

Coexistence states of a prey-predator model with population flux by attractive transition *

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1 Introduction

This article is concerned with the following Lotka-Volterra prey-predator model with nonlinear diffusion terms:

$$\begin{cases} u_t = d_1 \Delta u + \alpha \Delta(uv) + u(m_1 - u - cv), & (x, t) \in \Omega \times (0, T), \\ v_t = d_2 \Delta v + \beta \nabla \cdot \left[u^2 \nabla \left(\frac{v}{u} \right) \right] + v(m_2 + bu - v), & (x, t) \in \Omega \times (0, T), \\ u = v = 0, & (x, t) \in \partial\Omega \times (0, T), \\ u(x, 0) = u_0(x) \geq 0, \quad v(x, 0) = v_0(x) \geq 0, & x \in \Omega. \end{cases} \quad (1.1)$$

Here $\Omega \subset \mathbb{R}^N$ is a bounded domain with a smooth boundary $\partial\Omega$. Unknown functions $u(x, t)$ and $v(x, t)$, respectively, denote the population densities of the prey and the predator at location $x \in \Omega$ and time $t > 0$. The homogeneous Dirichlet boundary conditions assume a hostile environment for both species surrounding the habitat Ω . All coefficients are assumed to be spatial and temporal homogeneous; d_i , m_1 , b and c are positive constants; α and β are nonnegative constants; m_2 is a real constant which is allowed to be negative. Ecologically, m_1 and m_2 represent the growth rates of the prey and the predator, respectively; b and c denote the inter-specific interactions due to the predation; d_1 and d_2 are usual dispersal rates of the prey and the predator based on the Fick law. System (1.1) contains two nonlinear diffusion terms of prototype arising in ecology (Okubo-Levin [3]). One is the term $\alpha \Delta(uv)$ referred as the *cross-diffusion*

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term since Shigesada-Kawasaki-Teramoto [4] proposed a competition model with cross-diffusion terms to mathematically realize the segregation of two competing species. For the prey-predator relationship as (1.1), the cross-diffusion term $\alpha\Delta(uv)$ models an ecological situation that individuals of the prey diffuse from the high density area to the low density area of the enemy (predator). Another is the term $\beta\nabla \cdot [u^2\nabla(v/u)]$ which is not widely known as the cross-diffusion term in spite of the description parallel to the cross-diffusion in the book by Okubo-Levin [3]. The nonlinear diffusion term $\beta\nabla \cdot [u^2\nabla(v/u)]$ models an ecological situation that individuals of the predator move towards the high density area of the feed (prey). In the next section, following [3], we will explain reasons why such a couple of nonlinear diffusion terms appear from the micro-scopic modelling viewpoint.

Our interest is to derive the effect of nonlinear diffusion terms on the set of positive steady states. Then we will study the following stationary problem:

$$\begin{cases} d_1\Delta u + \alpha\Delta(uv) + u(m_1 - u - cv) = 0, & x \in \Omega, \\ d_2\Delta v + \beta\nabla \cdot \left[u^2\nabla\left(\frac{v}{u}\right) \right] + v(m_2 + bu - v) = 0, & x \in \Omega, \\ u = v = 0, & x \in \partial\Omega, \\ u \geq 0, \quad v \geq 0, & x \in \Omega. \end{cases} \quad (1.2)$$

On the linear diffusion system when $\alpha = \beta = 0$, there are a lot of papers (e.g., [5] and references therein) which study the set of positive solutions.

The purpose of this article is to review some results obtained by the author's joint researches ([1, 2]). The following four results about effects of nonlinear diffusion terms on positive solutions of (1.2) will be introduced.

- (i) A sufficient condition $\mathcal{R}(\alpha, \beta)$ on the (m_1, m_2) plane for the existence of positive solutions.
- (ii) The asymptotic behavior of $\mathcal{R}(\alpha, \beta)$ as $\alpha \rightarrow \infty$.
- (iii) The asymptotic behavior of $\mathcal{R}(\alpha, \beta)$ as $\beta \rightarrow \infty$.
- (iv) In a special case when $\alpha = 0$, the asymptotic behavior of positive solutions as $\beta \rightarrow \infty$.

The contents of this article is as follows: In Section 2, a mechanism of nonlinear diffusion terms of (1.1) will be explained from an ecological modelling viewpoint. In Section 3, we exhibit a sufficient region on the (m_1, m_2) plane for the existence of positive solutions (Fig. 2). In Section 4, the asymptotic behavior stated as above (ii)-(iv) will be introduced. Throughout this article, the usual norms of the spaces $L^p(\Omega)$ for $p \in [1, \infty)$ and $C(\overline{\Omega})$ are defined by

$$\|u\|_p := \left(\int_{\Omega} |u(x)|^p \right)^{1/p} \quad \text{and} \quad \|u\|_{\infty} := \max_{x \in \overline{\Omega}} |u(x)|.$$

2 Formulation of nonlinear diffusion in ecology

In this section, following the book by Okubo-Levin [3], derivations of the couple of nonlinear diffusion terms in (1.1) will be explained from the micro-scopic modelling aspect.

By the standard modelling procedure, we employ the 1d-spatio-temporal discretization such as

$$(x, t) = (n\Delta x, j\Delta t) \in \mathbb{R} \times (0, \infty),$$

where $n \in \mathbb{Z}$, $j \in \mathbb{N} \cup \{0\}$; Δx and Δt are tiny meshes for the space and time, respectively. In this setting, $\{n\Delta x\}_{n \in \mathbb{Z}}$ is assumed to be a one-dimensional habitat of the prey and the predator, and each location $n\Delta x$ is called n -site. It is assumed that every individual of both species must to be positioned at some site $n\Delta x$ and necessarily moves to either of neighbouring site $(n-1)\Delta x$ or $(n+1)\Delta x$ in a unit time mesh Δt . Let $u(x, t)$ (resp. $v(x, t)$) be the number of individuals of the prey (resp. predator) at n -site $x = n\Delta x$ and time $t = j\Delta t$. Let $T(m, n)$ be the transition probability of each individual from $m\Delta x$ to $n\Delta x$ in time Δt , where $|m - n| = 1$ (see Fig. 1). Under this setting, we estimate the difference of the number of the prey at n -site in time Δt by

$$\begin{aligned} u(x, t + \Delta t) - u(x, t) = & T(n-1, n)u(x - \Delta x, t) + T(n+1, n)u(x + \Delta x, t) \\ & - (T(n, n-1) + T(n, n+1))u(x, t). \end{aligned} \quad (2.1)$$

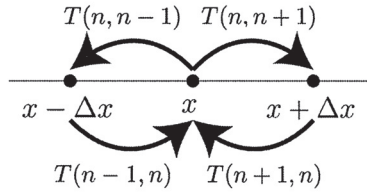


Figure 1: Transition rule

Here we derive the cross-diffusion term $(uv)_{xx}$ in the first equation of (1.1). For individuals of the prey, the low density location of the enemy (predator) is more favourable. So it is a natural situation that the transition probability $T(m, n)$ of individuals of the prey depends on the number of the predator at *departure* site such as

$$\text{Repulsive transition} \quad T(m, n) = \frac{\Delta t}{(\Delta x)^2} v(m\Delta x, t) \quad (|m - n| = 1),$$

where $\Delta t/(\Delta x)^2$ is related to the square root law for the Brownian motion. Substituting this T into the recurrent formula (2.1), we obtain the differential quotient

$$\begin{aligned} & \frac{u(x, t + \Delta t) - u(x, t)}{\Delta t} \\ = & \frac{u(x + \Delta x, t)v(x + \Delta x, t) - 2u(x, t)v(x, t) + u(x - \Delta x, t)v(x - \Delta x, t)}{(\Delta x)^2}. \end{aligned}$$

By passing to the limit $\Delta t \rightarrow 0$ and $\Delta x \rightarrow 0$, we obtain the partial differential equation

$$v_t = (uv)_{xx}.$$

This is the one dimensional version of the cross-diffusion part in (1.1).

Next we derive the nonlinear diffusion term $(u^2(v/u)_x)_x$ in the second equation of (1.1). For individuals of the predator, the high density location of the feed (prey) is more favourable. Then it is reasonable to assume that the transition probability $T(m, n)$ for individuals of the predator depends on the number of the prey at *arrival* site such as

$$\text{Attractive transition} \quad T(m, n) = \frac{\Delta t}{(\Delta x)^2} u(n\Delta x, t) \quad (|m - n| = 1).$$

We substituting this T into (2.1) (with u replaced by v) to obtain the differential quotient

$$\begin{aligned} \frac{v(x, t + \Delta t) - v(x, t)}{\Delta t} = & u(x, t) \frac{v(x + \Delta x, t) + v(x - \Delta x, t) - 2v(x, t)}{(\Delta x)^2} \\ & - \frac{u(x + \Delta x, t) + u(x - \Delta x, t) - 2u(x, t)}{(\Delta x)^2} v(x, t) \end{aligned}$$

By the continuation procedure as $\Delta t \rightarrow 0$ and $\Delta x \rightarrow 0$, we get the partial differential equation $v_t = u v_{xx} - u_{xx}v$, which is written by

$$v_t = \left(u^2 \left(\frac{v}{u} \right)_x \right)_x.$$

This is the one dimensional version of the nonlinear diffusion part in the second equation of (1.1).

In addition, we consider another model of T for the prey-predator relation. It is also reasonable to assume that the transition probability $T(m, n)$ of individuals of the predator depends on the *difference* of feed (prey) between at arrival and at departure as follows:

$$\text{Transition by chemotaxis} \quad T(m, n) = \frac{\Delta t}{2(\Delta x)^2} (u(n\Delta x, t) - u(m\Delta x, t)),$$

$T(m, n) \propto$	Diffusion	Famous PDE Model
$u (m \Delta x, t)$ Repulsive	$\Delta (uv)$	SKT model $\begin{cases} u_t = d_1 \Delta u + \alpha_1 \Delta (uv) + f_1(u, v), \\ v_t = d_2 \Delta v + \alpha_2 \Delta (uv) + f_2(u, v). \end{cases}$
$u (n \Delta x, t)$ Attractive	$\nabla \cdot \left(u^2 \nabla \left(\frac{v}{u} \right) \right)$	None
$u (n \Delta x, t) - u (m \Delta x, t)$ Difference	$-\nabla \cdot (v \nabla u)$	Keller-Segel model $\begin{cases} u_t = d_1 \Delta u - u + cv, \\ v_t = d_2 \Delta v - \alpha \nabla \cdot (v \nabla u). \end{cases}$

Table 1

where $|m - n| = 1$. Substituting this T into (2.1) (with u replaced by v), one can see

$$\begin{aligned} & \frac{v(x, t + \Delta t) - v(x, t)}{\Delta t} \\ = & - \frac{u(x + \Delta x, t) + u(x - \Delta x, t) - 2u(x, t)}{(\Delta x)^2} \frac{v(x, t) + v(x - \Delta x, t)}{2} \\ & - \frac{u(x + \Delta x, t) - u(x, t)}{\Delta x} \left(\frac{v(x + \Delta x, t) - v(x, t)}{2\Delta x} + \frac{v(x, t) - v(x - \Delta x, t)}{2\Delta x} \right). \end{aligned}$$

By the continuation procedure, we get the partial differential equation $v_t = -u_{xx}v - u_xv_x$, which can be written as

$$v_t = -(vu_x)_x.$$

This is an evolution equation driven by the so-called *chemotaxis* term.

These PDE modellings for typical three transitions of repulsive, attractive and difference types are generalized to the higher dimensional cases. We can summarize the correspondence table of transition type and nonlinear diffusion and famous PDE models with such nonlinear diffusion terms (Table 1).

3 Coexistence region

This section introduces a sufficient condition for the existence of positive solutions of (1.2). In order to show a bifurcation aspect of the sufficient condition, we have to collect semitrivial solutions of (1.2). Here we call (u, v) a semitrivial solution of (1.2) if one of the components identically vanishes over $\overline{\Omega}$ and the other is positive in Ω . Ecologically, semitrivial solutions are corresponding to steady states such as one of the species becomes extinct and the other survives. If v vanishes over

$\overline{\Omega}$, then u has to satisfy the following stationary logistic equation:

$$\begin{cases} d_1 \Delta u + u(m_1 - u) = 0 & \text{in } \Omega, \\ u = 0 & \text{on } \partial\Omega. \end{cases} \quad (3.1)$$

It is well known that (3.1) admits a unique positive solution if and only if $m_1 > d_1 \lambda_1$, where λ_1 is the least eigenvalue of $-\Delta$ with homogeneous Dirichlet boundary condition on $\partial\Omega$. Then we denote the positive solution by θ_{d_1, m_1} when $m_1 > d_1 \lambda_1$. Consequently, we see that (1.2) has a semitrivial solution $(u, v) = (\theta_{d_1, m_1}, 0)$ if $m_1 > d_1 \lambda_1$. Similarly, one can verify that (1.2) has another semitrivial solution $(u, v) = (0, \theta_{d_2, m_2})$ if $m_2 > d_2 \lambda_1$.

A sufficient condition for the existence of positive solutions of (1.2) can be shown in the (m_1, m_2) plane as Fig. 2:

Theorem 3.1 ([1, 2]). *If $m_1 \leq d_1 \lambda_1$, there is no positive solution of (1.2). In case $m_1 > d_1 \lambda_1$, for any fixed $(d_1, d_2, b, c) \in \mathbb{R}_+^4$, there exist two continuous functions*

$$m_2 = f(m_1, \beta), \quad m_2 = g(m_1, \alpha)$$

for $(m_1, \alpha, \beta) \in (d_1 \lambda_1, \infty) \times \overline{\mathbb{R}_+^2}$ with

$$\begin{aligned} \lim_{m_1 \downarrow d_1 \lambda_1} f(m_1, \beta) &= \lim_{m_1 \downarrow d_1 \lambda_1} g(m_1, \alpha) = d_2 \lambda_1, \\ \lim_{m_1 \rightarrow \infty} f(m_1, \beta) &= -\infty \quad \text{and} \quad \lim_{m_1 \rightarrow \infty} g(m_1, \alpha) = \infty \end{aligned}$$

such that (1.2) admits at least one positive solution if

$$\min\{f(m_1, \beta), g(m_1, \alpha)\} < m_2 < \max\{f(m_1, \beta), g(m_1, \alpha)\}.$$

Let us explain the bifurcation aspect of Theorem 3.1. Regarding m_2 as a real bifurcation parameter for any fixed $m_1 > d_1 \lambda_1$, $(u, v, m_2) = (\theta_{d_1, m_1}, 0, f(m_1, \beta))$ and $(u, v, m_2) = (0, \theta_{d_2, g(m_1, \alpha)}, g(m_1, \alpha))$ are bifurcation points from which positive solutions bifurcate. Furthermore, Theorem 3.1 ensures the existence of positive solutions of (1.2) if (m_1, m_2) belongs to the surrounded region by two curves $m_2 = f(m_1, \beta)$ and $m_2 = g(m_1, \alpha)$ (see Fig. 2). It should be noted that $f(m_1, \beta)$ (resp. $g(m_1, \alpha)$) is independent of α (resp. β).

Furthermore, in special cases when one of α and β vanishes, the existence of a bifurcation branch which connects these two semitrivial solutions was shown (see [1] for the case $\beta = 0$; [2] for the other case $\alpha = 0$). In this sense, the region

$$\begin{aligned} \mathcal{R}(\alpha, \beta) := & \{ (m_1, m_2) \in (d_1 \lambda_1, \infty) \times \mathbb{R} \mid \\ & \min\{f(m_1, \beta), g(m_1, \alpha)\} < m_2 < \max\{f(m_1, \beta), g(m_1, \alpha)\} \} \end{aligned}$$

exhibits a sufficient region for the existence of positive solutions.

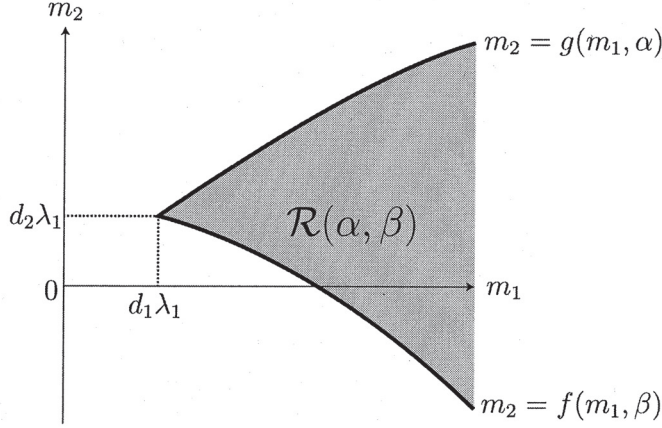


Figure 2: A sufficient region for the existence of positive solutions of (1.2)

4 Asymptotic analysis as $\alpha \rightarrow \infty$ or $\beta \rightarrow \infty$

In this section, we introduce the asymptotic behavior of $\mathcal{R}(\alpha, \beta)$ as the nonlinear diffusion coefficient α or β tends to infinity. In [1], the author and Yamada showed the following dependence of $\mathcal{R}(\alpha, \beta)$ on $\alpha > 0$ (see Fig. 3 (a)).

Theorem 4.1 ([1]). *For any fixed $m_1 > d_1\lambda_1$, $g(m_1, \alpha) \downarrow d_2\lambda_1$ as $\alpha \uparrow \infty$. In other words, it holds that*

$$\lim_{\alpha \rightarrow \infty} \mathcal{R}(\alpha, \beta) = \{ (m_1, m_2) \in (d_1\lambda_1, \infty) \times \mathbb{R} \mid \min\{f(m_1, \beta), d_2\lambda_1\} < m_2 < \max\{f(m_1, \beta), d_2\lambda_1\} \}.$$

In [2], Oeda and the author obtained the following asymptotic behavior of $\mathcal{R}(\alpha, \beta)$ as $\beta \rightarrow \infty$ (see Fig. 3 (b)).

Theorem 4.2 ([2]). *It holds true that*

$$\lim_{\beta \rightarrow \infty} \mathcal{R}(\alpha, \beta) := \{ (m_1, m_2) \in (d_1\lambda_1, \infty) \times \mathbb{R} \mid \min\{f^\infty(m_1), g(m_1, \alpha)\} < m_2 < \max\{f^\infty(m_1), g(m_1, \alpha)\} \},$$

where

$$f^\infty(m_1) := \lim_{\alpha \rightarrow \infty} f(m_1, \alpha) = \frac{d_2}{d_1}m_1 - \left(\frac{d_2}{d_1} + b\right) \frac{\|\theta_{d_1, m_1}\|_2^2}{\|\theta_{d_1, m_1}\|_1}.$$

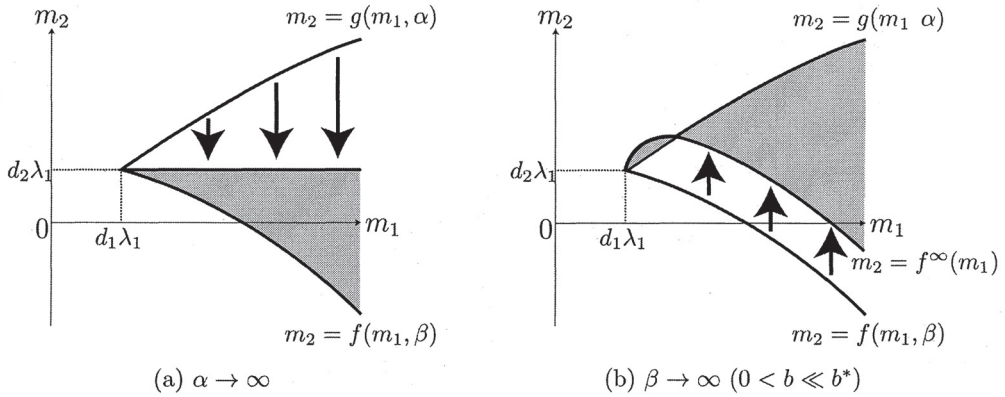


Figure 3: Asymptotic behaviors of $\mathcal{R}(\alpha, \beta)$ stated in Theorems 4.1 and 4.2.

We note the following asymptotic profile of $f^\infty(m_1)$ as $m_1 \downarrow d_1 \lambda_1$ and $m_1 \rightarrow \infty$ obtained in [2]:

$$\begin{aligned}
 \lim_{m_1 \downarrow d_1 \lambda_1} f^\infty(m_1) &= d_2 \lambda_1, \\
 \frac{d}{dm_1} f^\infty(d_1 \lambda_1) &:= \lim_{m_1 \downarrow d_1 \lambda_1} \frac{d}{dm_1} f^\infty(m_1) = \frac{d_2}{d_1} - \left(\frac{d_2}{d_1} + b \right) \frac{1}{\|\Phi\|_1 \|\Phi\|_3^3}, \\
 \lim_{m_1 \rightarrow \infty} f^\infty(m_1) &= -\infty,
 \end{aligned} \tag{4.1}$$

where Φ is the positive function satisfying

$$-\Delta \Phi = \lambda_1 \Phi \text{ in } \Omega, \quad \Phi = 0 \text{ on } \partial\Omega, \quad \|\Phi\|_2 = 1.$$

Since it is verified that $\|\Phi\|_1 \|\Phi\|_3^3 > 1$ by the Schwarz inequality, then (4.1) gives

$$\frac{d}{dm_1} f^\infty(d_1 \lambda_1) \begin{cases} > 0 & \text{if } 0 < b < b^* := \frac{d_2}{d_1} (\|\Phi\|_1 \|\Phi\|_3^3 - 1), \\ < 0 & \text{if } b > b^*. \end{cases}$$

Therefore, when $0 < b < b^*$, the curve $m_2 = f^\infty(m_1)$ is monotone increasing if $m_1 - d_1 \lambda_1 > 0$ is sufficiently small whereas it is monotone decreasing if $m_1 > 0$ is sufficiently large.

In the special case when $\alpha = 0$, we get the following limiting characterization of positive solutions as $\beta \rightarrow \infty$. The following result gives the asymptotic behavior of positive solutions of (1.2) as $\alpha \rightarrow \infty$.

Theorem 4.3 ([2]). Suppose that $\alpha = 0$ and $(m_1, m_2, d_1, d_2, b, c)$ satisfies

$$\begin{aligned} m_1 &> d_1 \lambda_1, \\ m_2 &\neq f^\infty(m_1), \\ m_2 &\neq \frac{d_2}{d_1} m_1 - \left(\frac{d_2}{d_1} - \frac{1}{c} \right) \frac{\|\theta_{d_1, m_1}\|_2^2}{\|\theta_{d_1, m_1}\|_1} (=: h(m_1)), \\ m_2 &\neq g(m_1, 0). \end{aligned}$$

Let $\{(u_n, v_n)\}$ be any sequence of positive solutions to (1.2) with $\alpha = 0$ and $\beta = \beta_n \rightarrow \infty$. Then the following alternative holds true.

- (i) If $\{\beta_n \|u_n\|_\infty\}$ is unbounded, then $f^\infty(m_1) < m_2 < h(m_1)$. In this case, for $s \in (0, 1)$ defined by

$$m_2 = (1 - s)f^\infty(m_1) + sh(m_1),$$

there exists a subsequence of $\{(u_n, v_n)\}$ (which is denoted by $\{(u_n, v_n)\}$ again) such that

$$\lim_{n \rightarrow \infty} (u_n, v_n) = \left(1 - s, \frac{s}{c}\right) \theta_{d_1, m_1} \quad \text{in } C^1(\overline{\Omega}) \times C^1(\overline{\Omega}).$$

- (ii) If $\{\beta_n \|u_n\|_\infty\}$ is bounded, there exists $(w, v) \in C^2(\overline{\Omega}) \times C^2(\overline{\Omega})$ such that

$$\lim_{n \rightarrow \infty} (\beta_n u_n, v_n) = (w, v) \quad \text{in } C^1(\overline{\Omega}) \times C^1(\overline{\Omega}),$$

passing to a subsequence, and moreover, (w, v) is a positive solution to

$$\begin{cases} d_1 \Delta w + w(m_1 - cv) = 0, & x \in \Omega, \\ d_2 \Delta v + \nabla \cdot \left[w^2 \nabla \left(\frac{v}{w} \right) \right] + v(m_2 - v) = 0, & x \in \Omega, \\ w = v = 0, & x \in \partial\Omega. \end{cases}$$

In the first situation (i) of Theorem 4.3, the set

$$\left\{ (u, v, m_2) = \left(\left(1 - s, \frac{s}{c}\right) \theta_{d_1, m_1}, (1 - s)f^\infty(m_1) + sh(m_1) \right) \mid 0 < s < 1 \right\}$$

of limit functions forms a line connects $(\theta_{d_1, m_1}, 0, f^\infty(m_1))$ with $(0, \theta_{d_1, m_1}/c, h(m_1))$. We should note that any (u, v) on this line satisfies the following limiting system of

(1.2) as $\beta_n \rightarrow \infty$ which consists of the equal diffusive Lotka-Volterra competition equations and an integral equation :

$$\begin{cases} d_1 \Delta u + u(m_1 - u - cv) = 0, & x \in \Omega, \\ d_1 \Delta v + v(m_1 - u - cv) = 0, & x \in \Omega, \\ u = v = 0, & x \in \partial\Omega, \\ \frac{d_2}{d_1} \int_{\Omega} v(m_1 - u - cv) = \int_{\Omega} v(m_2 + bu - v). \end{cases} \quad (4.2)$$

By Theorem 4.3, one can expect that almost all positive solution of (1.2) with large β can be characterized by either of type (i) or (ii). In view of the first type (i), the coexistence steady state (u, v) of prey and predator can be approximated by a coexistence steady state of the equal diffusive competition model (4.2) with an integral constraint. On the other hand, in the second type (ii), the component of prey shrinks with order $O(1/\beta)$ when β is sufficiently large.

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