2009

Stationary Pattern of a Ratio-Dependent Food Chain Model with Diffusion

Rui Peng

Junping Shi

Junping Shi
William & Mary, jxshix@wm.edu

Mingxin Wang

Recommended Citation

STATIONARY PATTERN OF A RATIO-DEPENDENT FOOD CHAIN MODEL WITH DIFFUSION*

RUI PENG†, JUNPING SHI‡, AND MINGXIN WANG§

Abstract. In the paper, we investigate a three-species food chain model with diffusion and ratio-dependent predation functional response. We mainly focus on the coexistence of the three species. For this coupled reaction-diffusion system, we study the persistent property of the solution, the stability of the constant positive steady state solution, and the existence and nonexistence of nonconstant positive steady state solutions. Both the general stationary pattern and Turing pattern are observed as a result of diffusion. Our results also exhibit some interesting effects of diffusion and functional responses on pattern formation.

Key words. food chain model, diffusion, ratio-dependent functional response, stationary pattern, Turing pattern, steady state solution

AMS subject classifications. 35J55, 92C15, 92D40

DOI. 10.1137/05064624X

1. Introduction. Understanding of spatial and temporal behaviors of interacting species in ecological systems is a central issue in population ecology. One aspect of great interest for a model with multispecies interactions is whether the involved species can persist or even stabilize at a coexistence steady state. In the case where the species are homogeneously distributed, this would be indicated by a constant positive solution of an ordinary differential equation (ODE) system. In the spatially inhomogeneous case, the existence of a nonconstant time-independent positive solution, also called stationary pattern, is an indication of the richness of the corresponding partial differential equation (PDE) dynamics. In recent years, stationary pattern induced by diffusion has been studied extensively, and many important phenomena have been observed.

In particular, starting with Turing's seminal 1952 paper [34], diffusion has been regarded as the driving force of the spontaneous emergence of spatiotemporal structure in a variety of nonequilibrium situations. To verify the influence of diffusion on this aspect, in the past decades, biologists and applied mathematicians have proposed a number of models, and much work has been devoted to the investigation of the existence of stationary pattern in chemical and biological dynamics theoretically as well as numerically. For example, chemical models include the activator-inhibitor Gierer–Meinhardt model [10, 23], the Sel'kov model [7, 35], the Gray–Scott model [32, 37], the Brusselator model [3, 30], the Noyes–Field model for Belousov–Zhabotinskii

reaction [29], and the chemotactic diffusion model [4, 18, 19, 22, 24, 37], and biological models include the competition model [14, 20] and the predator-prey model [8, 15, 16, 27, 28, 31, 36] (see also the references therein).

In his original paper [34], Turing proposed the notion of diffusion-driven instability (also called Turing instability) in his attempt at modeling, among other things, the regeneration phenomenon of hydra—one of the earliest examples of morphogenesis. That is, Turing claimed that the formation of spatial pattern during morphogenesis could be explained in terms of the instability of a homogeneous steady state solution to a reaction-diffusion network describing the growth and movement of a set of morphogens. Turing's original work was primarily concerned with the stability analysis of the uniform steady state solution of the system for the interacting morphogens.

In biology and chemistry, the more interesting question, however, is whether the spatially inhomogeneous solution may be generated by such instability. Strikingly, in some cases, Turing instability can indeed lead to stationary pattern (also called Turing pattern), a fascinating phenomenon in nonlinear science, which has been found in various mechanisms [4, 18, 26, 27, 28, 30, 35, 36, 37]. While linear stability analysis of the homogeneous steady state is a straightforward method for calculating conditions for the onset of Turing instability, the analysis of the existence of resulting nonhomogeneous steady states is mathematically challenging. In this paper, it is the question of the existence of nonhomogeneous steady states that we focus on.

In the present work, we will investigate a coupled reaction-diffusion food chain model with ratio-dependent functional response and analyze the coexistence of the three species. We attempt to further understand the influences of diffusion and functional responses on pattern formation. As a consequence, the existence and nonexistence results for nonconstant positive steady state solutions to this system indicate that stationary pattern arises as the diffusion coefficients enter into certain regions. In other words, diffusion does help to create stationary pattern. For this model, we also show that Turing instability occurs and prove the generation of Turing pattern in some cases.

On the other hand, our results also demonstrate that diffusion and functional response can become determining factors in the formation of pattern. Although our model is very different from the one considered by Lou, Martinez, and Ni in [20], their interesting observation that the introduction of a new species may qualitatively change the pattern structure of the original system is again present in our study. At the same time, our work corroborates recent numerical results implemented by Alonso, Bartumeus, and Catalan in [2]. We refer the reader to more detailed discussions in section 6.

Our paper is organized as follows. In section 2, we propose our mathematical model. In section 3, we discuss the persistence and stability of the unique constant positive steady state for the ODE and PDE systems. In section 4, we consider the nonexistence of nonconstant positive steady state solutions, while section 5 is devoted to the existence of nonconstant positive steady state solutions. In section 6, from the biological viewpoint we make some comments on our studies, indicating some interesting influences of diffusion and functional responses on pattern formation. Finally, in the appendix, we analyze some conditions, which are imposed in section 5 to obtain the nonconstant positive steady state solutions to the PDE system.

2. The derivation of the mathematical model. Numerous examples from biological control indicate that the classical prey-dependent predator-prey model is often contrary to actual observations, such as the well-known paradox of enrichment formulated by Rosenzweig [33]. The theory of Rosenzweig states that enriching a

predator-prey system (increasing the prey's carrying capacity) will cause an increase in the equilibrium density of the predator but not in that of the prey; it will destabilize the positive equilibrium as the prey's carrying capacity increases, and thus will increase the possibility of stochastic extinction of the predator. Recently there is growing evidence that in some situations, especially when predators have to search, share, and compete for food, a more suitable general predator-prey model should be a so-called ratio-dependent one (namely, the functional responses are ratio-dependent). Roughly speaking, this model states that the per capita predator growth rate should be a function of the ratio of prey to predator abundance (see, e.g., [1]).

In the case of multiple species interaction, the prey-dependent models such as those studied in [5, 9, 11, 17], while mathematically interesting, inherit the mechanism that generates the factitious paradox of enrichment and fail to produce the often observed extinction dynamics resulting in the collapse of the system. Consequently, a ratio-dependent food chain model, which is an ODE system with three equations whose species are hence assumed to be spatially homogeneous, was proposed by Hsu, Hwang, and Kuang in [13] to describe the growth of plant, pest, and top predator.

More precisely, the authors of [13] considered the following three–trophic-level food chain system with ratio-dependent functional response:

$$(2.1) \quad \begin{cases} \dfrac{du_1}{dt} = ru_1\left(1 - \dfrac{u_1}{k}\right) - \dfrac{1}{\eta_1}\dfrac{m_1 u_1 u_2}{u_1 + c_1 u_2}, & t > 0, \\[2ex] \dfrac{du_2}{dt} = \dfrac{m_1 u_1 u_2}{u_1 + c_1 u_2} - b_1 u_2 - \dfrac{1}{\eta_2}\dfrac{m_2 u_2 u_3}{u_2 + c_2 u_3}, & t > 0, \\[2ex] \dfrac{du_3}{dt} = \dfrac{m_2 u_2 u_3}{u_2 + c_2 u_3} - b_2 u_3, & t > 0, \\[2ex] u_1(0) > 0, \ \ u_2(0) > 0, \ \ u_3(0) > 0, \end{cases}$$

where u_i $(i = 1, 2, 3)$ are the respective population densities of prey, predator, and top predator. For $i = 1, 2$, η_i, m_i, c_i, and b_i represent the yield constants, maximal predator growth rates, half-saturation constants, and predator's death rates, respectively. Constants r and k are the prey intrinsic growth rate and carrying capacity, respectively. As observed in [13], u_3 preys on u_2 and only on u_2, and u_2 preys on u_1 and nutrient recycling is not accounted for, which produces the so-called simple food chain. A distinct feature of the simple food chain is the domino effect: if one species dies out, all the species at higher trophic levels die out as well.

As in [13], for simplicity, we use the following scaling to (2.1):

$$t \to rt, \qquad u_1 \to u_1/k, \qquad u_2 \to c_1 u_2/k, \qquad u_3 \to c_1 c_2 u_3/k,$$
$$m_1 \to m_1/r, \qquad b_1 \to b_1/r, \qquad m_2 \to m_2/r, \qquad b_2 \to b_2/r,$$

and (2.1) becomes the form

$$(2.2) \quad \begin{cases} \dfrac{du_1}{dt} = u_1(1 - u_1) - \dfrac{a_1 u_1 u_2}{u_1 + u_2}, & t > 0, \\[2ex] \dfrac{du_2}{dt} = \dfrac{m_1 u_1 u_2}{u_1 + u_2} - b_1 u_2 - \dfrac{a_2 u_2 u_3}{u_2 + u_3}, & t > 0, \\[2ex] \dfrac{du_3}{dt} = \dfrac{m_2 u_2 u_3}{u_2 + u_3} - b_2 u_3, & t > 0, \\[2ex] u_1(0) > 0, \ \ u_2(0) > 0, \ \ u_3(0) > 0, \end{cases}$$

where $a_i = m_i/(\eta_i c_i r)$ $(i = 1, 2)$, can be regarded as the respective predation rate of u_2 and u_3.

From [13], it is easily shown that (2.2) has a unique positive steady state solution if and only if the following are satisfied:

$$(2.3) \qquad m_2 > b_2, \quad A > 1 \quad \text{and} \quad 0 < a_1 < A/(A-1),$$

where

$$A \equiv m_1/(a_2(m_2 - b_2)/m_2 + b_1).$$

Moreover, the unique positive steady state $(u_1, u_2, u_3) = (\tilde{u}_1, \tilde{u}_2, \tilde{u}_3)$ can be expressed as

$$\tilde{u}_1 = [a_1 + A(1 - a_1)]/A, \quad \tilde{u}_2 = (A - 1)\tilde{u}_1, \quad \text{and} \quad \tilde{u}_3 = (m_2 - b_2)\tilde{u}_2/b_2.$$

We also note that $m_2 > b_2$ and $A > 1$ imply $m_1 > b_1$.

In [13], the authors dealt with (2.2). In particular, they obtained the extinction conditions of certain species and discussed the local asymptotical stability of $(\tilde{u}_1, \tilde{u}_2, \tilde{u}_3)$ and various scenarios where distinct solutions can be attracted to the origin, the pest-free steady state, and the positive steady state $(\tilde{u}_1, \tilde{u}_2, \tilde{u}_3)$. For more detail, we refer the reader to [13]. From their results, the authors pointed out that this ODE system is very rich in dynamics.

To take into account the inhomogeneous distribution of the predators and the prey in different spatial locations within a fixed bounded domain Ω in $\mathbf{R}^N$ with smooth boundary at any given time, and the natural tendency of each species to diffuse to a smaller population concentration, instead of (2.2), we need to consider the following reaction-diffusion (PDE) system:

$$(2.4) \quad \begin{cases} u_{1t} - d_1 \Delta u_1 = u_1(1 - u_1) - \dfrac{a_1 u_1 u_2}{u_1 + u_2} & \text{in } \Omega \times (0, \infty), \\[2mm] u_{2t} - d_2 \Delta u_2 = \dfrac{m_1 u_1 u_2}{u_1 + u_2} - b_1 u_2 - \dfrac{a_2 u_2 u_3}{u_2 + u_3} & \text{in } \Omega \times (0, \infty), \\[2mm] u_{3t} - d_3 \Delta u_3 = \dfrac{m_2 u_2 u_3}{u_2 + u_3} - b_2 u_3 & \text{in } \Omega \times (0, \infty), \\[2mm] \partial_\nu u_i = 0, \quad i = 1, 2, 3, & \text{on } \partial\Omega \times (0, \infty), \\[2mm] u_i(x, 0) = u_{i0}(x) \geq 0, \not\equiv 0, \ i = 1, 2, 3, & \text{in } \Omega. \end{cases}$$

Here ν is the outward unit normal vector on the boundary $\partial\Omega$ and $\partial_\nu = \partial/\partial\nu$, and d_i $(i = 1, 2, 3)$ are called the diffusion coefficients of the corresponding species u_i and hence are assumed to be positive constants. The initial data u_{i0} $(i = 1, 2, 3)$ are continuous functions, and the homogeneous Neumann boundary condition means that model (2.4) is self-contained and has no population flux across the boundary $\partial\Omega$.

In our work here, we are mainly concerned with the effect of diffusion on stationary pattern generated by (2.4). Hence, this leads us to study the steady state problem of

(2.4), which satisfies

(2.5)
$$\begin{cases} -d_1\Delta u_1 = u_1\left(1 - u_1\right) - \dfrac{a_1 u_1 u_2}{u_1 + u_2} & \text{in } \Omega, \\[2mm] -d_2\Delta u_2 = \dfrac{m_1 u_1 u_2}{u_1 + u_2} - b_1 u_2 - \dfrac{a_2 u_2 u_3}{u_2 + u_3} & \text{in } \Omega, \\[2mm] -d_3\Delta u_3 = \dfrac{m_2 u_2 u_3}{u_2 + u_3} - b_2 u_3 & \text{in } \Omega, \\[2mm] \partial_\nu u_i = 0, \ i = 1, 2, 3, & \text{on } \partial\Omega. \end{cases}$$

It is evident that only nonnegative solutions of (2.5) are of real interest. The positive solution (u_1, u_2, u_3) of (2.5) to be mentioned throughout this paper always refers to a classical solution with $u_i > 0$ $(i = 1, 2, 3)$ on $\bar{\Omega}$. It should also be noted that the well-known maximum principle ensures that a nonnegative classical solution of (2.5) with $u_i \not\equiv 0$ $(i = 1, 2, 3)$ must be a positive one.

For (2.4) and the steady state problem (2.5), we will mainly concentrate on the coexistence of the three species and consider the case of $a_1 < 1$. In particular, some results for the existence and nonexistence of nonconstant positive solutions to (2.5) are derived. In establishing the existence of nonconstant positive solutions, due to the lack of variational structure for (2.5), our mathematical tool is the topology degree theory incorporated with the calculation of the fixed point index.

3. Persistence and stability. For simplicity of presentation, we introduce some notation. Throughout this section, let

$$\mathbf{u}(t) = (u_1(t), u_2(t), u_3(t))^T \quad \text{and} \quad \mathbf{u}(x, t) = (u_1(x, t), u_2(x, t), u_3(x, t))^T$$

be the respective solutions of (2.2) and (2.4). Denote $\mathbf{u} = (u_1, u_2, u_3)^T$, $\tilde{\mathbf{u}} = (\tilde{u}_1, \tilde{u}_2, \tilde{u}_3)^T$. From classical theories of ODEs and parabolic equations, $\mathbf{u}(t)$ and $\mathbf{u}(x, t)$ exist globally and are positive; namely, $u_i(t)$, $u_i(x, t) > 0$ $(i = 1, 2, 3)$ for all $t > 0$ and $x \in \bar{\Omega}$.

First we state some simple facts about the asymptotical behavior of solutions to (2.4). The proof is similar to that of Theorem 2.5 in [28] and so is omitted here.

PROPOSITION 3.1. *The solution $(u_1(x, t), u_2(x, t), u_3(x, t))$ of (2.4) satisfies the following:*
  (i) *If $m_1 \leq b_1$, then $(u_2(x, t), u_3(x, t)) \rightarrow (0, 0)$ uniformly on $\bar{\Omega}$ as $t \rightarrow \infty$.*
  (ii) *If $m_2 \leq b_2$, then $u_3(x, t) \rightarrow 0$ uniformly on $\bar{\Omega}$ as $t \rightarrow \infty$.*
  (iii) *If $a_1 \leq 1$ and $m_1 \leq b_1$, then $u_1(x, t) \rightarrow 1$ and $(u_2(x, t), u_3(x, t)) \rightarrow (0, 0)$ uniformly on $\bar{\Omega}$ as $t \rightarrow \infty$. As a consequence, if $m_1 \leq b_1$ or $m_2 \leq b_2$, problem (2.5) has no positive solutions.*

As shown in Proposition 3.1, if $m_1 \leq b_1$ or $m_2 \leq b_2$, the two predators or the top predator will become extinct, respectively. Moreover, if $a_1 \leq 1$ and $m_1 \leq b_1$, then only the plant will exist eventually.

In this paper, since our main goal is to analyze the coexistence of the three species, from now on, unless otherwise specified, it is always assumed that $(\tilde{u}_1, \tilde{u}_2, \tilde{u}_3)$ exists, which implies that $m_1 > b_1$ and $m_2 > b_2$ as indicated in section 2.

We have the following basic persistence property of the solutions $\mathbf{u}(t)$ and $\mathbf{u}(x, t)$, which shows that the three species always coexist at any time and any location of the habitat domain, no matter how fast or slowly they diffuse, under certain conditions on parameters. This result is even new for the ODE system (2.2).

PROPOSITION 3.2. *Assume that $a_1 < 1$, $a_2 + b_1 < m_1$ hold. Then, for any $0 < \varepsilon \ll 1$, there exists $T \gg 1$ such that $\mathbf{u}(t)$ and $\mathbf{u}(x,t)$ satisfy*

$$K - \varepsilon < u_1(t), \quad u_1(x,t) < 1 + \varepsilon,$$

$$\frac{K(m_1 - (a_2 + b_1))}{a_2 + b_1} - \varepsilon < u_2(t), \quad u_2(x,t) < \frac{m_1 - b_1}{b_1} + \varepsilon,$$

$$\frac{K(m_1 - (a_2 + b_1))(m_2 - b_2)}{(a_2 + b_1)b_2} - \varepsilon < u_3(t), \quad u_3(x,t) < \frac{(m_1 - b_1)(m_2 - b_2)}{b_1 b_2} + \varepsilon$$

for all $x \in \bar{\Omega}$ and $t > T$. Here, K is given by

$$K = \frac{1}{2}\left\{ 2 - \frac{m_1}{b_1} + \sqrt{\left(2 - \frac{m_1}{b_1}\right)^2 + 4(1 - a_1)\left(\frac{m_1}{b_1} - 1\right)} \right\}.$$

Proof. The proof is based on comparison principles. We first prove that the estimates hold for $\mathbf{u}(t)$. For $0 < \varepsilon \ll 1$ and $t \gg 1$, from the first equation in (2.2) it is clear that $u_1(t) < 1 + \varepsilon$ by the comparison principle for ODEs.

In the following, we always consider that $0 < \varepsilon \ll 1$ and $t \geq T \gg 1$, and the values of ε and T may be different from line to line. Since $u_2(t)$ satisfies

$$u_2'(t) < \frac{(m_1 - b_1)(1 + \varepsilon) - b_1 u_2}{1 + \varepsilon + u_2} u_2,$$

by the comparison principle for ODEs again, we have that

$$u_2(t) < \frac{(m_1 - b_1)(1 + \varepsilon)}{b_1} + \varepsilon = \frac{m_1 - b_1}{b_1} + \frac{m_1}{b_1}\varepsilon.$$

Thus we can assume the following holds:

$$(3.1) \qquad\qquad u_2(t) < \frac{m_1 - b_1}{b_1} + \varepsilon.$$

Combining (3.1) and the first equation in (2.2), we deduce that

$$u_1'(t) > \frac{-u_1^2 + (2 - m_1/b_1 - \varepsilon)u_1 + (1 - a_1)[(m_1 - b_1)/b_1 + \varepsilon]}{(m_1 - b_1)/b_1 + \varepsilon + u_1} u_1.$$

Therefore

$$(3.2) \quad u_1(t) > \frac{1}{2}\left\{ 2 - \frac{m_1}{b_1} - \varepsilon + \sqrt{\left(2 - \frac{m_1}{b_1} - \varepsilon\right)^2 + 4(1 - a_1)\left(\frac{m_1}{b_1} - 1 + \varepsilon\right)} \right\}$$
$$- \varepsilon > K - \varepsilon.$$

Similarly, applying (3.2) to the second equation in (2.2), we obtain

$$(3.3) \qquad\qquad u_2(t) > \frac{K(m_1 - (a_2 + b_1))}{a_2 + b_1} - \varepsilon.$$

Together with (3.1) and (3.3), the third equation in (2.2) results in

$$(3.4) \qquad \frac{K[m_1 - (a_2 + b_1)](m_2 - b_2)}{(a_2 + b_1)b_2} - \varepsilon < u_3(t) < \frac{(m_1 - b_1)(m_2 - b_2)}{b_1 b_2} + \varepsilon.$$

To sum up, (3.1)–(3.4) deduce our result for $\mathbf{u}(t)$. In a similar manner, by the comparison principle for parabolic equations, one can establish the desired estimates for $\mathbf{u}(x, t)$. □

In particular Proposition 3.2 and the maximum principle imply a priori upper and lower bounds for the positive solutions of (2.5), which will play crucial roles in the later sections. To prove that we recall the following maximum principle (for example, Lemma 2.1 in [21]).

LEMMA 3.1. *Suppose that $g \in C(\bar{\Omega} \times \mathbf{R})$.*
(i) *Assume that $w \in C^2(\Omega) \cap C^1(\bar{\Omega})$ and satisfies*

$$\Delta w(x) + g(x, w(x)) \geq 0 \quad in \ \Omega, \quad \partial_\nu w \leq 0 \quad on \ \partial\Omega.$$

If $w(x_0) = \max_{\bar{\Omega}} w$, then $g(x_0, w(x_0)) \geq 0$.
(ii) *Assume that $w \in C^2(\Omega) \cap C^1(\bar{\Omega})$ and satisfies*

$$\Delta w(x) + g(x, w(x)) \leq 0 \quad in \ \Omega, \quad \partial_\nu w \geq 0 \quad on \ \partial\Omega.$$

If $w(x_0) = \min_{\bar{\Omega}} w$, then $g(x_0, w(x_0)) \leq 0$.
Now we have the following a priori estimates for steady state solutions.

THEOREM 3.1. *Assume that $a_1 < 1$ and $a_2 + b_1 < m_1$ hold. Let K be defined as in Proposition 3.2. Then any positive solution (u_1, u_2, u_3) of (2.5) satisfies the following: for all $x \in \bar{\Omega}$,*

$$K < u_1(x) < 1,$$

$$\frac{K(m_1 - (a_2 + b_1))}{a_2 + b_1} < u_2(x) < \frac{m_1 - b_1}{b_1},$$

$$\frac{K(m_1 - (a_2 + b_1))(m_2 - b_2)}{(a_2 + b_1)b_2} < u_3(x) < \frac{(m_1 - b_1)(m_2 - b_2)}{b_1 b_2}.$$

Proof. From Proposition 3.2, stated results hold if strict inequalities are replaced by nonstrict inequalities. Thus we only need to show the strict inequalities. Let (u_1, u_2, u_3) be a positive solution of (2.5) and set

$$u_i(x_i) = \max_{\bar{\Omega}} u_i \quad \text{and} \quad u_i(y_i) = \min_{\bar{\Omega}} u_i, \quad i = 1, 2, 3.$$

Applying Lemma 3.1 to the first equation in (2.5), we find that

$$1 - u_1(x_1) - \frac{a_1 u_2(x_1)}{u_1(x_1) + u_2(x_1)} \geq 0.$$

Thus when $a_1 < 1$, it follows that $u_1(y_1) < 1$. Following the same order in the proof of Proposition 3.2, we can show that the stated results with strict inequalities hold. □

When the population persistence holds for the food chain, the constant steady state $\tilde{\mathbf{u}}$ is always in the attracting region given in Proposition 3.2 and Theorem 3.1. Next we discuss the stability of $\tilde{\mathbf{u}}$ with respect to (2.4). To this end, we need to collect some known facts from [13]. For sake of simplicity, we denote

$$\mathbf{G}(\mathbf{u}) = \begin{pmatrix} u_1(1 - u_1) - \dfrac{a_1 u_1 u_2}{u_1 + u_2} \\ \dfrac{m_1 u_1 u_2}{u_1 + u_2} - b_1 u_2 - \dfrac{a_2 u_2 u_3}{u_2 + u_3} \\ \dfrac{m_2 u_2 u_3}{u_2 + u_3} - b_2 u_3 \end{pmatrix} \quad \text{and} \quad \mathbf{G_u}(\tilde{\mathbf{u}}) = \begin{pmatrix} a_{11} & a_{12} & 0 \\ a_{21} & a_{22} & a_{23} \\ 0 & a_{32} & a_{33} \end{pmatrix},$$

where

$$
\begin{cases}
a_{11} = \tilde{u}_1\Big[-1 + \dfrac{a_1\tilde{u}_2}{(\tilde{u}_1 + \tilde{u}_2)^2}\Big], \quad a_{22} = \tilde{u}_2\Big[-\dfrac{m_1\tilde{u}_1}{(\tilde{u}_1 + \tilde{u}_2)^2} + \dfrac{a_2\tilde{u}_3}{(\tilde{u}_2 + \tilde{u}_3)^2}\Big], \\[3mm]
a_{33} = -\dfrac{m_2\tilde{u}_2\tilde{u}_3}{(\tilde{u}_2 + \tilde{u}_3)^2} < 0, \quad a_{12} = -\dfrac{a_1\tilde{u}_1^2}{(\tilde{u}_1 + \tilde{u}_2)^2} < 0, \quad a_{21} = \dfrac{m_1\tilde{u}_2^2}{(\tilde{u}_1 + \tilde{u}_2)^2} > 0, \\[3mm]
a_{23} = -a_2\tilde{u}_2^2/(\tilde{u}_2 + \tilde{u}_3)^2 < 0, \quad a_{32} = m_2\tilde{u}_3^2/(\tilde{u}_2 + \tilde{u}_3)^2 > 0.
\end{cases}
$$

In Proposition 3.1 in [13], it was proved that if $a_{11} \le 0$ and $a_{22} \le 0$, $\tilde{\mathbf{u}}$ is locally asymptotically stable for (2.2). Indeed even with the presence of the diffusion, $\tilde{\mathbf{u}}$ is uniformly asymptotically stable for (2.4) under the same conditions. More precisely, we have the following theorem.

THEOREM 3.2. *Assume that $a_{11} \le 0$ and $a_{22} \le 0$ hold; then $\tilde{\mathbf{u}}$ is locally uniformly asymptotically stable for* (2.4) *in the sense of* [12]. *As a consequence,* (2.5) *has no nonconstant positive solution in a neighborhood of $\tilde{\mathbf{u}}$. Moreover, if $a_1 < 1$ and $a_2 + b_1 < m_1$, then $a_{11} < 0$ and $a_{22} < 0$; hence $\tilde{\mathbf{u}}$ is locally uniformly asymptotically stable.*

Proof. The proof of stability when $a_{11} \le 0$ and $a_{22} \le 0$ is similar to that of Theorem 2 in [36], and we omit the details here. We note that if $a_1 < 1$, then $a_{11} < 0$. Moreover, the inequality $a_{22} \le 0$ is equivalent to

$$
(3.5) \qquad m_1 \ge \Big(b_1 + a_2\frac{m_2 - b_2}{m_2}\Big)^2\Big/\Big(b_1 + a_2\Big(\frac{m_2 - b_2}{m_2}\Big)^2\Big).
$$

It is also noted that

$$
\Big(b_1 + a_2\frac{m_2 - b_2}{m_2}\Big)^2\Big/\Big(b_1 + a_2\Big(\frac{m_2 - b_2}{m_2}\Big)^2\Big) < a_2 + b_1.
$$

Hence if $a_1 < 1$ and $a_2 + b_1 < m_1$, we have $a_{11}, a_{22} < 0$ by (3.5). □

Remark 3.1. Theorem 3.2 and the previous arguments show that no Turing instability or diffusion-driven instability phenomenon occurs when $a_{11} \le 0$ and $a_{22} \le 0$ hold. On the other hand, if we take $m_1 = (b_1 + a_2(m_2 - b_2)/m_2)^2/(b_1 + a_2(m_2 - b_2)^2/m_2^2) - o(b_1)$, and $b_1 \to 0$, a_2, b_2, m_2 are properly chosen and either $a_1 \to 1/2$ or $a_1 \to 1$, as in Proposition 3.1 in [13], together with some meticulous computations, the well-known Roth–Hurwitz criterion ensures that $\tilde{\mathbf{u}}$ is still stable for the ODE system (2.2). However, by fixing these parameters including d_1 and d_2, and then letting the diffusion d_3 be large enough, similar to the proof of Theorem 2 in [36], one can show that $\tilde{\mathbf{u}}$ is unstable with respect to the PDE system (2.4). Thus Turing instability could occur when the conditions of Theorem 3.2 are not satisfied.

From Theorem 3.2, $\tilde{\mathbf{u}}$ is locally uniformly asymptotically stable when $a_1 < 1$ and $a_2 + b_1 < m_1$. In this case it is unlikely that nonconstant positive solutions (stationary pattern) of (2.5) exist. Indeed with more restrictive conditions on the parameters, we can show the global stability of $\tilde{\mathbf{u}}$ for systems (2.2) and (2.4). Our result below is independent of the diffusion rates d_i; that is, the constant coexistence state $\tilde{\mathbf{u}}$ is globally asymptotically stable. Hence when the conditions on the parameters are satisfied, $\tilde{\mathbf{u}}$ is stabilized under arbitrary spatially inhomogeneous perturbation.

THEOREM 3.3. *Let K be defined as in Proposition* 3.2. *Assume that the following hold:*

   (i) $a_1 < 1$ *and* $a_2 + b_1 < m_1$;

   (ii) $a_1(A - 1)/A < m_1K/(a_2 + b_1)$;

(iii) $a_2 b_2 m_1 (m_2 - b_2)(a_2 + b_1) < b_1 m_2 K[m_1 - (a_2 + b_1)][b_1 m_2 + a_2(m_2 - b_2)]$.

Then the constant positive steady state $\tilde{\mathbf{u}}$ is globally asymptotically stable for systems (2.2) *and* (2.4) *for all initial nonnegative conditions which are not steady states. In particular,* (2.5) *has no nonconstant positive solution if conditions* (i)–(iii) *hold.*

Proof. We use Lyapunov functionals for the proof. First, we verify the result for system (2.2). For our purpose, we first recall the following basic Lyapunov functionals:

$$E(u_i) = u_i - \tilde{u}_i - \tilde{u}_i \ln \frac{u_i}{\tilde{u}_i}, \quad i = 1, 2, 3.$$

Note that $E(u_i(t))$ are nonnegative, and $E(u_i(t)) = 0$ $(i = 1, 2, 3)$ if and only if $(u_1(t), u_2(t), u_3(t)) = (\tilde{u}_1, \tilde{u}_2, \tilde{u}_3)$. Hence, letting

$$E(t) = E(u_1(t)) + \frac{a_1 \tilde{u}_1}{m_1 \tilde{u}_2} E(u_2(t)) + \frac{a_1 a_2 \tilde{u}_1}{m_1 m_2 \tilde{u}_3} E(u_3(t)),$$

we have

$$
\begin{aligned}
\frac{dE}{dt} = {} & \left\{ -1 + \frac{a_1 \tilde{u}_2}{(\tilde{u}_1 + \tilde{u}_2)(u_1 + u_2)} \right\}(u_1 - \tilde{u}_1)^2 + \frac{a_1 \tilde{u}_1}{m_1 \tilde{u}_2}\left\{ -\frac{m_1 \tilde{u}_1}{(\tilde{u}_1 + \tilde{u}_2)(u_1 + u_2)} \right. \\
& \left. + \frac{a_2 \tilde{u}_3}{(\tilde{u}_2 + \tilde{u}_3)(u_2 + u_3)} \right\}(u_2 - \tilde{u}_2)^2 - \frac{a_1 a_2 \tilde{u}_1 \tilde{u}_2}{m_1 \tilde{u}_3 (\tilde{u}_2 + \tilde{u}_3)(u_2 + u_3)}(u_3 - \tilde{u}_3)^2.
\end{aligned}
$$
(3.6)

Under our assumptions (i)–(iii), we can claim that for $t \gg 1$ the following hold:

$$(3.7) \quad \frac{a_1 \tilde{u}_2}{(\tilde{u}_1 + \tilde{u}_2)(u_1 + u_2)} \le 1 \quad \text{and} \quad \frac{a_2 \tilde{u}_3}{(\tilde{u}_2 + \tilde{u}_3)(u_2 + u_3)} \le \frac{m_1 \tilde{u}_1}{(\tilde{u}_1 + \tilde{u}_2)(u_1 + u_2)}.$$

In fact, by Proposition 3.2, to satisfy (3.7), for $t \gg 1$ it is sufficient to require

$$\frac{a_1 \tilde{u}_2}{(\tilde{u}_1 + \tilde{u}_2)} < \frac{m_1 K}{a_2 + b_1} \quad \text{and} \quad \frac{a_2 \tilde{u}_3}{(\tilde{u}_2 + \tilde{u}_3)} \cdot \frac{m_1}{b_1} < \frac{m_1 \tilde{u}_1}{(\tilde{u}_1 + \tilde{u}_2)} \cdot \frac{K m_2(m_1 - (a_2 + b_1))}{(a_2 + b_1) b_2}.$$

Therefore by the definition of $(\tilde{u}_1, \tilde{u}_2, \tilde{u}_3)$, we easily see that the above two inequalities are equivalent to assumptions (ii) and (iii), respectively. Thus (3.6) implies that $E'(t) < 0$ for $t \gg 1$. Now for $t \gg 1$, $E(t)$ is a Lyapunov functional for system (2.2); namely, for $t \gg 1$, $E'(t) < 0$ along trajectories and $E(t) > 0$ except at $\tilde{\mathbf{u}}$. Hence $\tilde{\mathbf{u}}$ is globally asymptotically stable for (2.2) following the well-known theorem of Lyapunov stability.

Based on the proof of Theorem 3.3, by Proposition 3.2, it is not hard to see that for $t \gg 1$

$$E^*(t) = \int_\Omega \left\{ E(u_1(x,t)) + \frac{a_1 \tilde{u}_1}{m_1 \tilde{u}_2} E(u_2(x,t)) + \frac{a_1 a_2 \tilde{u}_1}{m_1 m_2 \tilde{u}_3} E(u_3(x,t)) \right\} \mathrm{d}x$$

is a Lyapunov functional for system (2.4) and $\tilde{\mathbf{u}}$ is globally asymptotically stable for system (2.4) under our assumptions. $\square$

Remark 3.2. Simple analysis shows that Theorem 3.3 holds if one of the following holds: (1) $a_1 \to 0$, $a_2 \to 0$; (2) $a_1 < 1$, m_1 is large and $m_2 \to b_2$; or (3) $a_1 < 1$, m_1 is large, and $a_2 b_2(m_2 - b_2)(a_2 + b_1) < (1 - a_1) b_1 m_2[b_1 m_2 + a_2(m_2 - b_2)]$. Indeed in case (1), K defined in Proposition 3.2 tends to 1 as $a_1 \to 0$, and the lower and upper bounds in Proposition 3.2 and Theorem 3.1 tend to the same value as $a_2 \to 0$.

This shows that the a priori estimate in Proposition 3.2 and Theorem 3.1 are sharp when a_1 and a_2 are small.

Results in this section have interesting and significant biological implications. Regarding the impact of the diffusion, all results in this section (Propositions 3.1 and 3.2 and Theorems 3.1, 3.2, and 3.3) are independent of diffusion coefficients d_i, $i = 1, 2, 3$. In these parameter ranges, diffusion usually enhances the stability of the constant steady states. Proposition 3.1 gives conditions of total extinction of all three species and conditions of the extinction of both middle and top predators. Comparison can be made with results in section 2 of [13], where the ODE system is studied in more detail.

When the constant coexistence steady state $\tilde{\mathbf{u}}$ exists, our main persistence and stability results are proved under the assumptions

$$(3.8) \qquad\qquad a_1 < 1 \quad \text{and} \quad a_2 + b_1 < m_1.$$

These conditions are evidently stronger than the conditions (2.3) under which $\tilde{\mathbf{u}}$ exists. But with (3.8) satisfied, persistence holds for the whole food chain, and all three species coexist regardless of initial conditions (see Proposition 3.2). The persistence question is even open for the same ODE system, and here we prove it for the more general reaction-diffusion system with no-flux boundary condition. This answers an open question raised in [13] (see discussion on p. 80). Moreover, under (3.8), $\tilde{\mathbf{u}}$ is also locally uniformly asymptotically stable with respect to (2.4), and under strong conditions in Theorem 3.3, $\tilde{\mathbf{u}}$ is globally asymptotically stable. For the ODE systems, these results complement those in [13] in which the main concern is successful biological control. Indeed our results show that under (3.8), biological control of the pest cannot be achieved.

4. Nonexistence of nonconstant positive solutions of (2.5). In Theorem 3.3, the global stability of the constant coexistence steady state implies the nonexistence of nonconstant positive solutions of (2.5) regardless of diffusions. Several nonexistence results of nonconstant positive solutions to (2.5) will be presented in this section, and in these results, the diffusion coefficients do play important roles. The mathematical techniques to be employed are the implicit function theorem method and the energy method, respectively. From now on, let $0 = \mu_0 < \mu_1 \leq \mu_2 \leq \cdots$ be the eigenvalues of the operator $-\Delta$ on Ω with the homogeneous Neumann boundary condition.

4.1. The energy method. In this subsection, we apply the energy method to establish some results on the nonexistence of nonconstant positive solutions of (2.5). For convenience, let us denote the constants a_i, b_i, m_i $(i = 1, 2)$ collectively by Λ.

THEOREM 4.1. *Assume that $a_1 < 1$ and $a_2 + b_1 < m_1$.*

(i) *There exists $\hat{D}_{1,2} = \hat{D}_{1,2}(\Lambda)$ which is independent of d_3 and Ω, such that (2.5) has no nonconstant positive solution provided that $\min\{\mu_1 d_1,\ \mu_1 d_2\} \geq \hat{D}_{1,2}$.*

(ii) *If, in addition, $a_1(a_2 + b_1)^2(m_1 - b_1) \leq (1 - a_1)^2 b_1 m_1^2$, then there exists $\hat{D}_2 = \hat{D}_2(\Lambda)$ which is independent of d_1, d_3, and Ω, such that (2.5) has no nonconstant positive solution provided that $\mu_1 d_2 \geq \hat{D}_2$.*

(iii) *If, in addition, $a_2(a_2 + b_1)^2 b_2 m_1(m_1 - b_1)(m_2 - b_2) \leq (1 - a_1)^3 b_1^3 m_2^2(m_1 - (a_2 + b_1))^2$, then there exists $\hat{D}_{1,3} = \hat{D}_{1,3}(\Lambda)$ which is independent of d_2 and Ω, such that (2.5) has no nonconstant positive solution provided that $\min\{\mu_1 d_1,\ \mu_1 d_3\} \geq \hat{D}_{1,3}$.*

Proof. Let (u_1, u_2, u_3) be a positive solution of (2.5) and let $\bar{g} = |\Omega|^{-1} \int_\Omega g \, \mathrm{d}x$. Then, multiplying the corresponding equation in (2.5) by $\frac{1}{u_i}(u_i - \bar{u}_i)$, $i = 1, 2, 3$, integrating over Ω, and adding the results, we get

$$\int_\Omega \left\{ \sum_{i=1}^3 \frac{d_i \bar{u}_i |\nabla(u_i - \bar{u}_i)|^2}{u_i^2} \right\} \mathrm{d}x$$

$$= \int_\Omega \left\{ (u_1 - \bar{u}_1)^2 \left(-1 + \frac{a_1 \bar{u}_2}{(u_1 + u_2)(\bar{u}_1 + \bar{u}_2)} \right) \right.$$

$$+ (u_1 - \bar{u}_1)(u_2 - \bar{u}_2) \frac{-a_1 \bar{u}_1 + m_1 \bar{u}_2}{(u_1 + u_2)(\bar{u}_1 + \bar{u}_2)}$$

$$+ (u_2 - \bar{u}_2)^2 \left(\frac{-m_1 \bar{u}_1}{(u_1 + u_2)(\bar{u}_1 + \bar{u}_2)} + \frac{a_2 \bar{u}_3}{(u_2 + u_3)(\bar{u}_2 + \bar{u}_3)} \right)$$

$$(4.1) \quad + (u_2 - \bar{u}_2)(u_3 - \bar{u}_3) \frac{-a_2 \bar{u}_2 + m_2 \bar{u}_3}{(u_2 + u_3)(\bar{u}_2 + \bar{u}_3)} - (u_3 - \bar{u}_3)^2 \frac{m_2 \bar{u}_2}{(u_2 + u_3)(\bar{u}_2 + \bar{u}_3)} \left. \right\} \mathrm{d}x.$$

By Theorem 3.1 and the Young inequality, from (4.1) it follows that

$$\int_\Omega \sum_{i=1}^3 d_i |\nabla(u_i - \bar{u}_i)|^2 \, \mathrm{d}x \leq C \int_\Omega \left\{ (u_1 - \bar{u}_1)^2 \left(-1 + \frac{a_1 \bar{u}_2}{(u_1 + u_2)(\bar{u}_1 + \bar{u}_2)} + \varepsilon \right) \right.$$

$$+ C(\varepsilon)(u_2 - \bar{u}_2)^2$$

$$(4.2) \qquad\qquad + (u_3 - \bar{u}_3)^2 \left(-\frac{m_2 \bar{u}_2}{(u_2 + u_3)(\bar{u}_2 + \bar{u}_3)} + \varepsilon \right) \left. \right\} \mathrm{d}x.$$

Here, C depends only on Λ, and $C(\varepsilon)$ depends only on Λ and ε. By Theorem 3.1 again, we can choose $0 < \varepsilon \ll 1$ which depends only on Λ such that

$$-\frac{m_2 \bar{u}_2}{(u_2 + u_3)(\bar{u}_2 + \bar{u}_3)} + \varepsilon < 0.$$

Thus, with (4.2) and the Poincaré inequality,

$$\mu_1 \int_\Omega (g - \bar{g})^2 \, \mathrm{d}x \leq \int_\Omega |\nabla(g - \bar{g})|^2 \, \mathrm{d}x,$$

we find that

$$\mu_1 \int_\Omega \sum_{i=1}^3 d_i (u_i - \bar{u}_i)^2 \, \mathrm{d}x \leq C(\varepsilon) \int_\Omega \sum_{i=1}^2 (u_i - \bar{u}_i)^2 \, \mathrm{d}x.$$

By the above inequality, it is clear that there exists $\hat{D}_{1,2}$ depending only on Λ, such that when $\min\{\mu_1 d_1, \, \mu_1 d_2\} \geq \hat{D}_{1,2}$, $u_i \equiv \bar{u}_i = \text{constant}$, $i = 1, 2, 3$, which asserts our result (i).

If, in addition, we assume $a_1(a_2 + b_1)^2(m_1 - b_1) \leq (1 - a_1)^2 b_1 m_1^2$, then Theorem 3.1 implies

$$-1 + \frac{a_1 \bar{u}_2}{(u_1 + u_2)(\bar{u}_1 + \bar{u}_2)} < 0.$$

Therefore, for $0 < \varepsilon \ll 1$ satisfying

$$-1 + \frac{a_1 \bar{u}_2}{(u_1 + u_2)(\bar{u}_1 + \bar{u}_2)} + \varepsilon < 0 \quad \text{and} \quad -\frac{m_2 \bar{u}_2}{(u_2 + u_3)(\bar{u}_2 + \bar{u}_3)} + \varepsilon < 0,$$

as before, (4.2) implies

$$(4.3) \qquad \int_\Omega \sum_{i=1}^3 d_i |\nabla(u_i - \bar{u}_i)|^2 \, \mathrm{d}x \le C(\varepsilon) \int_\Omega (u_2 - \bar{u}_2)^2 \, \mathrm{d}x.$$

Similar to arguments above, from (4.3) and the Poincaré inequality, there exists $\hat{D}_2 = \hat{D}_2(\Lambda)$ such that (2.5) has no nonconstant positive solution if $\mu_1 d_2 > \hat{D}_2$. Thus (ii) holds.

To prove (iii), as in the arguments above, it is enough to verify that

$$(4.4) \qquad a_2 \bar{u}_3(u_1 + u_2)(\bar{u}_1 + \bar{u}_2) < m_1 \bar{u}_1(u_2 + u_3)(\bar{u}_2 + \bar{u}_3).$$

By Theorem 3.1 again, to ensure (4.4), it suffices to require that the third condition in (iii) holds. This completes our proof. $\square$

THEOREM 4.2.

(i) *Let d_1^*, d_3^* be fixed positive constants satisfying $\mu_1 d_1^* > 1$ and $\mu_1 d_3^* > m_2 - b_2$. Then there exists a positive constant $D_2^* = D_2^*(d_1^*, d_3^*, \Lambda)$ such that (2.5) has no non-constant positive solution provided that $\mu_1 d_2 \ge D_2^*$, $d_1 \ge d_1^*$, and $d_3 \ge d_3^*$.*

(ii) *Let d_2^* be a fixed positive constant satisfying $\mu_1 d_2^* > m_1 - b_1$. Then there exists a positive constant $D_{1,3}^* = D_{1,3}^*(d_2^*, \Lambda)$ such that (2.5) has no nonconstant positive solution provided that $\min\{\mu_1 d_1, \, \mu_1 d_3\} \ge D_{1,3}^*$ and $d_2 \ge d_2^*$.*

Proof. We prove only (i), and the verification of (ii) is similar. Suppose that (u_1, u_2, u_3) and $(\bar{u}_1, \bar{u}_2, \bar{u}_3)$ are the same as in the proof of Theorem 4.1. Multiplying the corresponding equation of (2.5) by $u_i - \bar{u}_i$, $i = 1, 2, 3$, the analysis similar to the proof of Theorem 4.1 deduces

$$\mu_1 \sum_{i=1}^3 \int_\Omega d_i (u_i - \bar{u}_i)^2 \mathrm{d}x \le \int_\Omega \{ (1 + \varepsilon)(u_1 - \bar{u}_1)^2$$
$$+ C(u_2 - \bar{u}_2)^2 + (m_2 - b_2 + \varepsilon)(u_3 - \bar{u}_3)^2 \} \mathrm{d}x$$

for some positive constant $C = C(\Lambda, \varepsilon)$. Choose $\varepsilon > 0$ to be so small that $d_1 \mu_1 \ge 1 + \varepsilon$, $d_3 \mu_1 \ge m_2 - b_2 + \varepsilon$; then there exists D_2^* such that $(u_1, u_2, u_3) = (\bar{u}_1, \bar{u}_2, \bar{u}_3)$ must hold if $d_2 \ge D_2^*$, and so our conclusion holds. $\square$

The results in this subsection demonstrate such a phenomenon: when all diffusion coefficients are large, no patterns exist. Here either d_1, d_3, or d_2 has a lower bound (see Theorem 4.2). If, in addition, the conditions (3.8) are satisfied, then the patterns do not exist even if only one or two diffusion coefficients are large. Such results for general reaction-diffusion systems appeared in [6], and our results here show more delicate dependence on the diffusion coefficients only for the food chain system (2.4) and (2.5).

4.2. The implicit function theorem method. In this subsection, we use the implicit function theorem to obtain some further results for the nonexistence of nonconstant positive solutions of (2.5). We will need the following a priori estimate.

THEOREM 4.3. *Let $a_1 < 1$ and let d be a fixed positive number. Assume that for any positive constants $\tilde{d}_2$ and $\tilde{d}_3$, the boundary value problem*

$$(4.5) \quad \begin{cases} -\tilde{d}_2 \Delta w_2 = (m_1 - b_1)w_2 - \dfrac{a_2 w_2 w_3}{w_2 + w_3} & in \ \ \Omega, \\[2mm] -\tilde{d}_3 \Delta w_3 = \dfrac{m_2 w_2 w_3}{w_2 + w_3} - b_2 w_3 & in \ \ \Omega, \\[2mm] \partial_\nu w_2 = \partial_\nu w_3 = 0 & on \ \ \partial\Omega \end{cases}$$

has no positive solution satisfying $|w_2|_\infty + |w_3|_\infty = 1$. Then there exist positive constants $C_1(\Lambda, \Omega, d)$ and $C_2(\Lambda, \Omega, d)$ such that any positive solution (u_1, u_2, u_3) of (2.5) satisfies

$$C_1(\Lambda, \Omega, d) \ \leq u_i \leq \ C_2(\Lambda, \Omega, d), \quad i = 1, \ 2, \ 3,$$

provided that $d_1, d_2, d_3 \geq d$.

Proof. Since $a_1 < 1$, from the proof of Theorem 3.1, we see that

$$(4.6) \quad 1 - a_1 < u_1 < 1, \quad u_2 < (m_1 - b_1)/b_1, \quad \text{and } u_3 < (m_1 - b_1)(m_2 - b_2)/(b_1 b_2),$$

so $C_2(\Lambda, \Omega, d)$ has been found. Similarly to the proof of Theorem 3.4 in [28], from the second and third equations in (2.5), the desired $C_1(\Lambda, \Omega, d)$ can be obtained. ☐

The assumption that (4.5) has no positive solution is satisfied in some important parameter ranges.

LEMMA 4.1. *Problem* (4.5) *has no positive solution if one of the following holds*:
(i) $a_2 + b_1 \leq m_1$; *or*
(ii) $a_2 + b_1 > m_1$ *and* $\sqrt{a_2 + m_2} < \sqrt{m_1 - b_1} + \sqrt{b_2}$.
In particular, if $a_1 < 1$ and either (i) *or* (ii) *holds, the a priori estimate in Theorem* 4.3 *holds.*

Proof. If condition (i) holds, our conclusion is derived from (ii) of Lemma 3.1; if condition (ii) is satisfied, the proof is the same as that of Corollary 3.5 in [28]. ☐

In this subsection, we will prove a result which considerably improves Theorem 4.2 if the estimates in Theorem 4.3 hold. We note that the conditions (i) and (ii) include (3.8); thus the results are along the same lines as those in the last subsection. To prove our result, we first prepare two lemmas.

LEMMA 4.2. *Assume that $f(u)$ is a continuous function in $[0, \infty)$ and for some positive constant a, $f(u) > 0$ in $(0, a)$ and $f(u) < 0$ in (a, ∞). Then the problem*

$$-\Delta u = u f(u) \ \ in \ \ \Omega, \qquad \partial_\nu u = 0 \ \ on \ \ \partial\Omega$$

has a unique positive solution $u(x) \equiv a$.

Proof. The above result is easily obtained by the direct application of Lemma 3.1. ☐

LEMMA 4.3. (i) *Assume that $a_1 < 1$ and that assumptions in Theorem* 4.3 *hold. Let (u_{1i}, u_{2i}, u_{3i}) be a sequence of positive solutions of* (2.5) *with $d_2 = d_{2i}$ and $d_{2i} \to \infty$ as $i \to \infty$. Then (u_{1i}, u_{2i}, u_{3i}) converges to $\tilde{\mathbf{u}}$ in $[C(\bar{\Omega})]^3$ as $i \to \infty$.*

(ii) *Assume that $a_1 < 1$ and that assumptions in Theorem* 4.3 *hold. Let (u_{1i}, u_{2i}, u_{3i}) be a sequence of positive solutions of* (2.5) *with $(d_1, d_3) = (d_{1i}, d_{3i})$ and $d_{1i}, d_{3i} \to \infty$ as $i \to \infty$. Then (u_{1i}, u_{2i}, u_{3i}) converges to $\tilde{\mathbf{u}}$ in $[C(\bar{\Omega})]^3$ as $i \to \infty$.*

Proof. We prove only (i), and (ii) can be proved similarly by using Theorem 3.1 and Lemma 3.1.

From Theorem 4.3, the sequence $\{(u_{1i}, u_{2i}, u_{3i})\}$ is bounded in $[C(\bar{\Omega})]^3$ with the bound independent of d_2. Then some standard arguments show that there is a subsequence of (u_{1i}, u_{2i}, u_{3i}) (still labelled by itself), such that $(u_{1i}, u_{2i}, u_{3i}) \to (u_1, u_2, u_3)$ in $[C(\bar{\Omega})]^3$ as $i \to \infty$. Furthermore, $u_2 \equiv c$, which is a positive constant; $u_1, u_3 > 0$ on $\bar{\Omega}$; and (u_1, c, u_3) solves

$$(4.7) \quad \begin{cases} -d_1 \Delta u_1 = u_1(1 - u_1) - \dfrac{a_1 c u_1}{u_1 + c} & \text{in } \Omega, \quad \partial_\nu u_1 = 0 \ \text{ on } \partial\Omega, \\[3mm] \displaystyle\int_\Omega \left\{ \dfrac{m_1 u_1}{u_1 + c} - b_1 - \dfrac{a_2 u_3}{c + u_3} \right\} \, \mathrm{d}x = 0, \\[3mm] -d_3 \Delta u_3 = \dfrac{c m_2 u_3}{c + u_3} - b_2 u_3 & \text{in } \Omega, \quad \partial_\nu u_3 = 0 \ \text{ on } \partial\Omega. \end{cases}$$

By Lemma 4.2, from the first and third equations in (4.7), we find that u_1 and u_3 are both constants:

$$(4.8) \qquad u_1 \equiv \frac{1}{2}\Big\{ 1 - c + \sqrt{(1 - c)^2 + 4c(1 - a_1)} \ \Big\} \quad \text{and} \quad u_3 \equiv \frac{m_2 - b_2}{b_2} c.$$

Substituting (4.8) into the second equation in (4.7), we find that $(u_1, c, u_3) = \tilde{\mathbf{u}}$. This verifies that the convergence holds for a subsequence of (u_{1i}, u_{2i}, u_{3i}). But the limit is a fixed point; thus the convergence holds for the whole sequence (u_{1i}, u_{2i}, u_{3i}). $\square$

Now we state our main result in this subsection.

THEOREM 4.4. *Assume that $a_1 < 1$ and that assumptions in Theorem 4.3 hold.*

(i) *Let ϵ_1 be an arbitrary positive constant. Then there exists $D_2 = D_2(\epsilon_1, \Lambda, \Omega)$ such that (2.5) has no nonconstant positive solution provided that $\min\{d_1, d_3\} \geq \epsilon_1$ and $d_2 \geq D_2$.*

(ii) *Let ϵ_2 be an arbitrary positive constant. Then there exists $D_{1,3} = D_{1,3}(\epsilon_2, \Lambda, \Omega)$ such that (2.5) has no nonconstant positive solution provided that $d_2 \geq \epsilon_2$ and $\min\{d_1, d_3\} \geq D_{1,3}$.*

Proof. We first prove (i). By (i) of Theorem 4.2, for a fixed large constant $D_{1,3}$ depending only on Λ and Ω, there exists $D_2^* = D_2^*(\Lambda, \Omega)$ such that (2.1) has no positive nonconstant solution when $d_1, d_3 \geq D_{1,3}$ and $d_2 \geq D_2^*$. As a result, it suffices to consider the case $d_1, d_3 \in [\epsilon_1/2, D_{1,3}]$.

We make a decomposition: $u_2 = w_2 + \xi$ with $\int_\Omega w_2 = 0$ and $\xi \in \mathbf{R}^+$. We observe that finding the positive solution of (2.5) is equivalent to solving the following problem:

$$(4.9) \quad \begin{cases} d_1 \Delta u_1 + u_1(1 - u_1) - \dfrac{a_1 u_1 (w_2 + \xi)}{u_1 + w_2 + \xi} = 0 & \text{in } \Omega, \ \partial_\nu u_1 = 0 \text{ on } \partial\Omega, \\[3mm] \Delta w_2 + \rho \left\{ \dfrac{m_1 u_1 (w_2 + \xi)}{u_1 + w_2 + \xi} \right. \\[2mm] \qquad \left. - b_1(w_2 + \xi) - \dfrac{a_2 (w_2 + \xi) u_3}{w_2 + \xi + u_3} \right\} = 0 & \text{in } \Omega, \ \partial_\nu w_2 = 0 \text{ on } \partial\Omega, \\[3mm] \displaystyle\int_\Omega \left\{ \dfrac{m_1 u_1 (w_2 + \xi)}{u_1 + w_2 + \xi} - b_1(w_2 + \xi) \right. \\[2mm] \qquad \left. - \dfrac{a_2(w_2 + \xi)u_3}{w_2 + \xi + u_3} \right\} \, \mathrm{d}x = 0, \\[3mm] d_3 \Delta u_3 + \dfrac{m_2(w_2 + \xi)u_3}{w_2 + \xi + u_3} - b_2 u_3 = 0 & \text{in } \Omega, \ \partial_\nu u_3 = 0 \text{ on } \partial\Omega, \\[3mm] \xi > 0, u_1, u_3 > 0 & \text{in } \Omega, \end{cases}$$

where $\rho = d_2^{-1}$. Clearly, $(u_1, w_2, \xi, u_3) = (\tilde{u}_1, 0, \tilde{u}_2, \tilde{u}_3)$ is a solution of (4.9) for $\rho > 0$.

To prove our theorem, by the finite covering argument, it is sufficient to prove that, for any fixed $\tilde{d}_1, \tilde{d}_3 \in [\epsilon_1/2, D_{1,3}]$, there exists $\delta_0 > 0$ such that if $\rho \in (0, \delta_0)$, $(d_1, d_3) \in (\tilde{d}_1 - \delta_0, \tilde{d}_1 + \delta_0) \times (\tilde{d}_3 - \delta_0, \tilde{d}_3 + \delta_0)$, then $(\tilde{u}_1, 0, \tilde{u}_2, \tilde{u}_3)$ is the unique solution of (4.9). To this end, we define the following Banach spaces:

$$W_\nu^{2,2}(\Omega) = \{g \in W^{2,2}(\Omega) \mid \partial_\nu g = 0 \ \text{ on } \ \partial\Omega\}, \quad L_0^2(\Omega) = \left\{g \in L^2(\Omega) \mid \int_\Omega g \, \mathrm{d}x = 0\right\},$$

and denote

$$F(d_1, d_3, \rho, u_1, w_2, \xi, u_3) = (f_1, f_2, f_3, f_4)(d_1, d_3, \rho, u_1, w_2, \xi, u_3)$$

with

$$f_1(d_1, d_3, \rho, u_1, w_2, \xi, u_3) = d_1 \Delta u_1 + u_1(1 - u_1) - \frac{a_1 u_1 (w_2 + \xi)}{u_1 + w_2 + \xi},$$

$$f_2(d_1, d_3, \rho, u_1, w_2, \xi, u_3) = \Delta w_2 + \rho \left\{ \frac{m_1 u_1 (w_2 + \xi)}{u_1 + w_2 + \xi} - b_1(w_2 + \xi) \right.$$
$$\left. - \frac{a_2(w_2 + \xi)u_3}{w_2 + \xi + u_3} \right\},$$

$$f_3(d_1, d_3, \rho, u_1, w_2, \xi, u_3) = \int_\Omega \left\{ \frac{m_1 u_1(w_2 + \xi)}{u_1 + w_2 + \xi} - b_1(w_2 + \xi) - \frac{a_2(w_2 + \xi)u_3}{w_2 + \xi + u_3} \right\} \, \mathrm{d}x,$$

$$f_4(d_1, d_3, \rho, u_1, w_2, \xi, u_3) = d_3 \Delta u_3 + \frac{m_2(w_2 + \xi)u_3}{w_2 + \xi + u_3} - b_2 u_3.$$

Then

$$F : \mathbf{R}^+ \times \mathbf{R}^+ \times \mathbf{R}^+ \times W_\nu^{2,2}(\Omega) \times (L_0^2(\Omega) \cap W_\nu^{2,2}(\Omega))$$
$$\times \mathbf{R}^+ \times W_\nu^{2,2}(\Omega) \to L^2(\Omega) \times L_0^2(\Omega) \times \mathbf{R} \times L^2(\Omega)$$

is a well-defined mapping. It is clear that the solutions of (4.9) satisfy $F(d_1, d_3, \rho, u_1, w_2, \xi, u_3) = 0$. Moreover, (4.9) has a unique solution $(u_1, w_2, \xi, u_3) = (\tilde{u}_1, 0, \tilde{u}_2, \tilde{u}_3)$ when $\rho = 0$ and $(d_1, d_3) = (\tilde{d}_1, \tilde{d}_3)$ from the proof of (i) of Lemma 4.3. Obviously, F is a differentiable mapping, and its partial derivative with respect to the last four arguments is

$$\Psi \equiv D_{(u_1, w_2, \xi, u_3)} F(\tilde{d}_1, \tilde{d}_3, 0, \tilde{u}_1, 0, \tilde{u}_2, \tilde{u}_3),$$

$$\Psi : W_\nu^{2,2}(\Omega) \times (L_0^2(\Omega) \cap W_\nu^{2,2}(\Omega)) \times \mathbf{R} \times W_\nu^{2,2}(\Omega) \to L^2(\Omega) \times L_0^2(\Omega) \times \mathbf{R} \times L^2(\Omega)$$

with

$$\Psi(v_1, v_2, \tau, v_3) = \begin{pmatrix} \tilde{d}_1 \Delta v_1 + a_{11} v_1 + a_{12}(v_2 + \tau) \\ \Delta v_2 \\ \int_\Omega \{a_{21} v_1 + a_{22}(v_2 + \tau) + a_{23} v_3\} \, \mathrm{d}x \\ \tilde{d}_3 \Delta v_3 + a_{32}(v_2 + \tau) + a_{33} v_3 \end{pmatrix},$$

where a_{ij} are given in section 3.

We claim that Ψ is an isomorphism operator. Assume that $\Psi(v_1, v_2, \tau, v_3) = (0, 0, 0, 0)$; then $v_2 = 0$. Note that $a_1 < 1$ implies $a_{11} < 0$. Then from the equation of v_1, it follows that $v_1 \equiv -a_{12}\tau/a_{11}$. Similarly, $v_3 \equiv -a_{32}\tau/a_{33}$ since $a_{33} < 0$ and $\tau \in \mathbf{R}$. We substitute these results into the integral equations satisfied by (v_1, v_2, τ, v_3) and obtain that

$$\left(-\frac{a_{12}a_{21}}{a_{11}} + a_{22} - \frac{a_{23}a_{32}}{a_{33}} \right) \tau = 0.$$

This is equivalent to $\det\{\mathbf{G_u}(\tilde{\mathbf{u}})\}\tau = 0$, where

$$\det\{\mathbf{G_u}(\tilde{\mathbf{u}})\} = -(a_{12}a_{21}a_{33} + a_{11}a_{23}a_{32} - a_{11}a_{22}a_{33}) = -\frac{m_1 m_2 \tilde{u}_1^2 \tilde{u}_2^2 \tilde{u}_3}{(\tilde{u}_1 + \tilde{u}_2)^2(\tilde{u}_2 + \tilde{u}_3)^2} < 0$$

by some basic computations. Therefore $\tau = 0$, which implies that $(v_1, v_2, \tau, v_3) = (0, 0, 0, 0)$ and Ψ is injective. On the other hand, for a given $h_2 \in L_0^2(\Omega)$, the problem

$$-\Delta u_2 = h_2 \ \text{ in } \ \Omega, \quad u \in L_0^2(\Omega) \cap W_\nu^{2,2}(\Omega)$$

has a unique solution. By using $\det\{\mathbf{G_u}(\tilde{\mathbf{u}})\} < 0$ again, one can also check that Ψ is also surjective. Consequently Ψ is an isomorphism.

By the implicit function theorem, there exist positive constants ρ_0 and δ_0 such that, for each $\rho \in [0, \rho_0]$ and $(d_1, d_3) \in (\check{d}_1 - \delta_0, \check{d}_1 + \delta_0) \times (\check{d}_3 - \delta_0, \check{d}_3 + \delta_0)$, $(\tilde{u}_1, 0, \tilde{u}_2, \tilde{u}_3)$ is the unique solution of $F(d_1, d_3, \rho, u_1, w_2, \xi, u_3) = 0$ in $B_{\delta_0}(\tilde{u}_1, 0, \tilde{u}_2, \tilde{u}_3)$, where $B_{\delta_0}(\tilde{u}_1, 0, \tilde{u}_2, \tilde{u}_3)$ is the ball in $W_\nu^{2,2}(\Omega) \times (L_0^2(\Omega) \cap W_\nu^{2,2}(\Omega)) \times \mathbf{R} \times W_\nu^{2,2}(\Omega)$ centered at $(\tilde{u}_1, 0, \tilde{u}_2, \tilde{u}_3)$ with radius δ_0. Taking smaller ρ_0 and δ_0 if necessary, we can conclude (i) by use of Lemma 4.3(i).

In a similar manner, (ii) can be proved. In fact, we write $u_i = w_i + \xi_i$ with $\int_\Omega w_i = 0$ and $\xi_i \in \mathbf{R}^+$ $(i = 1, 3)$ and construct analogous operator

$$F(d_2, \rho_1, \rho_3, w_1, \xi_1, u_2, w_3, \xi_3) = (f_1, f_2, f_3, f_4, f_5)(d_2, \rho_1, \rho_3, w_1, \xi_1, u_2, w_3, \xi_3)$$

with

$$f_1(d_2, \rho_1, \rho_3, w_1, \xi_1, u_2, w_3, \xi_3) = \Delta w_1$$
$$+ \rho_1 \left\{ (w_1 + \xi_1)(1 - w_1 - \xi_1) - \frac{a_1(w_1 + \xi_1)u_2}{w_1 + \xi_1 + u_2} \right\},$$

$$f_2(d_2, \rho_1, \rho_3, w_1, \xi_1, u_2, w_3, \xi_3) = \int_\Omega \left\{ (w_1 + \xi_1)(1 - w_1 - \xi_1) - \frac{a_1(w_1 + \xi_1)u_2}{w_1 + \xi_1 + u_2} \right\} dx,$$

$$f_3(d_2, \rho_1, \rho_3, w_1, \xi_1, u_2, w_3, \xi_3) = d_2 \Delta u_2 + \frac{m_1(w_1 + \xi_1)u_2}{w_1 + \xi_1 + u_2} - b_1 u_2 - \frac{a_2(w_3 + \xi_3)u_2}{w_3 + \xi_3 + u_2},$$

$$f_4(d_2, \rho_1, \rho_3, w_1, \xi_1, u_2, w_3, \xi_3) = \Delta w_3 + \rho_3 \left\{ \frac{m_2(w_3 + \xi_3)u_2}{w_3 + \xi_3 + u_2} - b_2(w_3 + \xi_3) \right\},$$

$$f_5(d_2, \rho_1, \rho_3, w_1, \xi_1, u_2, w_3, \xi_3) = \int_\Omega \left\{ \frac{m_2(w_3 + \xi_3)u_2}{w_3 + \xi_3 + u_2} - b_2(w_3 + \xi_3) \right\} dx,$$

where $\rho_i = d_i^{-1}$ (i=1,3). For fixed $\tilde{d}_2 > 0$, we can verify that

$$D_{(w_1, \xi_1, u_2, w_3, \xi_3)} F(\tilde{d}_2, 0, 0, 0, \tilde{u}_1, \tilde{u}_2, 0, \tilde{u}_3) :$$

$$(L_0^2(\Omega) \cap W_\nu^{2,2}(\Omega)) \times \mathbf{R} \times W_\nu^{2,2}(\Omega) \times (L_0^2(\Omega) \cap W_\nu^{2,2}(\Omega))$$

$$\times \mathbf{R} \to L_0^2(\Omega) \times \mathbf{R} \times L^2(\Omega) \times L_0^2(\Omega) \times \mathbf{R}$$

is an isomorphism. As in the discussion of (i), by the implicit function theorem, Lemma 4.3(ii) and Theorem 4.2(ii), our result is obtained. The proof of Theorem 4.4 is complete. $\square$

5. Existence of nonconstant positive solutions of (2.5). This section is devoted to the existence of nonconstant positive solutions of (2.5) for certain values of diffusion coefficients d_1 and d_3, respectively, while the other parameters are fixed. Our results will show that, if the parameters are properly chosen, both the general stationary pattern and more interesting Turing pattern can arise as a result of diffusion.

For our purposes, we start with some preliminary results. First we study the linearization of (2.5) at $\tilde{\mathbf{u}}$. We denote

$$\mathbf{X} = \{\mathbf{u} \in [C^2(\bar{\Omega})]^3 \mid \partial_\nu \mathbf{u} = 0 \ \text{on} \ \partial\Omega\}$$

and

$$\mathbf{X}^+ = \{\mathbf{u} \in \mathbf{X} \mid u_i > 0 \ \text{on} \ \bar{\Omega}, \ i = 1, 2, 3\},$$

$$B(C) = \{\mathbf{u} \in \mathbf{X} \mid C^{-1} < u_i < C \ \text{on} \ \bar{\Omega}, \ i = 1, 2, 3\}, \ C > 0.$$

With the diffusion matrix $\mathcal{D} = \text{diag}(d_1, d_2, d_3)$, (2.5) can be written as

$$(5.1) \qquad \begin{cases} -\mathcal{D}\Delta\mathbf{u} = \mathbf{G}(\mathbf{u}) & \text{in} \ \Omega, \\ \partial_\nu \mathbf{u} = 0 & \text{on} \ \partial\Omega, \end{cases}$$

and $\mathbf{u}$ is a positive solution to (5.1) if and only if

$$\mathbf{F}(\mathbf{u}) \equiv \mathbf{u} - (\mathbf{I} - \Delta)^{-1}\{\mathcal{D}^{-1}\mathbf{G}(\mathbf{u}) + \mathbf{u}\} = 0 \ \text{for} \ \mathbf{u} \in \mathbf{X}^+,$$

where $(\mathbf{I} - \Delta)^{-1}$ is the inverse of $\mathbf{I} - \Delta$ in $\mathbf{X}$. As $\mathbf{F}(\cdot)$ is a compact perturbation of the identity operator, for any $B = B(C)$, the Leray–Schauder degree $\deg(\mathbf{F}(\cdot), 0, B)$ is well defined if $\mathbf{F}(\mathbf{u}) \neq 0$ on ∂B.

We also note that

$$D_\mathbf{u}\mathbf{F}(\tilde{\mathbf{u}}) = \mathbf{I} - (\mathbf{I} - \Delta)^{-1}\{\mathcal{D}^{-1}\mathbf{G}_\mathbf{u}(\tilde{\mathbf{u}}) + \mathbf{I}\},$$

and recall that if $D_\mathbf{u}\mathbf{F}(\tilde{\mathbf{u}})$ is invertible, the index of $\mathbf{F}$ at $\tilde{\mathbf{u}}$ is defined as $\text{index}(\mathbf{F}(\cdot), \tilde{\mathbf{u}}) = (-1)^\gamma$, where γ is the multiplicity of negative eigenvalues of $D_\mathbf{u}\mathbf{F}(\tilde{\mathbf{u}})$ [25, Theorem 2.8.1].

For the sake of convenience, we denote

$$(5.2) \qquad H(d_1, d_2, d_3; \mu) \equiv \det\{\mu\mathbf{I} - \mathcal{D}^{-1}\mathbf{G}_\mathbf{u}(\tilde{\mathbf{u}})\} = \frac{1}{d_1 d_2 d_3}\det\{\mu\mathcal{D} - \mathbf{G}_\mathbf{u}(\tilde{\mathbf{u}})\},$$

By arguments similar to those in [28], it can be shown that the following proposition holds.

PROPOSITION 5.1. *Suppose that, for all $n \geq 0$, the matrix $\mu_n \mathbf{I} - \mathcal{D}^{-1} \mathbf{G_u}(\tilde{\mathbf{u}})$ is nonsingular. Then*

$$\mathrm{index}(\mathbf{F}(\cdot), \ \tilde{\mathbf{u}}) = (-1)^\gamma, \quad \textit{where} \ \ \gamma = \sum_{n \geq 0, \ H(d_1, d_2, d_3; \mu_n) < 0} \dim E(\mu_n).$$

To compute $\mathrm{index}(\mathbf{F}(\cdot), \ \tilde{\mathbf{u}})$, we have to consider the sign of $H(d_1, d_2, d_3; \mu)$. Direct calculation gives

$$(5.3) \qquad \det\{\mu \mathcal{D} - \mathbf{G_u}(\tilde{\mathbf{u}})\} = A_3(d_1, d_3)\mu^3 + A_2(d_1, d_3)\mu^2 + A_1(d_1, d_3)\mu$$

$$- \det\{\mathbf{G_u}(\tilde{\mathbf{u}})\} \equiv \mathcal{A}(d_1, d_3; \ \mu),$$

with

$$\begin{cases} A_3(d_1, d_3) = d_1 d_2 d_3, \quad A_2(d_1, d_3) = -\{a_{33} d_1 d_2 + (a_{11} d_2 + a_{22} d_1)d_3\}, \\ A_1(d_1, d_3) = a_{11} a_{33} d_2 + (a_{22} a_{33} - a_{23} a_{32})d_1 + (a_{11} a_{22} - a_{12} a_{21})d_3, \end{cases}$$

where a_{ij} are defined in section 3.

We first consider the dependence of $\mathcal{A}$ on d_1. Let $\tilde{\mu}_i(d_1; \ d_2, d_3)$, $i = 1, 2, 3$, be the three roots of $\mathcal{A}(d_1, d_3; \ \mu) = 0$ satisfying $\mathrm{Re}\{\tilde{\mu}_1(d_1; \ d_2, d_3)\} \leq \mathrm{Re}\{\tilde{\mu}_2(d_1; \ d_2, d_3)\} \leq \mathrm{Re}\{\tilde{\mu}_3(d_1; \ d_2, d_3)\}$. Since $\det\{\mathbf{G_u}(\tilde{\mathbf{u}})\} < 0$ and $A_3(d_1, d_3) > 0$, one of $\tilde{\mu}_i(d_1; \ d_2, d_3)$ is real and negative, and the product of the other two is positive.

In addition, we have

$$\lim_{d_1 \to \infty} \mathcal{A}(d_1, d_3; \ \mu)/d_1 = \mu[d_2 d_3 \mu^2 - (a_{33} d_2 + a_{22} d_3)\mu + a_{22} a_{33} - a_{23} a_{32}].$$

Note that $a_{22} a_{33} - a_{23} a_{32} > 0$. If $a_{22} > 0$ or the reverse inequality of (3.5),

$$(5.4) \qquad m_1 < \left(b_1 + a_2 \frac{m_2 - b_2}{m_2}\right)^2 \bigg/ \left(b_1 + a_2 \left(\frac{m_2 - b_2}{m_2}\right)^2\right),$$

holds, and the parameters d_2 and d_3 satisfy

$$(5.5) \quad a_{33} d_2 + a_{22} d_3 > 0, \quad \Delta_1 \equiv (a_{33} d_2 + a_{22} d_3)^2 - 4 d_2 d_3 (a_{22} a_{33} - a_{23} a_{32}) > 0,$$

we can establish the following proposition.

PROPOSITION 5.2. *Assume that (5.4) holds and that d_2 and d_3 satisfy (5.5). Then there exists a positive constant D_1^* such that when $d_1 \geq D_1^*$, the three roots $\tilde{\mu}_i(d_1; \ d_2, d_3)$, $i = 1, 2, 3$, of $\mathcal{A}(d_1, d_3; \ \mu) = 0$ are all real and satisfy*

$$(5.6) \quad \begin{cases} \lim_{d_1 \to \infty} \tilde{\mu}_1(d_1; \ d_2, d_3) = 0, \\ \lim_{d_1 \to \infty} \tilde{\mu}_2(d_1; \ d_2, d_3) = \frac{1}{2 d_2 d_3}\left\{a_{33} d_2 + a_{22} d_3 - \sqrt{\Delta_1}\right\} \equiv \mu_2^*(d_2, d_3) > 0, \\ \lim_{d_1 \to \infty} \tilde{\mu}_3(d_1; \ d_2, d_3) = \frac{1}{2 d_2 d_3}\left\{a_{33} d_2 + a_{22} d_3 + \sqrt{\Delta_1}\right\} \equiv \mu_3^*(d_2, d_3) > 0. \end{cases}$$

Moreover, when $d_1 \geq D_1^*$,

$$(5.7) \quad \begin{cases} -\infty < \tilde{\mu}_1(d_1; d_2, d_3) < 0 < \tilde{\mu}_2(d_1; d_2, d_3) < \tilde{\mu}_3(d_1; d_2, d_3), \\ \mathcal{A}(d_1, d_3; \mu) < 0 \ \text{if} \ \mu \in (-\infty, \tilde{\mu}_1(d_1; d_2, d_3)) \cup (\tilde{\mu}_2(d_1; d_2, d_3), \tilde{\mu}_3(d_1; d_2, d_3)), \\ \mathcal{A}(d_1, d_3; \mu) > 0 \ \text{if} \ \mu \in (\tilde{\mu}_1(d_1; d_2, d_3), \tilde{\mu}_2(d_1; d_2, d_3)) \cup (\tilde{\mu}_3(d_1; d_2, d_3), \infty). \end{cases}$$

Similarly, we consider d_3 as the parameter, and d_1 and d_2 satisfy

$$(5.8) \quad a_{11}d_2 + a_{22}d_1 > 0, \quad \Delta_2 \equiv (a_{11}d_2 + a_{22}d_1)^2 - 4d_1d_2(a_{11}a_{22} - a_{12}a_{21}) > 0;$$

then we have the following proposition.

PROPOSITION 5.3. *Assume that* (5.4) *holds and that d_1 and d_2 satisfy* (5.8). *Then there exists a positive constant D_3^* such that when $d_3 \geq D_3^*$, the three roots $\tilde{\mu}_1(d_3; d_1, d_2)$, $i = 1, 2, 3$, of $\mathcal{A}(d_1, d_3; \mu) = 0$ are all real and satisfy*

$$\begin{cases} \lim_{d_3 \to \infty} \tilde{\mu}_1(d_3; d_1, d_2) \leq 0, \\ \displaystyle\lim_{d_3 \to \infty} \tilde{\mu}_2(d_3; d_1, d_2) = \frac{1}{2d_1d_2}\Big\{a_{11}d_2 + a_{22}d_1 - \sqrt{\Delta_2}\Big\} \equiv \mu_2^*(d_1, d_2) \geq 0, \\ \displaystyle\lim_{d_3 \to \infty} \tilde{\mu}_3(d_3; d_1, d_2) = \frac{1}{2d_1d_2}\Big\{a_{11}d_2 + a_{22}d_1 + \sqrt{\Delta_2}\Big\} \equiv \mu_3^*(d_1, d_2) > 0. \end{cases}$$

Moreover, when $d_3 \geq D_3^*$,

$$\begin{cases} -\infty < \tilde{\mu}_1(d_3; d_1, d_2) < 0 < \tilde{\mu}_2(d_3; d_1, d_2) < \tilde{\mu}_3(d_3; d_1, d_2), \\ \mathcal{A}(d_1, d_3; \mu) < 0 \;\; if \;\; \mu \in (-\infty, \tilde{\mu}_1(d_3; d_1, d_2)) \cup (\tilde{\mu}_2(d_3; d_1, d_2), \tilde{\mu}_3(d_3; d_1, d_2)), \\ \mathcal{A}(d_1, d_3; \mu) > 0 \;\; if \;\; \mu \in (\tilde{\mu}_1(d_3; d_1, d_2), \tilde{\mu}_2(d_3; d_1, d_2)) \cup (\tilde{\mu}_3(d_3; d_1, d_2), \infty). \end{cases}$$

Remark 5.1. Simple computations show that $\mu_2^*(d_1, d_2) = 0$ if and only if $a_{11}a_{22} - a_{12}a_{21} \leq 0$.

In virtue of Theorems 4.3 and 4.2 and Propositions 5.1 and 5.2, the first result of the existence of nonconstant positive solutions of (2.5) can be stated as follows.

THEOREM 5.1. *Assume that $a_1 < 1$, (5.4), (5.5), and assumptions in Theorem* 4.3 *hold. If $\mu_2^*(d_2, d_3) \in (\mu_i, \mu_{i+1})$ and $\mu_3^*(d_2, d_3) \in (\mu_j, \mu_{j+1})$ for some $j > i \geq 0$, where $\mu_2^*(d_2, d_3)$, $\mu_3^*(d_2, d_3)$ are defined in Proposition 5.2, and the sum $\sum_{n=i+1}^{j} \dim E(\mu_n)$ is odd, then there exists a positive constant $\tilde{D}_1$ such that, if $d_1 \geq \tilde{D}_1$, (2.5) admits at least one nonconstant positive solution.*

Proof. By Proposition 5.2 and our assumptions, there exists a positive constant $\tilde{D}_1$, such that when $d_1 \geq \tilde{D}_1$, (5.7) holds and

$$(5.9) \qquad \mu_i < \tilde{\mu}_2(d_1; d_2, d_3) < \mu_{i+1}, \quad \mu_j < \tilde{\mu}_3(d_1; d_2, d_3) < \mu_{j+1}.$$

According to Theorem 4.2, for $\hat{d}_1$ and $\hat{d}_3$ satisfying $\mu_1\hat{d}_1 > 1$, $\mu_1\hat{d}_3 > m_2 - b_2$, there exists a large $\hat{d}_2$ such that (2.5) has no constant positive solutions when $d_1 \geq \hat{d}_1$, $\mu_1d_2 \geq \hat{d}_2$, and $d_3 \geq \hat{d}_3$. In addition, since $\det\{\mathbf{G_u}(\tilde{\mathbf{u}})\} < 0$ and $\lim_{n \to \infty} \mu_n = \infty$, from (5.3), we can further choose $\hat{d}_1$, $\hat{d}_2$, and $\hat{d}_3$ to be so large that

$$(5.10) \qquad H(\hat{d}_1, \hat{d}_2, \hat{d}_3; \mu_n) > 0 \quad \text{for all} \;\; n \geq 0.$$

Now we show that for any $d_1 \geq \tilde{D}_1$, (2.5) has at least one nonconstant positive solution. The proof, which is accomplished by a contradiction argument, is based on the homotopy invariance of the topological degree. Suppose on the contrary that the assertion is not true for some $d_1 = \tilde{d}_1 \geq \tilde{D}_1$.

We fix $d_1 = \tilde{d}_1$. Let $d_i(t) = td_i + (1-t)\hat{d}_i$, $i = 1, 2, 3$, and define $\mathcal{D}(t) = \text{diag}(d_1(t), d_2(t), d_3(t))$. Now we consider the problem

$$(5.11) \qquad \begin{cases} -\mathcal{D}(t)\Delta\mathbf{u} = \mathbf{G}(\mathbf{u}) & \text{in} \;\; \Omega, \\ \partial_\nu\mathbf{u} = 0 & \text{on} \;\; \partial\Omega. \end{cases}$$

Then $\mathbf{u}$ is a positive solution of (2.5) if and only if it is a positive solution of (5.11) for $t = 1$. It is obvious that $\tilde{\mathbf{u}}$ is the unique constant positive solution of (5.11) for any $0 \le t \le 1$. For any $0 \le t \le 1$, $\mathbf{u}$ is a positive solution of (5.11) if and only if

$$\mathbf{F}(t;\mathbf{u}) \equiv \mathbf{u} - (\mathbf{I} - \Delta)^{-1}\left\{\mathcal{D}^{-1}(t)\mathbf{G}(\mathbf{u}) + \mathbf{u}\right\} = 0 \quad \text{for} \quad \mathbf{u} \in \mathbf{X}^{+}.$$

Clearly, $\mathbf{F}(1;\mathbf{u}) = \mathbf{F}(\mathbf{u})$. Theorem 4.2 shows that the only positive solution of $\mathbf{F}(0;\mathbf{u}) = 0$ is $\tilde{\mathbf{u}}$. From direct calculation,

$$D_{\mathbf{u}}\mathbf{F}(t;\tilde{\mathbf{u}}) = \mathbf{I} - (\mathbf{I} - \Delta)^{-1}\{\mathcal{D}^{-1}(t)\mathbf{G}_{\mathbf{u}}(\tilde{\mathbf{u}}) + \mathbf{I}\}.$$

In particular,

$$D_{\mathbf{u}}\mathbf{F}(0;\tilde{\mathbf{u}}) = \mathbf{I} - (\mathbf{I} - \Delta)^{-1}\{\hat{\mathcal{D}}^{-1}\mathbf{G}_{\mathbf{u}}(\tilde{\mathbf{u}}) + \mathbf{I}\},$$
$$D_{\mathbf{u}}\mathbf{F}(1;\tilde{\mathbf{u}}) = \mathbf{I} - (\mathbf{I} - \Delta)^{-1}\{\mathcal{D}^{-1}\mathbf{G}_{\mathbf{u}}(\tilde{\mathbf{u}}) + \mathbf{I}\} = D_{\mathbf{u}}\mathbf{F}(\tilde{\mathbf{u}}),$$

where $\hat{\mathcal{D}} = \text{diag}(\hat{d}_1, \hat{d}_2, \hat{d}_3)$. From (5.2) and (5.3) we see that

$$(5.12) \qquad\qquad H(d_1, d_2, d_3; \mu) = \frac{1}{d_1 d_2 d_3}\mathcal{A}(d_1, d_3; \mu).$$

In view of (5.7) and (5.9), it follows from (5.12) that

$$\begin{cases} H(d_1, d_2, d_3; \mu_0) = H(0) > 0, \\ H(d_1, d_2, d_3; \mu_n) < 0, \quad i + 1 \le n \le j, \\ H(d_1, d_2, d_3; \mu_n) > 0, \quad 1 \le n \le i \ \text{ and } \ n \ge j + 1. \end{cases}$$

Therefore, zero is not an eigenvalue of the matrix $\mu_i\mathbf{I} - \mathcal{D}^{-1}\mathbf{G}_{\mathbf{u}}(\tilde{\mathbf{u}})$ for all $n \ge 0$, and

$$\sum_{n \ge 0, H(d_1, d_2, d_3; \mu_n) < 0} \dim E(\mu_n) = \sum_{n=i+1}^{j} \dim E(\mu_n) = \text{an odd number}.$$

Then Proposition 5.1 shows that

$$(5.13) \qquad\qquad \text{index}(\mathbf{F}(1;\cdot),\tilde{\mathbf{u}}) = (-1)^{\gamma} = -1.$$

On the other hand, by (5.10) and Proposition 5.1 again, we obtain that

$$(5.14) \qquad\qquad \text{index}(\mathbf{F}(0;\cdot),\tilde{\mathbf{u}}) = (-1)^{0} = 1.$$

In view of $\tilde{d}_1 > \tilde{D}_1$, by Theorem 4.3, there exists a positive constant $C = C(\tilde{D}_1, d_2, d_3, \hat{d}_1, \hat{d}_2, \hat{d}_3, \Lambda)$ such that, for all $0 \le t \le 1$, the positive solutions of (5.11) satisfy $1/C < u_1, u_2, u_3 < C$. Therefore, $\mathbf{F}(t;\mathbf{u}) \ne 0$ on $\partial B(C)$ for all $0 \le t \le 1$. By the homotopy invariance of the topological degree,

$$(5.15) \qquad \deg\left(\mathbf{F}(1;\cdot),0,B(C)\right) = \deg\left(\mathbf{F}(0;\cdot),0,B(C)\right).$$

Moreover, under our assumptions, the only positive solution of both $\mathbf{F}(1;\mathbf{u}) = 0$ and $\mathbf{F}(0;\mathbf{u}) = 0$ in $B(C)$ is $\tilde{\mathbf{u}}$, and hence, by (5.13) and (5.14),

$$\deg\left(\mathbf{F}(0;\cdot),0,B(C)\right) = \text{index}(\mathbf{F}(0;\cdot),\tilde{\mathbf{u}}) = 1$$

and

$$\deg\left(\mathbf{F}(1;\cdot),0,B(C)\right) = \text{index}(\mathbf{F}(1;\cdot),\tilde{\mathbf{u}}) = -1.$$

This contradicts (5.15), and the proof is complete. $\qquad\square$

Remark 5.2. When d_3 is fixed, we note that $\lim_{d_2 \to 0} \mu_2^*(d_2, d_3) = (a_{22}a_{33} - a_{23}a_{32})/(a_{22}d_3)$, $\lim_{d_2 \to 0} \mu_3^*(d_2, d_3) = \infty$, and (5.5) is automatically fulfilled for small d_2. Therefore, if for all $i = 0, 1, 2, \dots, \mu_i$ are simple and $(a_{22}a_{33} - a_{23}a_{32})/(a_{22}d_3) \neq \mu_i$, by Theorem 5.1, when $a_1 < 1$ and the assertion of Theorem 4.3 hold, there exist two sequences of intervals $\{(\theta_n^1, \theta_n^2)\}_{n=1}^\infty$ and $\{(\Theta_n^1, \Theta_n^2)\}_{n=1}^\infty$ satisfying $\theta_{n+1}^1 < \theta_n^1$, $\Theta_n^2 < \Theta_{n+1}^1$, and $\theta_n^1, \theta_n^2 \to 0^+$ while $\Theta_n^1, \Theta_n^2 \to \infty$ as $n \to \infty$ such that (2.5) admits at least one nonconstant positive solution for all $d_1 \in (\Theta_n^1, \Theta_n^2)$ and $d_2 \in (\theta_n^1, \theta_n^2)$, $n = 1, 2, 3, \dots$. Recall that Theorem 4.3 holds when condition (i) or (ii) in Lemma 4.1 holds. When (i) (same as (3.8)) holds, (5.4) is not satisfied. But when (ii) in Lemma 4.1 holds, conditions in Theorem 5.1 can be satisfied.

Similarly, let us consider the case of large d_3. By Proposition 5.3 and Remark 5.1, we have the following theorem.

THEOREM 5.2. *Assume that $a_1 < 1$, (5.4), (5.8), and Theorem 4.3 hold.*

(i) *If $a_{11}a_{22} - a_{12}a_{21} > 0$, then $\mu_2^*(d_1, d_2) \in (\mu_i, \mu_{i+1})$, $\mu_3^*(d_1, d_2) \in (\mu_j, \mu_{j+1})$ for some $j > i \geq 0$, and $\sum_{n=i+1}^j \dim E(\mu_n)$ is odd.*

(ii) *If $a_{11}a_{22} - a_{12}a_{21} \leq 0$, $\mu_3^*(d_1, d_2) \in (\mu_j, \mu_{j+1})$ for some $j > 0$, and $\sum_{n=1}^j \dim E(\mu_n)$ is odd, where $\mu_2^*(d_1, d_2)$, $\mu_3^*(d_1, d_2)$ are defined in Proposition 5.3, then there exists a positive constant $\tilde{D}_3$ such that, if $d_3 \geq \tilde{D}_3$, (2.5) admits at least one nonconstant positive solution.*

Remark 5.3. By Proposition 5.3, regardless of the sign of $a_{11}a_{22} - a_{12}a_{21}$, we have a conclusion similar to that in Remark 5.2. In addition, we mention that the sign of $a_{11}a_{22} - a_{12}a_{21}$ is indefinite when $a_1 < 1$, $a_{22} > 0$, $\tilde{u}$ exists, and the assertion of Theorem 4.3 holds (note that, if $\sqrt{a_2 + m_2} < \sqrt{m_1 - b_1} + \sqrt{b_2}$, then Theorem 4.3 is true by Lemma 4.1). The detailed analysis on this claim is left to the appendix.

Remark 5.4. Fix d_1 and d_2; by Remark 3.1, if $m_1 = (b_1 + a_2(m_2 - b_2)/m_2)^2/(b_1 + a_2(m_2 - b_2)^2/m_2^2) - o(b_1)$, and $b_1 \to 0$, a_2, b_2, m_2 are properly chosen and either $a_1 \to 1/2$ or $a_1 \to 1$, and d_3 is sufficiently large, Turing instability actually happens. Furthermore, combined with the analysis of the appendix, Proposition A.2(i) also holds for such chosen parameters. With proper choices of d_1 and d_2, we can find certain parameter ranges guaranteeing the existence of both Turing instability and the nonconstant positive solution to (2.5) by Theorem 5.2(i). As a consequence, Turing patterns exist for these parameter ranges.

6. Conclusions. In this paper, we analyze a reaction-diffusion food chain model with ratio-dependent functional response. We are mainly concerned with the coexistence of the three species and focus on the case of a weak predation rate for the pest species (i.e., $a_1 < 1$). In particular, the existence and nonexistence of nonconstant positive steady states have been established. The existence results provide a theoretical support for pattern formation caused by diffusion.

We summarize our investigation here and hope to reveal some interesting phenomena of pattern formation in population ecology. We always assume the existence of a constant coexistence. The main results of sections 3 and 4 show that this constant coexistence steady state $\tilde{u}$ is the only steady state if (a) both of the predation rates a_1 and a_2 are small; (b) a_1 is small while a_2 is suitably chosen, and either the pest or the other two species diffuse quickly (Theorem 4.4). In the former case, we are also able to find a more restrictive parameter range so that $\tilde{u}$ is globally asymptotically stable (Theorem 3.3). This can also be seen from a bifurcation point of view. Here if we assume that a_1 is small, then stronger stability results of $\tilde{u}$ can be proved when a_2 is smaller. When a_2 is close to zero, then $\tilde{u}$ is globally asymptotically stable; when a_2

increases, $\tilde{\mathbf{u}}$ is still locally asymptotically stable but may not be globally asymptotically stable, and it is still the only steady state; and when a_2 further increases, $\tilde{\mathbf{u}}$ becomes unstable for both the ODE and the reaction-diffusion system, and nonconstant patterns exist in this case. In the latter case, the diffusion of the first or third species must be large enough (see Theorems 5.1 and 5.2). Thus for small a_1 and suitable a_2, the quick migration of the plant or top predator enhances the formation of spatial pattern for the system. In contrast, the quick migration of the pest or both the plant and top predators tends to prevent the system from generating pattern. It is well known that fast diffusion of all species in a biological system will not lead to spatial inhomogeneous patterns; see [6]. Our result shows the importance of the diffusion rate of the middle species in a food chain. The large diffusion rate of the pest (middle species) alone can lead to the nonexistence of spatial patterns, but if the pest diffusion rate is not large, then all other diffusion rates must be large to prevent the occurrence of patterns. On the other hand, a large diffusion rate of the top species or bottom species will help the generation of patterns. This demonstrates that, in an ecological model, different diffusions may play essentially different roles in developing spatial patterns. In addition, taking into account the close relationship between the time-dependent solutions to a reaction-diffusion system and the corresponding steady state solutions, to a great extent, the dynamical behaviors of (2.4) will be determined by the diffusions of the three species.

These conclusions can also be compared with those in [28] and [36]. In the absence of u_3, (2.4) becomes the prey-predator model studied by Pang and Wang in [28]. The results of the existence and nonexistence of nonconstant positive solutions there indicate that large d_2 contributes to the evolution of heterogeneousness for the dynamics, while large d_1 tends to increase the possibility of spatial uniform distribution. Therefore, combined with the our conclusions for (2.5), this suggests that the structure of solutions to the model in [28] will be significantly different due to the emergence of the top predator, which in turn leads to the qualitative change of the biological mechanism of the system. Such a phenomenon was also discussed by Lou, Martinez, and Ni for the classical Lotka–Volterra competition model in [20].

In [36], Wang investigated a three-species prey-predator model. In that model, the interaction between the lower and middle species is described by Holling II-type functional response (prey-dependent), while the functional response between the middle and top species is ratio-dependent (predator-dependent). It was proved that Turing pattern may appear if both d_1 and d_3 are large, but will not if d_2 is large. Therefore the results of the present paper and [36] show that the formation of Turing pattern in the biological models with the same degree of complexity depends on the choices of functional responses. In other words, the feeding strategy of predators may be one of the determining factors in producing Turing pattern. In a very recent work [2], Alonso, Bartumeus, and Catalan performed some numerical calculations indicating that predator-dependent models are sometimes capable of generating Turing pattern, while similar prey-dependent models are not. Hence our theoretical analysis for the food chain model rigorously confirms the outcome of computer simulation in [2].

Finally we point out that some of our mathematical techniques in sections 4 and 5 can be applied to deal with the prey-predator model proposed by Pang and Wang in [28] and derive some new a priori estimates for positive steady state solutions and nonexistence results for nonconstant positive steady state solutions.

Appendix A. In section 6, to prove the existence of nonconstant positive solutions to (2.5), we have made some hypotheses, namely, $a_1 < 1$, $a_{22} > 0$, $\tilde{\mathbf{u}}$ exists, and The-

orem 4.3 holds (in particular, $\sqrt{a_2 + m_2} < \sqrt{m_1 - b_1} + \sqrt{b_2}$ means that Theorem 4.3 is true). We list these conditions as follows:

$$(A.1) \begin{cases} a_1 < 1, \quad m_2 > b_2, \quad A > 1 \Longleftrightarrow a_2(m_2 - b_2)/m_2 + b_1 < m_1, \\[2mm] \sqrt{a_2 + m_2} < \sqrt{m_1 - b_1} + \sqrt{b_2} \Longleftrightarrow (\sqrt{a_2 + m_2} - \sqrt{b_2}\,)^2 + b_1 < m_1, \\[2mm] a_{22} > 0 \Longleftrightarrow m_1 < (b_1 + a_2(m_2 - b_2)/m_2)^2/(b_1 + a_2(m_2 - b_2)^2/m_2^2). \end{cases}$$

In the following, we will verify the claim made in Remark 5.3, which says that $a_{11}a_{22} - a_{12}a_{21}$ is indefinite when (A.1) holds. First of all, by the definitions of $a_{11}, a_{22}, a_{12}, a_{21}$, the direct computations yield the following proposition.

PROPOSITION A.1. *Define*

$$Q \equiv -(1 - a_1)a_2 b_2(m_2 - b_2)A^3 + (1 - a_1)m_1 m_2^2 A^2$$

$$+ [(2a_1 - 1)m_1 m_2^2 - a_1 a_2 b_2(m_2 - b_2)]A - a_1 m_1 m_2^2;$$

then $a_{11}a_{22} - a_{12}a_{21} > 0 \Longleftrightarrow Q > 0$. *Moreover, we note that*
   (i) *as* $a_1 \to 0$, $Q \to (m_1 m_2^2(A - 1) - a_2 b_2(m_2 - b_2)A^2)A$;
   (ii) *as* $a_1 \to 1/2$, $Q \to -\frac{1}{2}a_2 b_2(m_2 - b_2)A^3 - \frac{1}{2}a_2 b_2(m_2 - b_2)A + \frac{1}{2}m_1 m_2^2(A + 1)(A - 1)$;
   (iii) *as* $a_1 \to 1$, $Q \to m_1 m_2^2(A - 1) - a_2 b_2(m_2 - b_2)A$.
   PROPOSITION A.2. *The following results hold:*
   (i) *If we take* $m_1 = (b_1 + a_2(m_2 - b_2)/m_2)^2/(b_1 + a_2(m_2 - b_2)^2/m_2^2) - o(b_1)$, *then* (A.1) *can be satisfied and* $Q > 0$ *if* $b_1 \to 0$, a_2, b_2, m_2 *are properly chosen and either* $a_1 \to 1/2$ *or* $a_1 \to 1$.
   (ii) *If we take* $m_1 = b_1 + 1$, *then* (A.1) *can be satisfied and* $Q < 0$ *if* $b_1 \to \infty$, $a_2 > 1$, b_2, m_2 *are properly chosen and either* $a_1 \to 0$ *or* $a_1 \to 1/2$ *or* $a_1 \to 1$.

Proof. (i) As $b_1 \to 0$, $m_1 \to a_2$, and $A \to m_2/(m_2 - b_2)$, it is clear that $Q > 0$ provided that $b_1 \to 0$ and either $a_1 \to 1/2$ or $a_1 \to 1$ by Proposition A.1. On the other hand, it is clear that there are a_2, b_2, m_2 such that (i) holds.

Now, we verify (ii). If $a_1 \to 1$, $Q \to m_1 m_2^2(A-1) - a_2 b_2(m_2 - b_2)A$. Choosing $m_1 = b_1 + 1$ and letting $b_1 \to \infty$, we note that $A \to 1$ and $m_1(A - 1) \to 1 - a_2(m_2 - b_2)/m_2$. Therefore,

$$(A.2) \qquad Q < 0 \Longleftrightarrow 1 - a_2(m_2 - b_2)/m_2 < a_2 b_2(1 - b_2/m_2)/m_2.$$

By the above choice, (A.1) becomes equivalent to

$$(A.3) \qquad a_2(m_2 - b_2)/m_2 < 1,$$

$$1 + a_2(m_2 - b_2)^2/m_2^2 < 2a_2(m_2 - b_2)/m_2,$$

$$\sqrt{a_2 + m_2} < 1 + \sqrt{b_2}.$$

Claim. There exist a_2, b_2, m_2, and $b_2 < m_2$ such that (A.2) and (A.3) are true. In fact, let $b_2 = \alpha m_2$, where $\alpha \in (0, 1)$ will be determined later. If $a_2 > 1$, solving (A.3), we have

$$(a_2 - 1)/a_2 < \alpha < \sqrt{(a_2 - 1)/a_2} \quad \text{and} \quad \alpha > \left(\sqrt{1 + a_2/m_2} - \sqrt{1/m_2}\,\right)^2.$$

It is evident that if

$$(A.4) \qquad \sqrt{(a_2 - 1)/a_2} > \left(\sqrt{1 + a_2/m_2} - \sqrt{1/m_2} \; \right)^2,$$

there is α such that (A.3) holds. We verify that there exist a_2 and m_2 such that (A.4) is valid. Let $a_2 = \beta m_2$, where $\beta \in (0, \infty)$ will be determined later, and denote

$$f(\beta) = \sqrt[4]{1 - 1/a_2} + \sqrt{\beta/a_2} - \sqrt{1 + \beta}.$$

So, for some $\beta > 0$, $f(\beta) > 0 \Longleftrightarrow$ (A.4) holds for some a_2 and m_2. Simple analysis shows that $f(\beta)$ attains its maximal value at $\beta = 1/(a_2 - 1)$ and $f(1/(a_2 - 1)) > 0$. Take $\beta = 1/(a_2 - 1)$. According to our notation, (A.2) becomes equivalent to $a_2(1 - \alpha^2) - 1 > 0$. If $\alpha = \sqrt{(a_2 - 1)/a_2}$, $a_2(1 - \alpha^2) - 1 = 0$. Hence, we can find α which is close to but less than $\sqrt{(a_2 - 1)/a_2}$ such that (A.2) is valid. Consequently, our claim holds.

For $a_1 \to 0$ or $a_1 \to 1/2$, as above, similar analysis can be done. Therefore, from these arguments, it can follow that (ii) is also true under our requirements. $\square$

REFERENCES

[1] P. ABRAMS AND L. GINZBURG, *The nature of predation: Prey dependent, ratio dependent or neither?*, Trends Ecol. Evol., 15 (2000), pp. 337–341.

[2] D. ALONSO, F. BARTUMEUS, AND J. CATALAN, *Mutual interference between predators can give rise to Turing spatial patterns*, Ecology, 83 (2002), pp. 28–34.

[3] K. J. BROWN AND F. A. DAVIDSON, *Global bifurcation in the Brusselator system*, Nonlinear Anal., 24 (1995), pp. 1713–1725.

[4] T. K. CALLAHAN AND E. KNOBLOCH, *Pattern formation in three-dimensional reaction-diffusion systems*, Phys. D, 132 (1999), pp. 339–362.

[5] C. H. CHIU AND S. B. HSU, *Extinction of top predator in a three-level food-chain model*, J. Math. Biol., 37 (1998), pp. 372–380.

[6] E. CONWAY, D. HOFF, AND J. SMOLLER, *Large time behavior of solutions of systems of nonlinear reaction-diffusion equations*, SIAM J. Appl. Math., 35 (1978), pp. 1–16.

[7] F. A. DAVIDSON AND B. P. RYNNE, *A priori bounds and global existence of solutions of the steady-state Sel'kov model*, Proc. Roy. Soc. Edinburgh Sect. A, 130 (2000), pp. 507–516.

[8] Y. H. DU AND Y. LOU, *Qualitative behavior of positive solutions of a predator-prey model: Effects of saturation*, Proc. Roy. Soc. Edinburgh Sect. A, 131 (2001), pp. 321–349.

[9] H. I. FREEDMAN AND P. WALTMAN, *Mathematical analysis of some three-species food-chain models*, Math. Biosci., 33 (1977), pp. 257–277.

[10] A. GIERER, *Generation of biological patterns and form: Some physical, mathematical and logical aspects*, Prog. Biophys. Biol., 37 (1981), pp. 1–47.

[11] A. HASTINGS, T. POWELL, AND S. B. HSU, *Chaos in a three-species food chain*, Ecology, 72 (1991), pp. 896–903.

[12] D. HENRY, *Geometric Theory of Semilinear Parabolic Equations*, Lecture Notes in Math. 840, Springer-Verlag, Berlin, New York, 1993.

[13] S. B. HSU, T. W. HWANG, AND Y. KUANG, *A ratio-dependent food chain model and its applications to biological control*, Math. Biosci., 181 (2003), pp. 55–83.

[14] 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), pp. 4083–4094.

[15] Y. KAN-ON, *Existence and instability of Neumann layer solutions for a 3-component Lotka-Volterra model with diffusion*, J. Math. Anal. Appl., 243 (2000), pp. 357–372.

[16] Y. KAN-ON AND M. MIMURA, *Singular perturbation approach to a 3-component reaction-diffusion system arising in population dynamics*, SIAM J. Math. Anal., 29 (1998), pp. 1519–1536.

[17] A. KLEBANOFF AND A. HASTINGS, *Chaos in one-predator, two-prey models: General results from bifurcation theory*, Math. Biosci., 122 (1994), pp. 221–233.

[18] J. A. LEACH AND J. C. WEI, *Pattern formation in a simple chemical system with general orders of autocatalysis and decay.* I. *Stability analysis*, Phys. D, 180 (2003), pp. 185–209.

[19] C. S. LIN, W. M. NI, AND I. TAKAGI, *Large amplitude stationary solutions to a chemotaxis system*, J. Differential Equations, 72 (1988), pp. 1–27.

[20] Y. LOU, S. MARTINEZ, AND W. M. NI, *On 3×3 Lotka-Volterra competition systems with cross-diffusion*, Discrete Contin. Dyn. Syst., 6 (2000), pp. 175–190.

[21] Y. LOU AND W. M. NI, *Diffusion vs cross-diffusion: An elliptic approach*, J. Differential Equations, 154 (1999), pp. 157–190.

[22] M. MIMURA AND Y. NISHIURA, *Pattern formation in coupled reaction-diffusion systems*, Japan J. Indust. Appl. Math., 12 (1995), pp. 385–424.

[23] W. M. NI AND I. TAKAGI, *On the Neumann problem for some semilinear elliptic equations and systems of activator-inhibitor type*, Trans. Amer. Math. Soc., 297 (1986), pp. 351–368.

[24] W. M. NI AND J. C. WEI, *On positive solutions concentrating on spheres for the Gierer-Meinhardt system*, J. Differential Equations, 221 (2006), pp. 158–189.

[25] L. NIRENBERG, *Topics in Nonlinear Functional Analysis*, American Mathematical Society, Providence, RI, 2001.

[26] K. PAGE, P. K. MAINI, AND N. A. M. MONK, *Pattern formation in spatially heterogeneous Turing reaction-diffusion models*, Phys. D, 181 (2003), pp. 80–101.

[27] P. Y. H. PANG AND M. X. WANG, *Non-constant positive steady states of a predator-prey system with non-monotonic functional response and diffusion*, Proc. London Math. Soc. (3), 88 (2004), pp. 135–157.

[28] P. Y. H. PANG AND M. X. WANG, *Qualitative analysis of a ratio-dependent predator-prey system with diffusion*, Proc. Roy. Soc. Edinburgh Sect. A, 133 (2003), pp. 919–942.

[29] R. PENG AND M. X. WANG, *Positive steady-state solutions of the Noyes-Field model for Belousov-Zhabotinskii reaction*, Nonlinear Anal., 56 (2004), pp. 451–464.

[30] R. PENG AND M. X. WANG, *Pattern formation in the Brusselator system*, J. Math. Anal. Appl., 309 (2005), pp. 151–166.

[31] R. PENG AND M. X. WANG, *Positive steady-states of the Holling-Tanner prey-predator model with diffusion*, Proc. Roy. Soc. Edinburgh Sect. A, 135 (2005), pp. 149–164.

[32] R. PENG AND M. X. WANG, *On pattern formation in the Gray-Scott model*, Sci. China Ser. A, 50 (2007), pp. 377–386.

[33] M. L. ROSENZWEIG, *Paradox of enrichment: Destabilization of exploitation systems in ecological time*, Science, 171 (1969), pp. 385–387.

[34] A. TURING, *The chemical basis of morphogenesis*, Philos. Trans. R. Soc. Lond. Ser. B., 237 (1952), pp. 37–72.

[35] M. X. WANG, *Non-constant positive steady states of the Sel'kov model*, J. Differential Equations, 190 (2003), pp. 600–620.

[36] M. X. WANG, *Stationary patterns for a prey-predator model with prey-dependent and ratio-dependent functional responses and diffusion*, Phys. D, 196 (2004), pp. 172–192.

[37] J. C. WEI AND M. WINTER, *Existence and stability of multiple-spot solutions for the Gray-Scott model in R^2*, Phys. D, 176 (2003), pp. 147–180.

ERRATUM: STATIONARY PATTERN OF A RATIO-DEPENDENT FOOD CHAIN MODEL WITH DIFFUSION*

RUI PENG†, JUNPING SHI‡, AND MINGXIN WANG§

Abstract. The main purpose of this erratum is to correct an error in the proof of Theorem 4.4 in [R. Peng, J. Shi, and M. Wang, *SIAM J. Appl. Math.*, 67 (2007), pp. 1479–1503].

Key words. food chain model, diffusion, stationary pattern

AMS subject classifications. 35J55, 35K57, 92C15, 92C40

DOI. 10.1137/090752845

In the proof of Theorem 4.4 of [1, pages 1492–1493], we used the method of the implicit function theorem. On page 1493, in the course of constructing the operator F, we made an error, because for the operator F defined there, we cannot guarantee that the range of the second component f_2 is in $L_0^2(\Omega)$. We now need to make a minor change to the definition of the operator F as follows.

To this end, we first introduce the projection operator from $L^2(\Omega)$ to $L_0^2(\Omega)$. That is, for any $g \in L^2(\Omega)$, we set

$$\mathbf{P}(g) = g - \frac{1}{|\Omega|} \int_\Omega g \, \mathrm{d}x.$$

Then the corrected operator F should be given in the following form:

$$F(d_1, d_3, \rho, u_1, w_2, \xi, u_3) = (f_1, f_2, f_3, f_4)(d_1, d_3, \rho, u_1, w_2, \xi, u_3),$$

with the same definitions for f_1, f_3, and f_4 as on page 1493, but the definition of f_2 is changed to

$$f_2(d_1, d_3, \rho, u_1, w_2, \xi, u_3) = \Delta w_2 + \rho \mathbf{P} \left\{ \frac{m_1 u_1 (w_2 + \xi)}{u_1 + w_2 + \xi} - b_1 (w_2 + \xi) - \frac{a_2 (w_2 + \xi) u_3}{w_2 + \xi + u_3} \right\}.$$

Then

$$F : \mathbf{R}^+ \times \mathbf{R}^+ \times \mathbf{R}^+ \times W_\nu^{2,2}(\Omega) \times (L_0^2(\Omega) \cap W_\nu^{2,2}(\Omega)) \times \mathbf{R}^+ \times W_\nu^{2,2}(\Omega)$$
$$\rightarrow L^2(\Omega) \times L_0^2(\Omega) \times \mathbf{R} \times L^2(\Omega)$$

is well defined and the remaining part of the proof for assertion (i) of Theorem 4.4 can proceed as in the paper. For the proof of assertion (ii) of Theorem 4.4, a similar but obvious modification is also needed for the operator F defined on page 1494.

REFERENCE

[1] R. PENG, J. SHI, AND M. WANG, *Stationary pattern of a ratio-dependent food chain model with diffusion*, SIAM J. Appl. Math., 67 (2007), pp. 1479–1503.

†Institute of Nonlinear Complex Systems, College of Science, China Three Gorges University, Yichang, 443002, Hubei, P. R. China (pengrui_seu@163.com).

‡Department of Mathematics, College of William and Mary, Williamsburg, VA 23187-8795, and Department of Mathematics, Harbin Normal University, Harbin, 150080, Helongjiang, P. R. China (shij@math.wm.edu).

§Department of Mathematics, Southeast University, Nanjing, 210018, Jiangsu, P. R. China (mxwang@seu.edu.cn).