) can be obtained by perturbing $\alpha = b_0$ to $\alpha = b_0 + \epsilon$, it is easy to check that if we perturb (4.16) by replacing $b_0(x)$ with $b_0(x) + \epsilon$, then no positive solution $(u_\epsilon; v_\epsilon)$ of the perturbed (4.16) develops a sharp pattern as $\epsilon \to 0$. In fact, it is easy to show that $(u_\epsilon; v_\epsilon)$ is close to a positive solution of the unperturbed (4.16) when ϵ is small. One important reason for this fact is that the range of λ for the existence of a positive solution of (4.16) is **enlarged** by the vanishing of $b(x)$ in D. In contrast, Theorems 4.4 and 4.6 imply that the range of λ where (4.7) has a positive solution is **reduced** by the vanishing of α in D.

References

1. S. W. Ali and C. Cosner, Models for the effects of individual size and spatial scale on competition between species in heterogeneous environments, *Math. Biosci.*, **127** (1995), 45-76.

2. J. Blat and K. J. Brown, Bifurcation of steady-state solutions in predator-prey and competition systems, *Proc. R. Soc. Edinb.*, **97A** (1984), 21-34.

3. K. J. Brown and Y. Du, Bifurcation and monotonicity in competition reaction-diffusion systems, *Nonlinear Anal.*, **23** (1994), 1-13.

4. R. S. Cantrell and C. Cosner, Should a park be an island? *SIAM J. Appl. Math.*, **53** (1993), 219-252.

5. R. S. Cantrell, C. Cosner and V. Hutson, Ecological models, permanence and spatial heterogeneity, *Rocky Mountain J. Math.*, **26** (1996), 1-35.

6. E. N. Dancer, On positive solutions of some pairs of differential equations, *Trans. Amer. Math. Soc.*, **284** (1984), 729-743.

7. E. N. Dancer, On positive solutions of some pairs of differential equations, II, *J. Diff. Eqns.*, **60** (1985), 236-258.

8. E. N. Dancer, On the existence and uniqueness of positive solutions for competing species models with diffusion, *Trans. Amer. Math. Soc.*, **326** (1991), 829-859.

9. E. N. Dancer, Upper and lower stability and index theory for positive mappings and applications, *Nonlinear Anal.*, **17** (1991), 205-217.

10. E. N. Dancer, Multiple fixed points of positive mappings, *J. Rein Angew. Math.*, **371** (1986), 46-66.

11. E. N. Dancer, On the indices of fixed points of mappings in cones and applications, *J. Math. Anal. Appl.*, **91** (1983), 131-151.

12. E. N. Dancer and Y. Du, Competing species equations with diffusion, large interactions, and jumping nonlinearities, *J. Diff. Eqns.*, **114** (1994), 434-475.

13. E. N. Dancer and Y. Du, Effects of certain degeneracies in the predator-prey model, *SIAM J. Math. Anal.*, **34** (2002), 292-314.

14. E. N. Dancer and P. Hess, Stability of fixed points for order-preserving discrete-time dynamical systems, *J. Reine Angew. Math.*, **419** (1991), 125-139.

15. Y. Du, Effects of a degeneracy in the competition model, part I. classical and generalized steady-state solutions, *J. Diff. Eqns.*, **181** (2002), 92-132.

16. Y. Du, Effects of a degeneracy in the competition model, part II. perturbation and dynamical behaviour, *J. Diff. Eqns.*, **181** (2002), 133-164.

17. Y. Du, Realization of prescribed patterns in the competition model, *J. Diff. Eqns.*, **193** (2003), 147-179.

18. Y. Du, The structure of solution set of a class of nonlinear eigenvalue problems, *J. Math. Anal. Appl.*, **170** (1992), 567-580.

19. Y. Du and S.-B. Hsu, *A diffusive predator-prey model in heterogeneous environment*, preprint, 2003.

20. Y. Du and Q. Huang, Blow-up solutions for a class of semilinear elliptic and parabolic equations, *SIAM J. Math. Anal.*, **31** (1999), 1-18.

21. Y. Du and Shujie Li, Positive solutions with prescribed patterns in some simple semilinear equations, *Diff. Integral Eqns.*, **15** (2002), 805-822.

22. Y. Du and Y. Lou, Some uniqueness and exact multiplicity results for a predator-prey model, *Trans. Amer. Math. Soc.*, **349** (1997), 2443-2475.

23. Y. Du and Y. Lou, S-shaped global bifurcation curve and Hopf bifurcation of positive solutions to a predator-prey model, *J. Diff. Eqns.*, **144** (1998), 390-440.

24. Y. Du and Y. Lou, Qualitative behaviour of positive solutions of a predator-prey model: effects of saturation, *Proc. Royal Soc. Edinburgh*, **131A** (2001), 321-349.

25. J. Eilbeck, J. Furter and J. López-Gómez, Coexistence in a competition model with diffusion, *J. Diff. Eqns.*, **107** (1994), 96-139.

26. J. M. Fraile, P. Koch Medina, J. López-Gómez and S. Merino, Elliptic eigenvalue problems and unbounded continua of positive solutions of a semilinear elliptic problem, *J. Diff. Eqns.*, **127** (1996), 295-319.

27. C.Gui and Y. Lou, Uniqueness and nonuniqueness of coexistence states in the Lotka-Volterra competition model, *Comm. Pure Appl. Math.*, **Vol. XLVII** (1994), 1-24.

28. P. Hess and A. C. Lazer, On an abstract competition model and applications, *Nonlinear Anal.*, **16** (1991), 917-940.

29. M. Hirsch, Stability and convergence in strongly monotone dynamical systems, *J. reine angew. Math.*, **383** (1988), 1-53.

30. S. B. Hsu, Steady states of a system of partial differential equations modeling microbial ecology, *SIAM J. Math. Anal.,* **14** (1983), 1130-1138.

31. S. B. Hsu and T. W. Hwang, Global stability for a class of predator-prey systems, *SIAM J. Appl. Math.*, **55** (1995), 763-783.

32. S. B. Hsu and T. W. Hwang, Uniqueness of limit cycles for a predator-prey system of Holling and Leslie type, *Canad. Appl. Math. Quart.* **6(2)** (1998), 91-117.

33. S.B. Hsu, H.L. Smith and P. Waltman, Competitive exclusion and coexistence for competitive systems on ordered Banach spaces, *Trans. Amer. Math. Soc.,* **348** (1996), 4083-4094.

34. V. Hutson, Y. Lou and K. Mischaikow, Spatial heterogeneity of resources versus Lotka-Volterra dynamics, *J. Diff. Eqns.*, **185** (2002), 97-136.

35. V. Hutson, Y. Lou, K. Mischaikow and P. Polacik, *Competing species near a degenerate limit*, preprint, 2002.

36. V. Hutson, K. Mischaikow and P. Polacik, The evolution of dispersal rates in a heterogeneous time-periodic environment, *J. Math. Biol.,* **43** (2001), 501-533.

37. Y. Kan-on and E. Yanagida, Existence of non-constant stable equilibria in competition diffusion equations, *Hiroshima Math. J.,* **23** (1993), 193-221.

38. K. Kishimoto and H. F. Weinberger, The spatial homogeneity of stable equilibria of some reaction-diffusion systems on convex domains. *J. Differential Equations*, **58** (1985), 15–21.

39. P. Koman and A. W. Leung, A general monotone scheme for elliptic systems with applications to ecological models, *Proc. Roy. Soc. Edinb.*, **102A** (1986), 315-325.

40. J. Lopez-Gomez, On the structure of the permanence region for competing species models with general diffusivities and transport effects, *Discrete and Continuous Dynamical Systems*, **2** (1996), 525-542.

41. J. Lopez-Gomez and R. M. Pardo, Invertibility of linear noncooperative elliptic systems, *Nonlinear Anal.,* **31** (1998), 687-699.

42. J. Lopez-Gomez and J. Sabina de Lis, Coexistence states and global attractivity for some convective diffusive competing species models, *Trans. Amer. Math. Soc.,* **347** (1995), 3797-3833.

43. Y. Lou and W. M. Ni, Diffusion vs cross-diffusion: an elliptic approach, *J. Diff. Eqns.,* **154** (1999), 157-190.

44. Y. Lou and W. M. Ni, Diffusion, self-diffusion and cross diffusion, *J. Diff. Eqns.*, **131** (1996), 79-131.

45. H. Matano, Existence of nontrivial unstable sets for equilibriums of strongly order-preserving systems. *J. Fac. Sci. Univ. Tokyo Sect. IA Math.* **30** (1984), 645-673.

46. H. Matano and M. Mimura, Pattern formation in competition-diffusion systems in non-convex domains, *Publ. RIMS Kyoto Univ.*, **19** (1983), 1049-1079.

47. M. Mimura, Stationary patterns of some density-dependent diffusion systems with competitive dynamics, *Hiroshima Math. J.*, **11** (1981), 621-635.

48. M. Mimura and K. Kawasaki, *Spatial segregation in competitive interaction-diffusion equations*, J. Math. Biol., 9(1980), 49-64.

49. T. Ouyang,On the positive solutions of semilinear equations $\Delta u + \lambda u - hu^p = 0$ on the compact manifolds, *Trans. Amer. Math. Soc.*, **331** (1992), 503-527.

50. C. V. Pao, On nonlinear reaction-diffusion systems, *J. Math. Anal. Appl.*, **87** (1982), 165-198.

51. W. H. Ruan and C. V. Pao, Positive steady-state solutions of a competing reaction-diffusion system, *J. Diff. Eqns.*, **117** (1995), 401-427.

52. H. L. Smith, Monotone Dynamical Systems, Math. Surveys and Monographs, *Amer. Math. Soc.*, **41** 1995.

53. Y. Yamada, Stability of steady-states for prey-predator diffusion equations with homogeneous Dirichlet conditions, *SIAM J. Math. Anal.*, **21** (1990), 327-345.

Yihong Du
School of Mathematics,
Statistics and Computer Science,
University of New England,
Armidale, NSW 2351,
Australia
E-mail: ydu@turing.une.edu.au