

SPATIOTEMPORAL DYNAMICS OF A DIFFUSIVE PREDATOR-PREY MODEL WITH GENERALIST PREDATOR

DINGYONG BAI AND JIANSHE YU*

School of Mathematics and Information Science
Guangzhou University, Guangzhou 510006, China
Center for Applied Mathematics
Guangzhou University, Guangzhou 510006, China

YUN KANG

Science and Mathematics Faculty, College of Integrative Sciences and Arts
Arizona State University, Mesa, AZ 85212, USA
Simon A. Levin Mathematical, Computational, and Modeling Sciences Center
Arizona State University, Tempe, AZ 85281, USA

ABSTRACT. In this paper, we study the spatiotemporal dynamics of a diffusive predator-prey model with generalist predator subject to homogeneous Neumann boundary condition. Some basic dynamics including the dissipation, persistence and non-persistence (i.e., one species goes extinct), the local and global stability of non-negative constant steady states of the model are investigated. The conditions of Turing instability due to diffusion at positive constant steady states are presented. A critical value ρ of the ratio $\frac{d_2}{d_1}$ of diffusions of predator to prey is obtained, such that if $\frac{d_2}{d_1} > \rho$, then along with other suitable conditions Turing bifurcation will emerge at a positive steady state, in particular so it is with the large diffusion rate of predator or the small diffusion rate of prey; while if $\frac{d_2}{d_1} < \rho$, both the reaction-diffusion system and its corresponding ODE system are stable at the positive steady state. In addition, we provide some results on the existence and non-existence of positive non-constant steady states. These existence results indicate that the occurrence of Turing bifurcation, along with other suitable conditions, implies the existence of non-constant positive steady states bifurcating from the constant solution. At last, by numerical simulations, we demonstrate Turing pattern formation on the effect of the varied diffusive ratio $\frac{d_2}{d_1}$. As $\frac{d_2}{d_1}$ increases, Turing patterns change from spots pattern, stripes pattern into spots-stripes pattern. It indicates that the pattern formation of the model is rich and complex.

1. Introduction. Recently, Kang and Fewell [18] studied a host-parasite coevolutionary model, in which the relationship between host (prey) and parasite (predator) is described by the following ecological model with Holling Type II functional response

$$\begin{cases} \frac{du}{dt} = u \left[r_1 \left(1 - \frac{u}{K_1} \right) - \frac{av}{1+hau} \right], \\ \frac{dv}{dt} = v \left[r_2 \left(1 - \frac{v}{K_2} \right) - d + \frac{eau}{1+hau} \right], \end{cases} \quad (1)$$

2020 *Mathematics Subject Classification.* Primary: 35B36, 45M10; Secondary: 92C15.

Key words and phrases. Generalist predator, stability, Turing instability, non-constant solution, pattern formation.

* Corresponding author: Jianshe Yu.

where u and v represent the population densities of prey and predator at time t , respectively, $r_i, K_i (i = 1, 2), a, e, h, d$ are positive constants with specific ecological interpretations : r_1 and r_2 denote the intrinsic growth rate of species u and v , respectively, in the absence of other species; K_1 and K_2 are the carrying capacities of species u and v individuals, respectively; d stands for the dead rate of predator individuals due to hunting or attacking all potential prey resources; a is the capturing efficiency of a predator and h is the predator handling time. In [18], the ecological dynamics for model (1), including the boundedness, permanence, stability of boundary and interior equilibria, and extinction of one species, were performed.

In system (1), both species u and v follow Logistic growth in the absence of other species, which indicates that species v has alternative food resources and could persist in the absence of prey u , i.e., predator species v is generalist. In natural, many predators are in fact generalist, and their prey consists of different species(see, for example, [30, 34, 33, 2]). In the last couple of decades, the study on prey-predator work involving generalist predators has attracted more and more attentions, and provided additional biological insights on dynamical outcomes for models with predator being generalist versus specialist. For example, the study of Symondson et al [35] shows that generalist predators could be effective control agents and have some unique biocontrol functions that are denied to specialists. The work of Kang et.al. [18, 19] indicates that models with generalist predator could exhibit more complicate dynamics and more likely to have “top down” regulation by comparing to the similar models with specialist predator. We also refer to [14, 13, 31, 9, 24, 29, 6] for some references on the study of predator-prey models with generalist predators.

The interactions between predator and prey generally occur over a wide range of spatial and temporal scales and the spatial diffusions of generalist predator and its preys play important roles in shaping ecological communities. The parabolic and elliptic predator-prey models with generalist predators also have been widely studied. Blat and Brown [1] studied the non-negative steady-state solutions of a reaction-diffusion system with generalist predator under Dirichlet boundary condition. Treating prey and predator birth-rates as bifurcation parameters in [1], the ranges of parameters were given for which there exist non-trivial steady-state solutions. In spatially heterogeneous environment, the reaction-diffusion systems with generalist predators were studied in [7, 28], and some results on the existence, non-existence and multiplicity of positive steady states and global bifurcation were obtained. In [8, 15], the reaction-diffusion models with generalist predators and protection zones for preys were studied. We also refer to [17, 36] for the study on the positive steady-state solutions of coupled reaction-diffusion Lotka-Volterra systems, and [23] for the study of the travelling wave solutions of a reaction-diffusion system with generalist predator. In this paper, we study the spatiotemporal dynamics of the reaction-diffusion predator-prey model corresponding to ODE model (1)

$$\begin{cases} \frac{\partial u}{\partial t} - d_1 \Delta u = u \left[r_1 \left(1 - \frac{u}{K_1} \right) - \frac{av}{1+hau} \right], & x \in \Omega, t > 0, \\ \frac{\partial v}{\partial t} - d_2 \Delta v = v \left[r_2 \left(1 - \frac{v}{K_2} \right) - d + \frac{eau}{1+hau} \right], & x \in \Omega, t > 0, \\ \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = 0, & x \in \partial\Omega, t > 0, \\ u(x, 0) = u_0(x) \geq 0, v(x, 0) = v_0(x) \geq 0, & x \in \Omega, \end{cases} \quad (2)$$

where, Ω is a bounded domain of $\mathbb{R}^N (N \geq 1)$ with smooth boundary $\partial\Omega$, $\frac{\partial}{\partial \nu}$ is the outward directional derivative normal to $\partial\Omega$, $u_0, v_0 \in C(\bar{\Omega})$ stand for the initial

conditions, d_1 and d_2 are positive constants and stand for the random diffusive rates of the prey and predator, respectively.

When $r_2 > d$ and Ω is a two-dimensional bounded connected square domain, by changing $r_2 - d$ and $\frac{r_2}{K_2}$ into r_2 and m , respectively, (2) becomes the model studied by Chakraborty [5]. In [5], the condition of Turing bifurcation at positive constant steady state due to diffusion was given, and different pattern formations and spatiotemporal chaos were presented by numerical simulation. In this paper, we discuss the dissipation, persistence and non-persistence (i.e., one species goes extinct), the local and global stability of non-negative constant steady states of (2). The conditions of Turing bifurcation at positive constant steady state of (2) are presented. A critical value ρ of $\frac{d_2}{d_1}$ is obtained such that if $\frac{d_2}{d_1} > \rho$, then along with other suitable conditions Turing bifurcation emerges at a positive steady state, in particular so it is with the large diffusion rate d_2 of predator or the small diffusion rate d_1 of prey; while if $\frac{d_2}{d_1} < \rho$, (2) has the same stability to ODE system (1). We refer reader to [12, 37, 4, 38, 32, 20] for some references on the recent study of Turing bifurcation and spatiotemporal pattern formation of some ecological models.

In order to study the stationary pattern induced by diffusions, we also consider the existence and non-existence of positive non-constant solutions of the steady state of (2), i.e., the following semi-linear elliptic system

$$\begin{cases} -d_1 \Delta u = u \left[r_1 \left(1 - \frac{u}{K_1} \right) - \frac{av}{1+hav} \right], & x \in \Omega, \\ -d_2 \Delta v = v \left[r_2 \left(1 - \frac{v}{K_2} \right) - d + \frac{eau}{1+hav} \right], & x \in \Omega, \\ \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = 0, & x \in \partial \Omega. \end{cases} \quad (3)$$

In [27], the non-existence of non-constant positive steady state solutions of the following reaction-diffusion predator-prey model with Holling type-II functional response and generalist predator was studied

$$\begin{cases} -d_1 \Delta u = u(\alpha - u) - \frac{muv}{1+u}, & x \in \Omega, \\ -d_2 \Delta v = v(\beta - v) + \frac{muv}{1+u}, & x \in \Omega, \\ \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = 0, & x \in \partial \Omega, \end{cases} \quad (4)$$

where the constant β may be non-positive. It was proved under $N \leq 3$ in [27] that for any given $d_1, d_2, \alpha, \beta, \Omega$, there exists a positive constant M , which depends on $d_1, d_2, \alpha, \beta, \Omega$, such that if $m \geq M$, then (4) has no non-constant positive solution when $\beta \leq 0$ and has no positive solution when $\beta > 0$. For model (3), we are interested in the effect of diffusion rates d_1 and d_2 on the stationary pattern. It is proved that if $r_2 < d < r_2 + \frac{eaK_1}{1+haK_1}$ and $d_2 > \frac{1}{\mu_1} \left(r_2 - d + \frac{eaK_1}{1+ahK_1} \right)$, where μ_1 is the smallest positive eigenvalue of $-\Delta$ on Ω with zero-flux boundary conditions, (3) has no non-constant positive steady state solution for sufficiently large d_1 . In addition, some existence results of at least one non-constant positive steady state solution of (3) are obtained by the index formula given by Pang and Wang [26] and Leray-Schauder topological degree theory. These existence results indicate that the occurrence of Turing instability at a positive constant steady state of reaction-diffusion system, along with other suitable conditions, implies the existence of non-constant positive steady state bifurcating from the constant solution.

The remaining sections of this paper is organized as follows. In Section 2, we show the results on the dissipation, permanence, non-persistence, and the local and global stability of non-negative constant steady states of model (2), as well as Turing instability at positive constant solutions of (2). In Section 3, we first give a priori

upper and lower bounds for the positive solutions of (3) in order to calculate the topological degree, then present the non-existence and existence of positive non-constant solutions of (3). In Section 4, we perform a series of numerical simulation to show the occurrence of Turing patterns caused by diffusions. It is found that the model dynamics exhibit spatiotemporal Turing complexity of pattern formation, including spots, strips and spots-stripes Turing patterns. At last, we end the paper with a brief discussion in Section 5.

2. Permanence, stability, Turing instability. In this section, we study the dissipation, persistence and non-persistence, the local and global stability of non-negative constant steady states of model (2). Also, Turing instability at the positive constant solution is studied.

2.1. Permanence. First, we show the dissipation and permanence of (2). Define

$$M_v = \frac{K_2}{r_2} \left[r_2 - d + \frac{eaK_1}{1+haK_1} \right], \quad m_u = \frac{K_1}{r_1} (r_1 - aM_v),$$

$$m_v = \frac{K_2}{r_2} \left[r_2 - d + \frac{eam_u}{1+ham_u} \right].$$

Theorem 2.1. (Dissipation) *The non-negative solution $(u(x, t), v(x, t))$ of system (2) satisfies*

$$\limsup_{t \rightarrow \infty} \max_{\Omega} u(x, t) \leq K_1, \quad \limsup_{t \rightarrow \infty} \max_{\Omega} v(x, t) \leq \max\{0, M_v\}.$$

Proof. Since $u \left[r_1 \left(1 - \frac{u}{K_1} \right) - \frac{av}{1+ha u} \right] \leq r_1 u \left(1 - \frac{u}{K_1} \right)$ in $\Omega \times [0, \infty)$, we can directly get the first assertion from the comparison argument for parabolic problems [11]. Thus, there exists $T > 0$ such that $u(x, t) \leq K_1 + \epsilon$ for $(x, t) \in \Omega \times [T, \infty)$. It follows that $v(x, t)$ satisfies

$$\begin{cases} \frac{\partial v}{\partial t} - d_2 \Delta v \leq v \left[r_2 \left(1 - \frac{v}{K_2} \right) - d + \frac{ea(K_1 + \epsilon)}{1+ha(K_1 + \epsilon)} \right], & x \in \Omega, t > T, \\ \frac{\partial v}{\partial \nu} = 0, & x \in \partial\Omega, t > T, \\ v(x, T) > 0, & x \in \Omega. \end{cases}$$

If $d \leq r_2 + \frac{eaK_1}{1+haK_1}$, let $z(t)$ be a solution of the ODE

$$\begin{cases} z'(t) = z \left[r_2 \left(1 - \frac{z}{K_2} \right) - d + \frac{ea(K_1 + \epsilon)}{1+ha(K_1 + \epsilon)} \right], & t > T, \\ z(T) = \max_{x \in \Omega} v(x, T) > 0. \end{cases}$$

Then

$$\lim_{t \rightarrow \infty} z(t) = \frac{K_2}{r_2} \left(r_2 - d + \frac{ea(K_1 + \epsilon)}{1 + ha(K_1 + \epsilon)} \right).$$

It follows from the comparison argument [11] that $v(x, t) \leq z(t)$, and hence

$$\limsup_{t \rightarrow \infty} \max_{\Omega} v(x, t) \leq \frac{K_2}{r_2} \left(r_2 - d + \frac{eaK_1}{1 + haK_1} \right).$$

by the arbitrariness of ϵ . If $d > r_2 + \frac{eaK_1}{1+haK_1}$, we have the differential inequality

$$\frac{\partial v}{\partial t} - d_2 \Delta v \leq -\frac{r_2 v}{K_2},$$

and the same argument above yields $\limsup_{t \rightarrow \infty} \max_{x \in \Omega} v(x, t) \leq 0$. In either case, the second assertion holds. This completes the proof. □

The following result gives the sufficient conditions for the permanence of (2).

Theorem 2.2. (Permanence) *If either*

(i) $r_2 > d$ and $\frac{r_1}{a} > M_v$; or

(ii) $r_2 \leq d$ and $\frac{r_1}{a} > M_v > m_v > 0$,

then any positive solution $(u(x, t), v(x, t))$ of system (2) satisfies

$$\liminf_{t \rightarrow \infty} \min_{x \in \bar{\Omega}} u(x, t) \geq m_u, \quad \liminf_{t \rightarrow \infty} \min_{x \in \bar{\Omega}} v(x, t) \geq m_v.$$

Proof. We only show the proof for the case $r_2 \leq d$. Choose any $\epsilon : 0 < \epsilon < m_u$ sufficiently small, such that $r_1 - a(M_v + \epsilon) > 0$ and $r_2 - d + \frac{ea(m_u - \epsilon)}{1 + ha(m_u - \epsilon)} > 0$. In view of Theorem 2.1, there exists $T > 0$ such that $v(x, t) \leq M_v + \epsilon$ in $\Omega \times [T, \infty)$. Thus, we have that $u(x, t)$ is an upper solution of

$$\begin{cases} \frac{\partial z}{\partial t} - d_1 \Delta z = z \left[r_1 \left(1 - \frac{z}{K_1} \right) - a(M_v + \epsilon) \right], & x \in \Omega, t > T, \\ \frac{\partial z}{\partial \nu} = 0, & x \in \partial\Omega, t > T, \\ z(x, T) = u(x, T) > 0, & x \in \Omega. \end{cases} \tag{5}$$

Let $w(t)$ be the unique positive solution of the following problem

$$\begin{cases} \frac{dw}{dt} = w \left[r_1 \left(1 - \frac{w}{K_1} \right) - a(M_v + \epsilon) \right], & t > T, \\ w(T) = \min_{\bar{\Omega}} u(x, T) > 0. \end{cases}$$

Then $w(t)$ is a lower solution of (5) and $\lim_{t \rightarrow \infty} w(t) = \frac{K_1}{r_1} (r_1 - aM_v) = m_u$ by the arbitrariness of ϵ . It follows from the comparison principle [11] that the desired first assertion holds. Hence, there exists $T_0 > T$ such that $u(x, t) \geq m_u - \epsilon$ in $\Omega \times [T_0, \infty)$. Thus, we have that $v(x, t)$ is an upper solution of

$$\begin{cases} \frac{\partial z}{\partial t} - d_2 \Delta z = z \left[r_2 \left(1 - \frac{z}{K_2} \right) - d + \frac{ea(m_u - \epsilon)}{1 + ha(m_u - \epsilon)} \right], & x \in \Omega, t > T_0, \\ \frac{\partial z}{\partial \nu} = 0, & x \in \partial\Omega, t > T_0, \\ z(x, T_0) = v(x, T_0) > 0, & x \in \Omega, \end{cases}$$

Again, using the comparison principle [11], we can get the second assertion. The proof is completed. □

2.2. Non-persistence. It is known from [18] that system (2) has two semi-trivial constant steady states $E_{10} = (K_1, 0)$ and $E_{01} = \left(0, \left(1 - \frac{d}{r_2} \right) K_2 \right)$ if $r_2 > d$. In this subsection, we discuss the global stability of the constant steady states E_{10} and E_{01} , which implies that one species goes extinct and system (2) has no positive non-constant steady state regardless of the diffusion coefficients.

Theorem 2.3. (Non-persistence) 1. *If $d > r_2 + \frac{eaK_1}{1 + haK_1}$, then any positive solution $(u(x, t), v(x, t))$ of (2) satisfies*

$$\lim_{t \rightarrow \infty} (u(x, t), v(x, t)) = (K_1, 0) \quad \text{uniformly on } \bar{\Omega}.$$

Thus $E_{10} = (K_1, 0)$ is globally uniformly asymptotically stable in \mathbb{R}_+^2 .

2. *If $d < r_2$ and one of the following conditions is satisfied*

(i) $ahK_1 \leq 1$ and $\frac{r_1}{a} < \tilde{m}_v$, or

(ii) $ahK_1 > 1$ and $\frac{r_1(1+ahK_1)^2}{4a^2hK_1} < \tilde{m}_v$,
 where, $\tilde{m}_v = \frac{K_2}{r_2}(r_2 - d)$, then any positive solution $(u(x, t), v(x, t))$ of (2) satisfies

$$\lim_{t \rightarrow \infty} (u(x, t), v(x, t)) = \left(0, \left(1 - \frac{d}{r_2} \right) K_2 \right) \quad \text{uniformly on } \bar{\Omega}.$$

Thus $E_{01} = \left(0, \left(1 - \frac{d}{r_2} \right) K_2 \right)$ is globally uniformly asymptotically stable in \mathbb{R}_+^2 .

Proof. 1. From the proof of Theorem 2.1, there exists a positive function $z(t)$ satisfying $\lim_{t \rightarrow \infty} z(t) = 0$ such that $\max_{x \in \Omega} v(x, t) \leq z(t)$. Thus, $v \rightarrow 0$ uniformly on $\bar{\Omega}$ as $t \rightarrow \infty$.

For any $\epsilon, 0 < \epsilon \ll 1$, there exists $T, 0 < T < \infty$, such that $v(x, t) \leq \epsilon, \forall x \in \bar{\Omega}, t \geq T$. Therefore,

$$\begin{cases} \frac{\partial u}{\partial t} - d_1 \Delta u \geq u \left[r_1 \left(1 - \frac{u}{K_1} \right) - a\epsilon \right], & x \in \Omega, t \geq T, \\ \frac{\partial u}{\partial \nu} = 0, & x \in \partial\Omega, t \geq T, \\ u(x, T) > 0, & x \in \bar{\Omega}, \end{cases}$$

Applying the comparison principle [11], we have that

$$\liminf_{t \rightarrow \infty} \min_{x \in \bar{\Omega}} u(x, t) \geq \frac{K_1}{r_1}(r_1 - a\epsilon).$$

The arbitrariness of ϵ then implies that $\liminf_{t \rightarrow \infty} \min_{x \in \bar{\Omega}} u(x, t) \geq K_1$. This, along with the result of Theorem 2.1, implies that $u \rightarrow K_1$ uniformly on $\bar{\Omega}$ as $t \rightarrow \infty$.

2. By the second equation of (2), we have

$$\begin{cases} \frac{\partial v}{\partial t} - d_2 \Delta v \geq v \left[r_2 \left(1 - \frac{v}{K_2} \right) - d \right], & x \in \Omega, t > 0, \\ \frac{\partial v}{\partial \nu} = 0, & x \in \partial\Omega, t > 0, \\ v(x, 0) = v_0(x) \geq 0, & x \in \Omega. \end{cases}$$

Since $r_2 > d$, it follows from a comparison argument that

$$\liminf_{t \rightarrow \infty} \min_{x \in \bar{\Omega}} v(x, t) \geq \frac{K_2}{r_2}(r_2 - d) = \tilde{m}_v. \tag{6}$$

This implies that for any $\epsilon, 0 < \epsilon \ll 1$, there exists $T, 0 < T < \infty$, such that $v(x, t) \geq \tilde{m}_v - \epsilon, \forall x \in \bar{\Omega}, t \geq T$. Therefore,

$$\begin{cases} \frac{\partial u}{\partial t} - d_1 \Delta u \leq \frac{u}{1+ah} \left[(r_1 - a(\tilde{m}_v - \epsilon)) + \frac{r_1(ahK_1-1)}{K_1}u - \frac{r_1ah}{K_1}u^2 \right], & x \in \Omega, t \geq T, \\ \frac{\partial u}{\partial \nu} = 0, & x \in \partial\Omega, t \geq T, \\ u(x, T) > 0, & x \in \bar{\Omega}. \end{cases}$$

Let $w(t)$ be the solution of the ODE

$$\begin{cases} w'(t) = \frac{w}{1+ahw} \left[(r_1 - a(\tilde{m}_v - \epsilon)) + \frac{r_1}{K_1}(ahK_1 - 1)w - \frac{r_1ah}{K_1}w^2 \right], & t \geq T, \\ w(T) = \max_{x \in \bar{\Omega}} u(x, T) > 0. \end{cases}$$

An application of the comparison principle gives $\max_{x \in \bar{\Omega}} u(x, t) \leq w(t)$.

If $ahK_1 \leq 1$ and $\frac{r_1}{a} < \tilde{m}_v$, we have $\lim_{t \rightarrow \infty} w(t) = 0$.

If $ahK_1 > 1$ and $\frac{r_1(1+ahK_1)^2}{4a^2hK_1} < \tilde{m}_v$, then

$$\left[\frac{r_1}{K_1}(ahK_1 - 1) \right]^2 + 4(r_1 - a(m_v - \epsilon)) \frac{r_1 ah}{K_1} < 0,$$

which also implies that $\lim_{t \rightarrow \infty} w(t) = 0$. Thus, $u \rightarrow 0$ uniformly on $\bar{\Omega}$ as $t \rightarrow \infty$. It follows that there exists $T_1 > T$ such that $u(x, t) \leq \epsilon, \forall x \in \bar{\Omega}, t \geq T_1$. Therefore,

$$\begin{cases} \frac{\partial v}{\partial t} - d_2 \Delta v \leq v \left[r_2 \left(1 - \frac{v}{K_2} \right) - d + ea\epsilon \right], & x \in \Omega, t > T_1, \\ \frac{\partial v}{\partial \nu} = 0, & x \in \partial\Omega, t > T_1, \\ v(x, T_1) > 0, & x \in \bar{\Omega}. \end{cases}$$

Again by a comparison argument, we have

$$\limsup_{t \rightarrow \infty} \max_{x \in \Omega} v(x, t) \leq \frac{K_2}{r_2} (r_2 - d + ea\epsilon).$$

The arbitrariness of ϵ then implies that $\limsup_{t \rightarrow \infty} \max_{x \in \Omega} v(x, t) \leq \frac{K_2}{r_2} (r_2 - d)$. This, along with (6), implies that $v \rightarrow \frac{K_2}{r_2} (r_2 - d)$ uniformly on $\bar{\Omega}$ as $t \rightarrow \infty$. The proof is completed. \square

2.3. Local stability and Turing bifurcation. Except the two semi-trivial constant steady states $E_{10} = (K_1, 0)$ and $E_{01} = \left(0, \left(1 - \frac{d}{r_2} \right) K_2 \right)$ ($r_2 > d$), system (2) has a trivial constant steady state $E_{00} = (0, 0)$, and at most three positive constant steady states $E^* = (u^*, v^*)$ (see [18]). The interior equilibrium $E^*(u^*, v^*)$ of system (1) satisfies the following two equations

$$\begin{aligned} r_1 \left(1 - \frac{u}{K_1} \right) - \frac{av}{1+ahu} = 0 &\Leftrightarrow v = \frac{r_1(K_1 - u)(1+ahu)}{aK_1}, \\ r_2 \left(1 - \frac{v}{K_2} \right) - d + \frac{eau}{1+ahu} = 0 &\Leftrightarrow v = \frac{K_2}{r_2} \left[\frac{eau}{1+ahu} + r_2 - d \right]. \end{aligned}$$

In this subsection, we analyze the local stability of these constant steady states. Also, Turing instability of the positive constant steady state $E^* = (u^*, v^*)$ is studied.

Assume that $0 = \mu_0 < \mu_1 < \dots$ are the eigenvalues of the operator $-\Delta$ on Ω with the homogeneous Neumann boundary condition. Set $S_p = \{\mu_0, \mu_1, \mu_2, \dots\}$ and $E(\mu_i)$ the eigenspace corresponding to μ_i in $C^1(\bar{\Omega})$. Let

$$\mathbf{X} = \{ \mathbf{w} \in [C^1(\bar{\Omega})]^2 \mid \partial_\nu \mathbf{w} = 0 \text{ on } \partial\Omega \}, \quad (7)$$

$\{\phi_{ij} \mid j = 1, \dots, \dim E(\mu_i)\}$ be an orthonormal basis of $E(\mu_i)$, $\mathbf{X}_{ij} = \{ \mathbf{c} \phi_{ij} \mid \mathbf{c} \in \mathbb{R}^2 \}$, then

$$\mathbf{X} = \bigoplus_{i=1}^{\infty} \mathbf{X}_i, \quad \text{where } \mathbf{X}_i = \bigoplus_{j=1}^{\dim E(\mu_i)} \mathbf{X}_{ij}.$$

For the sake of simplicity, we rewrite system (2) in a compact form

$$\begin{cases} \mathbf{w}_t = D\Delta \mathbf{w} + F(\mathbf{w}), & x \in \Omega, t > 0, \\ \frac{\partial \mathbf{w}}{\partial \nu} = 0, & x \in \partial\Omega, t > 0, \\ \mathbf{w}(x, 0) = (u_0(x), v_0(x))^T, & x \in \Omega, \end{cases} \quad (8)$$

where $\mathbf{w} = (u(x, t), v(x, t))^T$, $D = \text{diag}(d_1, d_2)$ and

$$F(\mathbf{w}) = \begin{pmatrix} r_1 u \left(1 - \frac{u}{K_1} \right) - \frac{avv}{1+ahu} \\ r_2 v \left(1 - \frac{v}{K_2} \right) - dv + \frac{eauv}{1+ahu} \end{pmatrix}.$$

For convenience, set

$$\begin{aligned} j_{11} &= -\frac{r_1 u^*}{K_1} \cdot \frac{2ahu^* - (ahK_1 - 1)}{1 + ah u^*}, & j_{12} &= -\frac{au^*}{1 + ah u^*}, \\ j_{21} &= \frac{eav^*}{(1 + ah u^*)^2}, & j_{22} &= -\frac{r_2 v^*}{K_2}, \end{aligned} \tag{9}$$

and

$$H(d_1, d_2, \mu) := d_1 d_2 \mu^2 - (d_1 j_{22} + d_2 j_{11}) \mu + (j_{11} j_{22} - j_{12} j_{21}). \tag{10}$$

Denote the discriminant of $H(d_1, d_2, \mu) = 0$ as follows

$$Q := Q(d_1, d_2) = (d_1 j_{22} + d_2 j_{11})^2 - 4d_1 d_2 (j_{11} j_{22} - j_{12} j_{21}). \tag{11}$$

If $Q(d_1, d_2) > 0$, then $H(d_1, d_2, \mu) = 0$ has two real roots, denoted by

$$\mu^\pm(d_1, d_2) := \frac{1}{2d_1 d_2} (d_1 j_{22} + d_2 j_{11} \pm \sqrt{Q}). \tag{12}$$

Define

$$B := B(d_1, d_2) = \{\mu : \mu \geq 0, \mu^-(d_1, d_2) < \mu < \mu^+(d_1, d_2)\}. \tag{13}$$

Now, we give the main results on the local stability of the non-negative constant steady states of system (2). For this, we make the following assumptions

$$\begin{cases} \frac{r_1 r_2}{K_1 K_2} (2ahu^* - ahK_1 + 1) + \frac{ea^2}{(1 + ah u^*)^2} > 0, \\ K_1 > 2u^* + \frac{1}{ah}. \end{cases} \tag{H}$$

We also take the following notations

$$\begin{aligned} N_1(u^*) &= \frac{u^*}{1 + ah u^*} \left[ea + \frac{r_1}{K_1} (2ahu^* - ahK_1 + 1) \right], \\ N_2(u^*) &= \frac{u^*}{1 + ah u^*} \left[\frac{d_2 r_1}{d_1 K_1} (2ahu^* - ahK_1 + 1) + ea \right], \\ N_3(u^*) &= 2 \left[\frac{d_2}{d_1} \cdot \frac{r_1 (K_1 - u^*) u^*}{a K_1} \left(\frac{r_1 r_2}{K_1 K_2} (2ahu^* - ahK_1 + 1) + \frac{ea^2}{(1 + ah u^*)^2} \right) \right]^{\frac{1}{2}}. \end{aligned}$$

Theorem 2.4. (Local stability and Turing instability)

1. For the positive constant steady state $E^* = (u^*, v^*)$ of system (2),
 - (i) if $K_1 \leq 2u^* + \frac{1}{ah}$, it is locally uniformly asymptotically stable;
 - (ii) under Condition (H), it is locally uniformly asymptotically stable if

$$0 < d < r_2 + \min\{N_1(u^*), N_2(u^*)\}; \tag{14}$$

- (iii) under Condition (H), it is locally uniformly asymptotically stable if

$$\max\{r_2 + N_2(u^*), 0\} < d < r_2 + \min\{N_1(u^*), N_2(u^*) + N_3(u^*)\}; \tag{15}$$

- (iv) under Condition (H) and

$$\max\{r_2 + N_2(u^*) + N_3(u^*), 0\} < d < r_2 + N_1(u^*), \tag{16}$$

it is locally uniformly asymptotically stable if $\overline{B(d_1, d_2)} \cap S_p = \emptyset$; while it is Turing instability if $B(d_1, d_2) \cap S_p \neq \emptyset$.

2. The semi-trivial constant steady state $E_{10} = (K_1, 0)$ of system (2) is locally uniformly asymptotically stable if $d > r_2 + \frac{eaK_1}{1 + ahK_1}$.
3. The semi-trivial constant steady state $E_{01} = (0, (1 - \frac{d}{r_2})K_2)$ of system (2) is locally uniformly asymptotically stable if $\frac{r_1}{aK_2} < 1 - \frac{d}{r_2}$.
4. The trivial constant steady state $E_{00} = (0, 0)$ of system (2) is always unstable.

Proof. The linearization of system (8) can be expressed by $\mathbf{w}_t = \mathcal{L}(\mathbf{w}) \equiv D\Delta\mathbf{w} + J|_E\mathbf{w}$, where

$$J|_E = \begin{pmatrix} r_1 - \frac{2r_1u}{K_1} - \frac{av}{(1+ahu)^2} & -\frac{au}{1+ahu} \\ \frac{eav}{(1+ahu)^2} & r_2 - \frac{2r_2v}{K_2} - d + \frac{eau}{1+ahu} \end{pmatrix}.$$

1. Consider the positive constant steady state $E^* = (u^*, v^*)$ of (2). The linearization of (8) at $E^* = (u^*, v^*)$ can be expressed by $\mathbf{w}_t = \mathcal{L}(\mathbf{w}) \equiv D\Delta\mathbf{w} + J|_{E^*}\mathbf{w}$, where $J|_{E^*} = (j_{mn})_{2 \times 2}$ with $j_{mn}(m, n = 1, 2)$ is given in (9).

Note that for each $i \geq 0$, \mathbf{X}_i is invariant under the operator \mathcal{L} . λ is an eigenvalue of \mathcal{L} if and only if λ is an eigenvalue of the matrix $A_i = -\mu_i D + J|_{E^*}$ for some $i \geq 0$. The characteristic polynomial $\text{Det}(\lambda I - A_i)$ is given by

$$\psi_i(\lambda) = \lambda^2 - \text{Tr}(A_i)\lambda + \text{Det}(A_i), \quad i = 0, 1, \dots, \tag{17}$$

where

$$\begin{aligned} \text{Tr}(A_i) &= -\mu_i(d_1 + d_2) + \text{Tr}(J|_{E^*}), \\ \text{Det}(A_i) &= H(d_1, d_2, \mu_i) = d_1d_2\mu_i^2 - (d_1j_{22} + d_2j_{11})\mu_i + \text{Det}(J|_{E^*}), \end{aligned}$$

and

$$\begin{aligned} \text{Tr}(J|_{E^*}) &= j_{11} + j_{22} \\ &= -\frac{r_1u^*}{K_1} \cdot \frac{2ahu^* - (ahK_1 - 1)}{1+ahu^*} - \frac{r_2v^*}{K_2} \\ &= -\frac{u^*}{1+ahu^*} \left(\frac{r_1}{K_1} (2ahu^* - ahK_1 + 1) + ea \right) - r_2 + d, \\ d_1j_{22} + d_2j_{11} &= -\frac{d_2r_1u^*}{K_1} \cdot \frac{2ahu^* - (ahK_1 - 1)}{1+ahu^*} - \frac{d_1r_2v^*}{K_2} \\ &= -\frac{d_1u^*}{1+ahu^*} \left(\frac{d_2r_1}{d_1K_1} (2ahu^* - ahK_1 + 1) + ea \right) - d_1(r_2 - d), \\ \text{Det}(J|_{E^*}) &= j_{11}j_{22} - j_{12}j_{21} \\ &= \frac{u^*v^*}{1+ahu^*} \left(\frac{r_1r_2}{K_1K_2} (2ahu^* - ahK_1 + 1) + \frac{ea^2}{(1+ahu^*)^2} \right). \end{aligned}$$

(i) If $K_1 \leq 2u^* + \frac{1}{ah}$, it is easy to see that $\text{Tr}(A_i) < 0, \text{Det}(A_i) > 0$ for all $i \geq 0$. Therefore, for each $i \geq 0$, the two roots λ_1^i and λ_2^i of $\psi_i(\lambda) = 0$ both have negative real parts. By a standard argument(see, for example, [10, 3]), one can prove that there exists an $\eta > 0$ such that

$$\text{Re}\{\lambda_1^i\} \leq -\eta, \quad \text{Re}\{\lambda_2^i\} \leq -\eta.$$

Therefore, the spectrum of \mathcal{L} , which consists of eigenvalues, lies in $\{ \text{Re}\lambda \leq -\eta \}$. In the sense of [16], $E^* = (u^*, v^*)$ is uniformly asymptotically stable.

In the following proofs for (ii)-(iv), we assume that Condition (H) holds. Then

$$\text{Det}(J|_{E^*}) > 0.$$

(ii) By (14), one can check that $d_1j_{22} + d_2j_{11} < 0$ and $\text{Tr}(J|_{E^*}) < 0$. It follows that $\text{Tr}(A_i) < 0, \text{Det}(A_i) > 0$ for all $i \geq 0$. Therefore, for each $i \geq 0$, the two roots λ_1^i and λ_2^i of $\psi_i(\lambda) = 0$ both have negative real parts. Similar to the arguments of case (i), $E^* = (u^*, v^*)$ is uniformly asymptotically stable.

(iii) From (15), it is easy to check that $d_1j_{22} + d_2j_{11} > 0$ by $d > r_2 + N_2(u^*)$, and

$$Q = (d_1j_{22} + d_2j_{11})^2 - 4d_1d_2\text{Det}(J|_{E^*}) < 0$$

by $d < r_2 + N_2(u^*) + N_3(u^*)$. Thus, combining with $\text{Det}(J|_{E^*}) > 0$, we have that $\text{Det}(A_i) > 0$ for all $i \geq 0$. Again, from (15), we have $\text{Tr}(J|_{E^*}) < 0$ by $d < r_2 + N_1(u^*)$ and hence $\text{Tr}(A_i) < 0$ for all $i \geq 0$. Therefore, for each $i \geq 0$, the two roots λ_1^i

and λ_2^i of $\psi_i(\lambda) = 0$ both have negative real parts and $E^* = (u^*, v^*)$ is uniformly asymptotically stable.

(iv) From (16), it is easy to verify that $d_1j_{22} + d_2j_{11} > 0$ and $Q > 0$ by $d > r_2 + N_2(u^*) + N_3(u^*) > r_2 + N_2(u^*)$. Thus, the equation $H(d_1, d_2, \mu) = 0$ has two positive real roots

$$0 < \mu^-(d_1, d_2) < \mu^+(d_1, d_2).$$

Therefore, if the set $B(d_1, d_2)$ defined by (13) satisfies $\overline{B(d_1, d_2)} \cap S_p = \emptyset$, then for all $i \geq 0$, $\text{Det}(A_i) > 0$. On the other hand, $\text{Tr}(A_i) < 0$ for all $i \geq 0$ by $d < r_2 + N_1(u^*)$. So, for each $i \geq 0$, the two roots λ_1^i and λ_2^i of $\psi_i(\lambda) = 0$ both have negative real parts and $E^* = (u^*, v^*)$ is uniformly asymptotically stable.

If $B(d_1, d_2) \cap S_p \neq \emptyset$, then there exists $i_0 \geq 1$ such that

$$\mu_{i_0} \in (\mu^-(d_1, d_2), \mu^+(d_1, d_2)),$$

which implies that $\text{Det}(A_{i_0}) < 0$. Thus, the equation $\psi_{i_0}(\lambda) = 0$ has a positive real root. On the other hand, according to the arguments above, one can easily obtain that ODE system (1) is locally asymptotically stable at the positive equilibrium $E^* = (u^*, v^*)$ if Condition (H) holds and $0 < d < r_2 + N_1(u^*)$. Therefore, the positive constant steady state $E^* = (u^*, v^*)$ of system (2) is Turing instability.

2. Consider the semi-trivial constant steady state $E_{10} = (K_1, 0)$. Clearly,

$$J|_{E_{10}} = \begin{pmatrix} -r_1 & -\frac{aK_1}{1+ahK_1} \\ 0 & r_2 - d + \frac{eaK_1}{1+ahK_1} \end{pmatrix}.$$

Since $d > r_2 + \frac{eaK_1}{1+ahK_1}$, we have $\text{Tr}(J|_{E_{10}}) < 0$ and $\text{Det}(J|_{E_{10}}) > 0$. The remaining arguments are rather similar as above. Therefore, E_{10} is uniformly asymptotically stable.

3. Consider the semi-trivial constant steady state $E_{01} = (0, (1 - \frac{d}{r_2})K_2)$ ($r_2 > d$). Clearly,

$$J|_{E_{01}} = \begin{pmatrix} r_1 - aK_2 \left(1 - \frac{d}{r_2}\right) & 0 \\ eaK_2 \left(1 - \frac{d}{r_2}\right) & d - r_2 \end{pmatrix}.$$

Since $\frac{r_1}{aK_2} < 1 - \frac{d}{r_2}$, we have $\text{Tr}(J|_{E_{01}}) < 0$ and $\text{Det}(J|_{E_{01}}) > 0$. Therefore, E_{01} is uniformly asymptotically stable.

4. Consider the trivial constant steady state $E_{00} = (0, 0)$. It is easy to see that

$$J|_{E_{00}} = \begin{pmatrix} r_1 & 0 \\ 0 & r_2 - d \end{pmatrix}.$$

Since $J|_{E_{00}}$ has a positive eigenvalue r_1 , $E_{00} = (0, 0)$ is unstable. The proof is completed. □

Notation. Theorem 2.4 and its proof indicates the follows.

1. The reaction-diffusion system (2) has the same local stabilities at E_{00}, E_{10} and E_{01} with ODE system (1)(see Kang and Fewell [18]). Therefore, the diffusions of prey and predator don't influence the stability of E_{00}, E_{10} and E_{01} ;
2. If $d_2 \leq d_1$, then $N_2(u^*) \geq N_1(u^*)$, and (15) and (16) fail while (14) holds. This implies that the reaction-diffusion system (2) has the same local stability at E^* with ODE system (1), and the spatial diffusions of species can't produce Turing

bifurcation. However, if $d_2 > d_1$ then the diffusions of species may drive Turing instability to occur when (16) and $B(d_1, d_2) \cap S_p \neq \emptyset$ hold.

The sufficient condition of Turing instability given in Theorem 2.4 doesn't explicitly show the effect of diffusion rates on the occurrence of Turing bifurcation. In the following result, a critical value ρ of $\frac{d_2}{d_1}$ is obtained such that if $\frac{d_2}{d_1} > \rho$, then along with other suitable conditions Turing bifurcation emerges at a positive steady state; while if $\frac{d_2}{d_1} < \rho$, (2) has the same stability to ODE system (1). Comparing to Theorem 2.4, the conditions given below is more easy to be checked.

Theorem 2.5. (Turing bifurcation) Assume that (H) holds and $0 < d < r_2 + N_1(u^*)$. Let

$$\rho = \frac{1}{(j_{11})^2} \left(\sqrt{\text{Det}(J|_{E^*})} + \sqrt{-j_{12}j_{21}} \right)^2. \tag{18}$$

Then $\rho > -\frac{j_{22}}{j_{11}} > 1$ and

- (1) if $\frac{d_2}{d_1} \in (0, \rho)$, the positive constant steady state $E^* = (u^*, v^*)$ of (2) is locally uniformly asymptotically stable;
- (2) if $\frac{d_2}{d_1} \in (\rho, \infty)$, $E^* = (u^*, v^*)$ of (2) is locally uniformly asymptotically stable provided that $\overline{B(d_1, d_2)} \cap S_p = \emptyset$; while it is Turing instability provided that $B(d_1, d_2) \cap S_p \neq \emptyset$.

Proof. First, we prove that $-\frac{j_{22}}{j_{11}} > 1$. Note $v^* = \frac{K_2}{r_2} \left(\frac{eau^*}{1+ahu^*} + r_2 - d \right)$, we have

$$-\frac{j_{22}}{j_{11}} = \frac{K_1 eau^* + (r_2 - d)(1 + ah u^*)}{r_1 u^*(ahK_1 - 2ahu^* - 1)}.$$

Then, by $ahK_1 - 2ahu^* - 1 > 0$ and $0 < d < r_2 + N_1(u^*)$, we get

$$\begin{aligned} -\frac{j_{22}}{j_{11}} &> \frac{K_1 eau^* - N_1(u^*)(1 + ah u^*)}{r_1 u^*(ahK_1 - 2ahu^* - 1)} \\ &= \frac{K_1 eau^* - u^* \left(ea + \frac{r_1}{K_1}(2ahu^* - ahK_1 + 1) \right)}{r_1 u^*(ahK_1 - 2ahu^* - 1)} \\ &= 1. \end{aligned}$$

The first inequality of Condition (H) is equivalent to $H(d_1, d_2, 0) = j_{11}j_{22} - j_{12}j_{21} > 0$. $0 < d < r_2 + N_1(u^*)$ implies that $\text{Tr}(J|_{E^*}) < 0$, and hence for all $i \geq 0$, $\text{Tr}(A_i) < 0$. Therefore, ODE system (1) is locally asymptotically stable at $E^* = (u^*, v^*)$.

If $d_1j_{22} + d_2j_{11} > 0$ and the discriminant (11) of $H(d_1, d_2, \mu) = 0$ satisfies $Q(d_1, d_2) > 0$, then $H(d_1, d_2, \mu) = 0$ has two positive roots $0 < \mu^- < \mu^+$. Clearly, if $\frac{d_2}{d_1} > -\frac{j_{22}}{j_{11}}$, which is equivalent to $d_1j_{22} + d_2j_{11} > 0$ since $j_{11} > 0$ and $j_{22} < 0$, then $Q(d_1, d_2) > 0$ is equivalent to $d_1j_{22} + d_2j_{11} > 2\sqrt{d_1d_2\text{Det}(J|_{E^*})}$, i.e.,

$$j_{11} \left(\sqrt{\frac{d_2}{d_1}} \right)^2 - 2\sqrt{\text{Det}(J|_{E^*})}\sqrt{\frac{d_2}{d_1}} + j_{22} > 0.$$

Set $\sqrt{\frac{d_2}{d_1}} = z$ and consider

$$\phi(z) = j_{11}z^2 - 2\sqrt{\text{Det}(J|_{E^*})}z + j_{22}, \quad z > 0,$$

which is a degree two polynomial, opening up since $j_{11} > 0$ by $2ahu^* - ahK_1 + 1 < 0$, satisfying $\phi(0) = j_{22} < 0$. Therefore, $\phi(z)$ has a unique root z^* in $(0, \infty)$ such that $\phi(z) < 0$ for $0 < z < z^*$ and $\phi(z) > 0$ for $z > z^*$. Clearly,

$$\begin{aligned} z^* &= \frac{1}{j_{11}} \left(\sqrt{\text{Det}(J|_{E^*})} + \sqrt{\text{Det}(J|_{E^*}) - j_{11}j_{22}} \right) \\ &= \frac{1}{j_{11}} \sqrt{\text{Det}(J|_{E^*})} + \sqrt{\frac{1}{(j_{11})^2} \text{Det}(J|_{E^*}) - \frac{j_{22}}{j_{11}}} \\ &> \sqrt{-\frac{j_{22}}{j_{11}}} > 1. \end{aligned}$$

It is easy to see that z^* also can be rewritten as

$$z^* = \frac{1}{j_{11}} \left(\sqrt{\text{Det}(J|_{E^*})} + \sqrt{-j_{12}j_{21}} \right).$$

Set $\rho = (z^*)^2$. Thus, if $\frac{d_2}{d_1} > \rho$, then $Q(d_1, d_2) > 0$. It follows that $H(d_1, d_2, \mu) = 0$ has two positive roots $0 < \mu^- < \mu^+$. In this case, if $[\mu^-, \mu^+] \cap S_p = \emptyset$, then for all $i \geq 0$, $\text{Det}(A_i) = H(d_1, d_2, \mu_i) > 0$, and hence all roots of $\psi_i(\lambda) = 0$ have negative real parts. Consequently, system (2) is locally asymptotically stable at E^* . While if $(\mu^-, \mu^+) \cap S_p \neq \emptyset$, then there exists $i_0 > 0$ such that $\mu_{i_0} \in (\mu^-, \mu^+)$, which implies that $\text{Det}(A_{i_0}) < 0$, and hence $\psi_{i_0}(\lambda) = 0$ have one positive real root. Thus, E^* is Turing instability.

If $\frac{d_2}{d_1} \in \left(-\frac{j_{22}}{j_{11}}, \rho\right)$, then $d_1j_{22} + d_2j_{11} > 0$ and $Q(d_1, d_2) < 0$. It follows that for all $\mu \geq 0$, $H(d_1, d_2, \mu) > 0$. If $\frac{d_2}{d_1} \leq -\frac{j_{22}}{j_{11}}$, we also have that $H(d_1, d_2, \mu) > 0$ holds for all $\mu \geq 0$. Thus, for each $i \geq 0$, the roots of $\psi_i(\lambda) = 0$ have negative real parts. As a consequence, system (2) is locally uniformly asymptotically stable at E^* . The proof is finished. \square

The following corollary is a direct application of Theorem 2.5. It indicates that the large diffusion rate d_2 of predator or the small diffusion rate d_1 of prey will lead to the occurrence of Turing instability at the positive constant steady state $E^* = (u^*, v^*)$ of (2).

Corollary 1. Assume that (H) holds and $0 < d < r_2 + N_1(u^*)$.

1. There exists $d_2^* > 0$ such that for $d_2 > d_2^*$, the positive constant steady state $E^* = (u^*, v^*)$ of (2) is locally uniformly asymptotically stable if $\frac{j_{11}}{d_1} < \mu_1$; while it is Turing instability if $\frac{j_{11}}{d_1} > \mu_1$.
2. There exists $d_1^* > 0$ such that for $d_1 < d_1^*$, the positive constant steady state $E^* = (u^*, v^*)$ of (2) is Turing instability.

Proof. 1. If d_2 is large enough then $d_1j_{22} + d_2j_{11} > 0$, $Q(d_1, d_2) > 0$, and $0 < \mu^- < \mu^+$. Furthermore,

$$\mu^-(d_1, d_2) \rightarrow 0, \quad \mu^+(d_1, d_2) \rightarrow \frac{j_{11}}{d_1} \quad \text{as } d_2 \rightarrow \infty.$$

Thus, there exists $d_2^* > 0$ such that for $d_2 > d_2^*$, $0 < \mu^- < \mu_1$.

If $\frac{j_{11}}{d_1} < \mu_1$, then $[\mu^-, \mu^+] \cap S_p = \emptyset$, which implies that for all $i \geq 0$, $\text{Det}(A_i) = H(d_1, d_2, \mu_i) > 0$, and hence all roots of $\psi_i(\lambda) = 0$ have negative real parts. Consequently, system (2) is locally uniformly asymptotically stable at E^* .

If $\frac{j_{11}}{d_1} > \mu_1$, then $\mu_1 \in (\mu^-, \mu^+)$, which implies that for $i = 1$, $\text{Det}(A_1) = H(d_1, d_2, \mu_1) < 0$, and hence $\psi_1(\lambda) = 0$ have one positive real root. Thus, E^* is Turing instability.

2. If d_1 is sufficiently small then $d_1 j_{22} + d_2 j_{11} > 0$, $Q(d_1, d_2) > 0$, and $0 < \mu^- < \mu^+$. Furthermore,

$$\mu^-(d_1, d_2) \rightarrow \frac{\text{Det}(J|_{E^*})}{j_{11}d_2}, \quad \mu^+(d_1, d_2) \rightarrow \infty \quad \text{as } d_1 \rightarrow 0.$$

Thus, for sufficiently small d_1 , $(\mu^-, \mu^+) \cap S_p \neq \emptyset$, and hence E^* is Turing instability. \square

2.4. Global stability at positive constant steady states. In this subsection, we establish the global asymptotic stability of the positive constant steady state of system (2), which implies the non-existence of non-constant steady state of (2) regardless of the diffusion coefficients.

Theorem 2.6. (*Global stability*) *The positive constant steady state $E^* = (u^*, v^*)$ of system (2) is globally uniformly asymptotically stable if $K_1 < u^* + \frac{1}{ah}$.*

Proof. Let $(u(x, t), v(x, t))$ be the solution of (2). Take the Lyapunov function

$$E(t) = \int_{\Omega} W(u(x, t), v(x, t)) dx,$$

where

$$W(u, v) = \int \frac{u - u^*}{u} du + \gamma \int \frac{v - v^*}{v} dv,$$

and $\gamma = \frac{1}{e}(1 + ah u^*)$. By simple computations, we have

$$\begin{aligned} \frac{dE}{dt} &= \int_{\Omega} [W_u \frac{\partial u}{\partial t} + W_v \frac{\partial v}{\partial t}] dx \\ &= - \int_{\Omega} \left[d_1 \frac{u^*}{u^2} |\nabla u|^2 + \gamma d_2 \frac{v^*}{v^2} |\nabla v|^2 \right] dx - \frac{\gamma r_2}{K_2} \int_{\Omega} (v - v^*)^2 dx \\ &\quad - \int_{\Omega} \left[\frac{r_1}{K_1} - \frac{a^2 h v^*}{(1 + ah u^*)(1 + ah u)} \right] (u - u^*)^2 dx. \end{aligned}$$

Since $K_1 < u^* + \frac{1}{ah}$ and $v^* = \frac{r_1(K_1 - u^*)(1 + ah u^*)}{a K_1}$, we have that for $x \in \bar{\Omega}$ and $t > 0$,

$$\frac{r_1}{K_1} - \frac{a^2 h v^*}{(1 + ah u^*)(1 + ah u)} \geq \frac{r_1}{K_1} - \frac{a^2 h v^*}{1 + ah u^*} > 0.$$

Thus, applying some standard arguments, together with Theorem 2.1 and Theorem 2.2, we have $(u(x, t), v(x, t)) \rightarrow (u^*, v^*)$ in $[L^\infty(\Omega)]^2$, which implies that (u^*, v^*) attracts all solution of (2). It follows from Theorem 2.4 that the positive constant steady state $E^* = (u^*, v^*)$ of system (2) is globally asymptotically stable. The proof is completed. \square

3. Non-constant positive steady-states. In order to study the stationary pattern of (2) induced by diffusions, in this section we discuss the existence and non-existence of non-constant positive solutions of system (3).

3.1. Bounds for positive steady state. In this subsection we give a priori upper and lower bounds for the positive solutions of (3). To this aim, we recall the following maximum principle [22] and Harnack Inequality [21].

Lemma 3.1. (*Maximum principle*[22]) *Let Ω be a bounded Lipschitz domain in \mathbb{R}^N and $g \in C(\bar{\Omega} \times \mathbb{R})$.*

1. Assume that $w \in C^2(\Omega) \cap C^1(\bar{\Omega})$ and satisfies

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

If $w(x_0) = \max_{x \in \bar{\Omega}} w(x)$, then $g(x_0, w(x_0)) \geq 0$.

2. Assume that $w \in C^2(\Omega) \cap C^1(\bar{\Omega})$ and satisfies

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

If $w(x_0) = \min_{x \in \bar{\Omega}} w(x)$, then $g(x_0, w(x_0)) \leq 0$.

Lemma 3.2. (Harnack Inequality[21]) Let $w \in C^2(\Omega) \cap C^1(\bar{\Omega})$ be a positive solution to $\Delta w(x) + c(x)w(x) = 0$, where $c \in C(\bar{\Omega})$, satisfying zero-flux boundary conditions on $\bar{\Omega}$. Then there exists a positive constant $C = C(\|c\|_\infty, N, \Omega)$, such that $\max_{x \in \bar{\Omega}} w(x) \leq C \min_{x \in \bar{\Omega}} w(x)$.

For convenience, set $\Lambda = (r_1, r_2, K_1, K_2, a, e, h, d)$. The results of bounds for positive solutions of (3) can be stated as follows.

Theorem 3.3. (The bounds of the solutions) Assume that $r_2 < d < r_2 + \frac{eaK_1}{1+ahK_1}$. For any positive solution $(u(x), v(x))$ of system (3),

1. $u(x) \leq K_1$, $v(x) \leq \frac{K_2}{r_2} \left(r_2 - d + \frac{eaK_1}{1+ahK_1} \right)$.
2. for arbitrary fixed positive number \bar{d} , there exists a positive constant $C = C(N, \Omega, \bar{d}, \Lambda)$ such that if $d_1, d_2 \geq \bar{d}$, $u(x), v(x) \geq C$.

Proof. Let $x_0, x_1 \in \bar{\Omega}$ such that $u(x_0) = \max_{x \in \bar{\Omega}} u(x)$ and $v(x_1) = \max_{x \in \bar{\Omega}} v(x)$. By Lemma 3.1, we have from the first equation of (3) that

$$r_1 \left(1 - \frac{u(x_0)}{K_1} \right) - \frac{av(x_0)}{1+ahu(x_0)} \geq 0,$$

which implies $u(x_0) = \max_{x \in \bar{\Omega}} u(x) \leq K_1$. It follows from the second equation of (3) that

$$\Delta v + \frac{v}{d_2} \left[r_2 \left(1 - \frac{v}{K_2} \right) - d + \frac{eaK_1}{1+haK_1} \right] \geq 0.$$

Then, again by Lemma 3.1, we have

$$r_2 \left(1 - \frac{v(x_1)}{K_2} \right) - d + \frac{eaK_1}{1+haK_1} \geq 0,$$

which implies that $v(x_1) \leq \frac{K_2}{r_2} \left(r_2 - d + \frac{eaK_1}{1+ahK_1} \right)$ since $r_2 - d + \frac{eaK_1}{1+ahK_1} > 0$. The first assertion is proved.

Let

$$c_1(x) = \frac{1}{d_1} \left[r_1 \left(1 - \frac{u}{K_1} \right) - \frac{av}{1+ahu} \right],$$

$$c_2(x) = \frac{1}{d_2} \left[r_2 \left(1 - \frac{v}{K_2} \right) - d + \frac{eau}{1+ahu} \right].$$

Clearly,

$$\|c_1(x)\|_\infty \leq \frac{r_1}{\bar{d}}, \quad \|c_2(x)\|_\infty \leq \frac{1}{\bar{d}} \left(r_2 - d + \frac{eaK_1}{1+ahK_1} \right)$$

provided that $d_1, d_2 \geq \tilde{d}$. Take

$$\tilde{C} = \max \left\{ \frac{r_1}{\tilde{d}}, \frac{1}{\tilde{d}} \left(r_2 - d + \frac{eaK_1}{1+ahK_1} \right) \right\}.$$

Then $\|c_1(x)\|_\infty \leq \tilde{C}$, $\|c_2(x)\|_\infty \leq \tilde{C}$, where \tilde{C} depends on $N, \Omega, \tilde{d}, \Lambda$. Thus, in view of Lemma 3.2, there exists a positive constant $C^* = C^*(N, \Omega, \tilde{d}, \Lambda)$ such that the Harnack inequality

$$\max_{x \in \Omega} u(x) \leq C^* \min_{x \in \Omega} u(x), \quad \max_{x \in \Omega} v(x) \leq C^* \min_{x \in \Omega} v(x). \quad (19)$$

holds provided $d_1, d_2 \geq \tilde{d}$.

Now, we verify the lower bounds of $u(x)$ and $v(x)$. On the contrary, suppose that the conclusion is not true, then there exist sequences $\{d_{1i}\}$ and $\{d_{2i}\}$ with $d_{1i}, d_{2i} \geq \tilde{d}$ and the positive solution $(u_i(x), v_i(x))$ of (3) corresponding to $(d_1, d_2) = (d_{1i}, d_{2i})$, such that

$$\max_{x \in \Omega} u_i(x) \rightarrow 0, \quad \text{or} \quad \max_{x \in \Omega} v_i(x) \rightarrow 0 \quad \text{as} \quad i \rightarrow \infty \quad (20)$$

by (19). Note that $(u_i(x), v_i(x))$ satisfies

$$\begin{cases} -d_{1i}\Delta u_i = u_i \left[r_1 \left(1 - \frac{u_i}{K_1} \right) - \frac{av_i}{1+ahu_i} \right], & x \in \Omega, \\ -d_{2i}\Delta v_i = v_i \left[r_2 \left(1 - \frac{v_i}{K_2} \right) - d + \frac{eau_i}{1+ahu_i} \right], & x \in \Omega, \\ \frac{\partial u_i}{\partial \nu} = \frac{\partial v_i}{\partial \nu} = 0, & x \in \partial\Omega. \end{cases}$$

Integrating by parts, we have that, for $i = 1, 2, \dots$,

$$\begin{cases} \int_{\Omega} \left[r_1 \left(1 - \frac{u_i}{K_1} \right) - \frac{av_i}{1+ahu_i} \right] u_i dx = 0, \\ \int_{\Omega} \left[r_2 \left(1 - \frac{v_i}{K_2} \right) - d + \frac{eau_i}{1+ahu_i} \right] v_i dx = 0. \end{cases} \quad (21)$$

By the regularity theory for elliptic equations [11], there exists a subsequence of $\{(u_i, v_i)\}_{i=1}^\infty$, which we shall still denote by $\{(u_i, v_i)\}_{i=1}^\infty$, and two non-negative functions $\tilde{u}, \tilde{v} \in C^2(\Omega)$, such that $(u_i, v_i) \rightarrow (\tilde{u}, \tilde{v})$ in $[C^2(\Omega)]^2$ as $i \rightarrow \infty$. By (20), we know that $\tilde{u} \equiv 0$ or $\tilde{v} \equiv 0$. Also, $\tilde{u} \leq K_1$. Furthermore, since u_i, v_i satisfy (19), so do \tilde{u}, \tilde{v} .

Let $i \rightarrow \infty$ in (21), we obtain that

$$\begin{cases} \int_{\Omega} \left[r_1 \left(1 - \frac{\tilde{u}}{K_1} \right) - \frac{a\tilde{v}}{1+a\tilde{h}\tilde{u}} \right] \tilde{u} dx = 0, \\ \int_{\Omega} \left[r_2 \left(1 - \frac{\tilde{v}}{K_2} \right) - d + \frac{ea\tilde{u}}{1+a\tilde{h}\tilde{u}} \right] \tilde{v} dx = 0. \end{cases} \quad (22)$$

Now, we distinguish three cases to finish the proof.

Case 1. $\tilde{u} \equiv 0$ and $\tilde{v} \not\equiv 0$. From the second inequality of (19), $\tilde{v} > 0$ on $\bar{\Omega}$. Then we have $\int_{\Omega} \left[r_2 \left(1 - \frac{\tilde{v}}{K_2} \right) - d \right] \tilde{v} dx < 0$ since $r_2 < d$, which contradicts the second equation of (22).

Case 2. $\tilde{v} \equiv 0$ and $\tilde{u} \not\equiv 0$. From the first inequality of (19), $0 < \tilde{u} \leq K_1$ on $\bar{\Omega}$. It follows from the first equation of (22) that $\tilde{u} \equiv K_1$ on $\bar{\Omega}$. By the second equation of (21), there exists $x_i^* \in \bar{\Omega}$, assuming $x_i^* \rightarrow x_0^* \in \bar{\Omega}$ as $i \rightarrow \infty$, such that

$$r_2 \left(1 - \frac{v_i(x_i^*)}{K_2} \right) - d + \frac{eau_i(x_i^*)}{1+ahu_i(x_i^*)} = 0. \quad (23)$$

Let $i \rightarrow \infty$ in (23), we have $r_2 - d + \frac{eaK_1}{1+ahK_1} = 0$, which contradicts the assumption that $d < r_2 + \frac{eaK_1}{1+ahK_1}$.

Case 3. $\tilde{v} \equiv 0$ and $\tilde{u} \equiv 0$. Similar to the arguments above, there exists $x_i^* \in \tilde{\Omega}$, assuming $x_i^* \rightarrow x_0^* \in \tilde{\Omega}$ as $i \rightarrow \infty$, such that (23) holds. Let $i \rightarrow \infty$ in (23), we have $r_2 - d = 0$, which contradicts the assumption that $r_2 < d$. The proof is completed. \square

3.2. Non-existence of non-constant positive steady states. From Theorem 2.3, we know that if either $d < r_2$ along with other suitable conditions or $d > r_2 + \frac{eaK_1}{1+haK_1}$, (3) has no non-constant positive solution regardless of diffusion coefficients. In this subsection, we consider the case $r_2 < d < r_2 + \frac{eaK_1}{1+haK_1}$ and establish the non-existence result for suitable ranges of diffusive rates d_1 and d_2 .

Theorem 3.4. (Non-existence of non-constant steady states) *Let μ_1 be the smallest positive eigenvalue of the operator $-\Delta$ on Ω with zero-flux boundary condition. Assume that $r_2 < d < r_2 + \frac{eaK_1}{1+ahK_1}$ and $d_2 > \frac{1}{\mu_1} \left(r_2 - d + \frac{eaK_1}{1+ahK_1} \right)$. Then there exists a positive constants $D_1 = D_1(N, \Omega, \Lambda)$ such that (3) has no positive non-constant steady-state provided that $d_1 \geq D_1$.*

Proof. Let $(u(x), v(x))$ be any positive solution of (3) and denote $\bar{g} = |\Omega|^{-1} \int_{\Omega} g dx$. By multiplying the first equation of (3) by $(u - \bar{u})$ and integrating over Ω , we have from Theorem 3.3 that

$$\begin{aligned} d_1 \int_{\Omega} |\nabla(u - \bar{u})|^2 dx &= \int_{\Omega} (u - \bar{u})u \left[r_1 - \frac{r_1}{K_1}u - \frac{av}{1+ahu} \right] dx \\ &= \int_{\Omega} (u - \bar{u})^2 \left[r_1 - \frac{r_1}{K_1}(u + \bar{u}) - \frac{av}{(1+ah\bar{u})(1+ahu)} \right] dx \\ &\quad - \frac{a\bar{u}}{1+ah\bar{u}} \int_{\Omega} (u - \bar{u})(v - \bar{v}) dx \\ &\leq r_1 \int_{\Omega} (u - \bar{u})^2 dx + \tilde{L}_1 \int_{\Omega} |u - \bar{u}| |v - \bar{v}| dx, \end{aligned}$$

where \tilde{L}_1 is a positive constant depending on N, Ω, Λ . Similarly, multiplying the second equation of (3) by $(v - \bar{v})$ and integrating over Ω , we have from Theorem 3.3 that

$$\begin{aligned} d_2 \int_{\Omega} |\nabla(v - \bar{v})|^2 dx &= \int_{\Omega} (v - \bar{v})v \left[r_2 - \frac{r_2}{K_2}v - d + \frac{eau}{1+ahu} \right] dx \\ &= \int_{\Omega} (v - \bar{v})^2 \left[r_2 - \frac{r_2}{K_2}(v + \bar{v}) - d + \frac{eau}{1+ah\bar{u}} \right] dx \\ &\quad + \int_{\Omega} \frac{eau}{(1+ah\bar{u})(1+ahu)} (u - \bar{u})(v - \bar{v}) dx \\ &\leq \left(r_2 - d + \frac{eaK_1}{1+ahK_1} \right) \int_{\Omega} (v - \bar{v})^2 dx + \tilde{L}_2 \int_{\Omega} |u - \bar{u}| |v - \bar{v}| dx, \end{aligned}$$

where the positive constant \tilde{L}_2 depending on N, Ω, Λ . Thus, we obtain

$$\begin{aligned} &d_1 \int_{\Omega} |\nabla(u - \bar{u})|^2 dx + d_2 \int_{\Omega} |\nabla(v - \bar{v})|^2 dx \\ &\leq \int_{\Omega} \left[r_1(u - \bar{u})^2 + \left(r_2 - d + \frac{eaK_1}{1+ahK_1} \right) (v - \bar{v})^2 \right] dx + 2L \int_{\Omega} |u - \bar{u}| |v - \bar{v}| dx, \end{aligned}$$

where $L = \frac{\tilde{L}_1 + \tilde{L}_2}{2}$. Applying the well-known ϵ -Young Inequality, we obtain

$$\begin{aligned} &d_1 \int_{\Omega} |\nabla(u - \bar{u})|^2 dx + d_2 \int_{\Omega} |\nabla(v - \bar{v})|^2 dx \\ &\leq \int_{\Omega} \left(r_1 + \frac{L}{\epsilon} \right) (u - \bar{u})^2 dx + \int_{\Omega} \left(r_2 - d + \frac{eaK_1}{1+ahK_1} + \epsilon L \right) (v - \bar{v})^2 dx, \end{aligned}$$

where ϵ is an arbitrary positive constant. It follows from the well-known Poincaré inequality that

$$\begin{aligned} & d_1 \int_{\Omega} |\nabla(u - \bar{u})|^2 dx + d_2 \int_{\Omega} |\nabla(v - \bar{v})|^2 dx \\ & \leq \frac{1}{\mu_1} \left(\left(r_1 + \frac{L}{\epsilon} \right) \int_{\Omega} |\nabla(u - \bar{u})|^2 dx + \left(r_2 - d + \frac{eaK_1}{1+ahK_1} + \epsilon L \right) \int_{\Omega} |\nabla(v - \bar{v})|^2 dx \right). \end{aligned}$$

By the assumption $d_2\mu_1 > r_2 - d + \frac{eaK_1}{1+ahK_1}$, we can choose $\epsilon > 0$ small sufficiently such that $d_2\mu_1 \geq r_2 - d + \frac{eaK_1}{1+ahK_1} + \epsilon L$. Taking $D_1 > \frac{1}{\mu_1} \left(r_1 + \frac{L}{\epsilon} \right)$, then one can conclude that $u \equiv \bar{u}, v \equiv \bar{v}$ if $d_1 \geq D_1$. The proof is completed. \square

3.3. Existence of non-constant positive steady states. In this subsection, we show the existence of non-constant positive solutions of system (3). From Theorem 2.5, we know that the large ratio of d_2 to d_1 along with other suitable conditions will lead to the occurrence of Turing instability at a constant positive steady state of (2). The existence results of this subsection indicate that the occurrence of Turing instability at a positive constant steady state of (2) would imply the existence of non-constant positive steady state bifurcating from the constant solution.

Let \mathbf{X} be the space defined in (7). Define

$$\mathbf{X}^+ = \{(u, v) \in \mathbf{X} | u > 0, v > 0 \text{ on } \bar{\Omega}\}.$$

System (3) can be written as follows

$$\begin{cases} -D\Delta \mathbf{w} = F(\mathbf{w}), & \mathbf{w} \in \mathbf{X}^+, \\ \partial_\nu \mathbf{w} = \mathbf{0}, & \text{on } \partial\Omega, \end{cases} \quad (24)$$

where $D = \text{diag}(d_1, d_2)$ and

$$F(\mathbf{w}) = \begin{pmatrix} r_1 u (1 - uK_1) - \frac{auv}{1+ahu} \\ r_2 v (1 - vK_2) - dv + \frac{eavv}{1+ahv} \end{pmatrix}.$$

It is easy to see that \mathbf{w} is a positive solution of (24) if and only if \mathbf{w} satisfies

$$G(\mathbf{w}) := \mathbf{w} - (\mathbf{I} - \Delta)^{-1}(D^{-1}F(\mathbf{w}) + \mathbf{w}) = \mathbf{0}, \quad \mathbf{w} \in \mathbf{X}^+,$$

where $(\mathbf{I} - \Delta)^{-1}$ is the inverse of $\mathbf{I} - \Delta$ subject to the zero-flux boundary condition, D^{-1} is the inverse of D and $G(\cdot)$ is a compact perturbation of the identity operator.

Denote $\mathbf{w}^* = E^*(u^*, v^*)$, which is the constant positive steady state of (24). We shall calculate the index of $\text{index}(G(\cdot), \mathbf{w}^*)$ by the similar arguments in [26, 3].

Notice that

$$G_{\mathbf{w}}(\mathbf{w}^*) = \mathbf{I} - (\mathbf{I} - \Delta)^{-1}(D^{-1}F_{\mathbf{w}}(\mathbf{w}^*) + \mathbf{I}),$$

where $F_{\mathbf{w}}(\mathbf{w}^*) = (j_{mn})_{2 \times 2}$ and $j_{mn}(m, n = 1, 2)$ is given in (9). We investigate the eigenvalues of the problem

$$G_{\mathbf{w}}(\mathbf{w}^*)\Psi + \lambda\Psi = \mathbf{0}, \quad \Psi \neq \mathbf{0}, \quad (25)$$

where $\Psi = (\Psi_1, \Psi_2)^T$. Clearly, (25) can be rewritten as

$$\begin{cases} \Delta\Psi + \frac{1}{\lambda+1}(D^{-1}F_{\mathbf{w}}(\mathbf{w}^*) - \lambda\mathbf{I})\Psi = \mathbf{0}, & x \in \Omega, \\ \partial_{\mathbf{n}}\Psi = \mathbf{0}, & x \in \partial\Omega, \\ \Psi \neq \mathbf{0}. \end{cases} \quad (26)$$

Thus, by a simple calculation, we know that λ is an eigenvalue of (25) if and only if λ is an eigenvalue of the matrix $(\mu_i + 1)^{-1}(D^{-1}F_{\mathbf{w}}(\mathbf{w}^*) - \mu_i\mathbf{I})$ for $i \geq 0$. Therefore,

$G_{\mathbf{w}}(\mathbf{w}^*)$ is invertible if and only if the matrix $\mathcal{M}_i := \mu_i \mathbf{I} - D^{-1}F_{\mathbf{w}}(\mathbf{w}^*)$ is invertible for $i \geq 0$. Note

$$\mathcal{M}_i = \mu_i \mathbf{I} - D^{-1}F_{\mathbf{w}}(\mathbf{w}^*) = \begin{pmatrix} \mu_i - \frac{1}{d_1}j_{11} & -\frac{1}{d_1}j_{12} \\ -\frac{1}{d_2}j_{21} & \mu_i - \frac{1}{d_2}j_{22} \end{pmatrix}.$$

A straightforward computation yields

$$\begin{aligned} \text{Det}(\mathcal{M}_i) &= \frac{1}{d_1 d_2} (d_1 d_2 \mu_i^2 - (d_1 j_{22} + d_2 j_{11}) \mu_i + j_{11} j_{22} - j_{12} j_{21}) \\ &:= \frac{1}{d_1 d_2} H(d_1, d_2, \mu_i). \end{aligned} \tag{27}$$

If $Q(d_1, d_2) = (d_1 j_{22} + d_2 j_{11})^2 - 4d_1 d_2 (j_{11} j_{22} - j_{12} j_{21}) > 0$, then the equation $H(d_1, d_2, \mu) = 0$ has two real roots μ^\pm given by (12), i.e.,

$$\mu^\pm(d_1, d_2) = \frac{1}{2d_1 d_2} \left(d_1 j_{22} + d_2 j_{11} \pm \sqrt{\Delta} \right).$$

Recall

$$\begin{aligned} B &:= B(d_1, d_2) = \{ \mu : \mu \geq 0, \mu^-(d_1, d_2) < \mu < \mu^+(d_1, d_2) \}, \\ S_p &= \{ \mu_0, \mu_1, \mu_2, \dots \}. \end{aligned}$$

Denote that $m(\mu_i)$ is the multiplicity of μ_i . In order to compute $\text{index}(G(\cdot), \mathbf{w}^*)$, we introduce the following conclusion by Pang and Wang[26]:

Lemma 3.5. *Suppose $H(d_1, d_2, \mu_i) \neq 0$ for all $\mu_i \in S_p$. Then $\text{index}(\mathbf{G}(\cdot), \mathbf{w}^*) = (-1)^\sigma$, where $\sigma = \sum_{\mu_i \in B \cap S_p} m(\mu_i)$ if $B \cap S_p \neq \emptyset$ and $\sigma = 0$ if $B \cap S_p = \emptyset$. In particular, if $H(d_1, d_2, \mu) > 0$ for all $\mu \geq 0$, then $\sigma = 0$.*

In order to state our main results of this subsection, we make the following assumption

$$\left\{ \begin{aligned} &\frac{r_1 r_2}{K_1 K_2} (2ah u^* - ah K_1 + 1) + \frac{ea^2}{(1+ah u^*)^2} > 0, \\ &ah K_1 > 1, r_2 < d < r_2 + \frac{ea(K_1 - \frac{1}{ah})}{2+ah(K_1 - \frac{1}{ah})} - \frac{r_1 r_2 (1+ah K_1)^2}{4a^2 h K_1 K_2}. \end{aligned} \right. \tag{H*}$$

Theorem 3.6. *(Existence of non-constant steady state) Assume that (H*) holds and ρ is defined in (18). Then for $\frac{d_2}{d_1} \in (\rho, +\infty)$, if $\mu^- \in (\mu_i, \mu_{i+1})$ and $\mu^+ \in (\mu_j, \mu_{j+1})$ for some $0 \leq i < j$, and $\sum_{k=i+1}^j m(\mu_k)$ is odd, system (3) has at least one non-constant positive solution.*

Proof. First, by the inequalities of the second line of Condition (H*), we know that system (3) has a unique positive constant steady state $\mathbf{w}^* = (u^*, v^*)$ with $u^* < \frac{1}{2} (K_1 - \frac{1}{ah})$. In fact, (u^*, v^*) is a positive constant steady state of (3) if and only if u^* is a positive positive intercept of $f(u)$ and $g(u)$, where

$$f(u) = \frac{r_1(K_1 - u)(1 + ah u)}{a K_1}, \quad g(u) = \frac{K_2}{r_2} \left[\frac{e a u}{1 + ah u} + r_2 - d \right].$$

Clearly, $f(u)$ is a degree two polynomial, opening down, with symmetry axis $u = \tilde{u} = \frac{1}{2}(K_1 - \frac{1}{ah})$ and two roots $-\frac{1}{ah}$ and K_1 , and $f(0) = \frac{r_1}{a} > 0, f(\tilde{u}) = \frac{r_1(1+ah K_1)^2}{4a^2 h K_1}$; $g(u)$ is an increasing function with a unique root $u_0 = \frac{d-r_2}{a[e-h(d-r_2)]}$, and $g(0) =$

$\frac{K_2(r_2-d)}{r_2}$, $\lim_{u \rightarrow -\frac{1}{ah}^+} g(u) = -\infty$, $\lim_{u \rightarrow \infty} g(u) = \frac{K_2}{r_2} \left(\frac{e}{h} + r_2 - d \right)$. If $0 < u_0 < \tilde{u}$ and $f(\tilde{u}) < g(\tilde{u})$, which is equivalent to

$$ahK_1 > 1, r_2 < d < r_2 + \frac{ea(K_1 - \frac{1}{ah})}{2 + ah(K_1 - \frac{1}{ah})} - \frac{r_1r_2(1 + ahK_1)^2}{4a^2hK_1K_2},$$

then $f(u)$ and $g(u)$ have a unique positive intercept u^* . Hence, (3) has a unique positive constant steady state $\mathbf{w}^* = (u^*, v^*)$, $v^* = f(u^*)$. Clearly, $u^* < \frac{1}{2} (K_1 - \frac{1}{ah})$.

The first inequality of Condition (H*) is equivalent to $H(d_1, d_2, 0) = \text{Det}F_{\mathbf{w}}(\mathbf{w}^*) = j_{11}j_{22} - j_{12}j_{21} > 0$. From the proof of Theorem 2.5, we know that if $\frac{d_2}{d_1} > \rho$, then $d_1j_{22} + d_2j_{11} > 0$ and the discriminant

$$Q(d_1, d_2) = (d_1j_{22} + d_2j_{11})^2 - 4d_1d_2(j_{11}j_{22} - j_{12}j_{21}) > 0.$$

Therefore, $H(d_1, d_2, \mu) = 0$ has two positive roots $0 < \mu^- < \mu^+$. By our assumptions, $\mu^- \in (\mu_i, \mu_{i+1})$ and $\mu^+ \in (\mu_j, \mu_{j+1})$ for some $0 \leq i < j$.

Now, on the contrary, we suppose that system (3) has no non-constant positive solution. Then Theorem 3.4 implies that we can choose d_1^* and d_2^* satisfying $d_1^* > d_1, d_2^* > d_2$ such that

- (i) system (3) with the pare of diffusive coefficient (d_1^*, d_2^*) has no non-constant solutions;
- (ii) $H(d_1^*, d_2^*, \mu) > 0$ for all $\mu \geq 0$.

For $\tau \in [0, 1]$, we define

$$D(\tau) = \begin{pmatrix} \tau d_1 + (1 - \tau)d_1^* & 0 \\ 0 & \tau d_2 + (1 - \tau)d_2^* \end{pmatrix}$$

and consider the problem

$$\begin{cases} -\Delta \mathbf{w} = D^{-1}(\tau)F(\mathbf{w}), & x \in \Omega, \\ \partial_n \mathbf{w} = 0, & x \in \partial\Omega, \end{cases} \tag{28}$$

Clearly, $\mathbf{w}^* = (u^*, v^*)$ is the unique positive constant solution of (28). For any $\tau \in [0, 1]$, \mathbf{w} is a non-constant positive solution of (28) if and only if \mathbf{w} satisfies

$$G^*(\mathbf{w}; \tau) := \mathbf{w} - (\mathbf{I} - \Delta)^{-1}(D^{-1}(\tau)F(\mathbf{w}) + \mathbf{w}) = 0, \quad \mathbf{w} \in \mathbf{X}^+.$$

By Theorem 3.3, there exists $\underline{C} = \underline{C}(d_1, d_2, d_1^*, d_2^*, N, \Omega, \Lambda)$ and $\overline{C} = \overline{C}(\Lambda)$ such that for all $\tau \in [0, 1]$ the positive solutions of (28) satisfy $\underline{C} < u(x), v(x) < \overline{C}$ on $\overline{\Omega}$. Set

$$\mathcal{B} = \{\mathbf{w} \in \mathbf{X} | \underline{C} < u(x), v(x) < \overline{C} \text{ on } \overline{\Omega}\}.$$

Then, $G^*(\mathbf{w}; \tau) \neq 0$, for all $\mathbf{w} \in \partial\mathcal{B}$ and $\tau \in [0, 1]$, and the Leray-Schauder topological degree $\text{deg}(G^*(\cdot; \tau), \mathcal{B}, 0)$ is well defined since $(\mathbf{I} - \Delta)^{-1}(D^{-1}(\tau)F(\mathbf{w}) + \mathbf{w})$ is compact. From the homotopy invariance of Leray-Schauder degree, we deduce

$$\text{deg}(G^*(\cdot; 0), \mathcal{B}, 0) = \text{deg}(G^*(\cdot; 1), \mathcal{B}, 0). \tag{29}$$

When $\tau = 1$, $G^*(\mathbf{w}; 1) = G(\mathbf{w})$, the equation $G^*(\mathbf{w}; 1) = 0$ has no other positive solutions in \mathcal{B} except the constant one \mathbf{w}^* . In view of $\mu^- \in (\mu_i, \mu_{i+1})$ and $\mu^+ \in (\mu_j, \mu_{j+1})$, we have $B(d_1, d_2) \cap S_p = \{\mu_{i+1}, \mu_{i+2}, \dots, \mu_j\}$ and $\sigma = \sum_{\mu_i \in B \cap S_p} m(\mu_i)$ is

odd. Thus, we have from Lemma 3.5 that

$$\text{deg}(G^*(\cdot; 1), \mathcal{B}, 0) = \text{index}(G(\cdot), \mathbf{w}^*) = (-1)^\sigma = -1. \tag{30}$$

When $\tau = 0$, we know, from the choice of (d_1^*, d_2^*) and (i) above, that the equation $G^*(\mathbf{w}; 0) = 0$ has the unique positive solution \mathbf{w}^* in \mathcal{B} . Also, (ii) above yields that

$B(d_1^*, d_2^*) \cap S_p = \emptyset$ which implies that $\sigma = 0$ in this case. Thus, we have from Lemma 3.5 that

$$\deg(G^*(\cdot; 0), \mathcal{B}, 0) = \text{index}(G^*(\cdot; 0), \mathbf{w}^*) = (-1)^\sigma = 1. \tag{31}$$

Thus, from (29)-(31), we get a contradiction. Therefore, system (3) has at least one non-constant positive solution. The proof is completed. \square

From the proofs of Theorem 3.6 and 1, we have the following corollary.

Corollary 2. *Assume that (H^*) holds.*

1. *If $\frac{j_{11}}{d_1} \in (\mu_j, \mu_{j+1})$ for some $j \geq 1$, and $\sum_{i=1}^j m(\mu_i)$ is odd, then there exists $d_2^* > 0$ such that system (3) has at least one non-constant positive solution if $d_2 > d_2^*$.*
2. *If $\frac{\text{Det}(J|_{E^*})}{j_{11}d_2} \notin S_p$, and all $\mu_i, i = 0, 1, 2, \dots$, are simple, then there exists a sequence of intervals*

$$\left\{ (d_1^-(j), d_1^+(j)) \right\}_{j=1}^\infty, \quad \text{with } d_1^+(j+1) < d_1^-(j), \quad d_1^-(j) \searrow 0^+ \quad \text{as } j \rightarrow \infty,$$

such that system (3) has at least one non-constant positive solution for every $d_1 \in (d_1^-(j), d_1^+(j))$.

4. Turing pattern formation. In Subsection 2.2, we obtain the conditions of Turing instability of the solutions to model (2). In this section, we show the Turing patterns caused by diffusion. Via numerical simulation, we find that the model dynamics exhibits spatiotemporal Turing complexity of pattern formation, including spots, strips and spots-stripes Turing patterns.

We take a discrete spatial domain of size 100×100 (the lattice size) with the lattice constant 0.2. The numerical integration of model (2) is performed by using a finite difference approximation for the spatial derivatives and an explicit Euler method for the time integration with a time step size of 0.01. All our numerical simulations employ the zero-flux boundary conditions. The initial condition is always a small amplitude random perturbation around the positive constant steady state solution $E^* = (u^*, v^*)$ of model (2). In numerical simulation, it is observed that the distributions of predator and prey are always of the same type. So, we only show our results of pattern formation to the distribution of prey u . We have taken some snapshots with red (blue) corresponding to the high (low) value of prey u .

In the numerical simulations, the following parameters are fixed as

$$r_1 = 2, r_2 = 0.2, K_1 = 8, K_2 = 0.18, a = 2, d = 0.35, h = 0.5, e = 2. \tag{32}$$

Then, model (1) has a unique positive equilibrium $E^* = (u^*, v^*) = (1.5934, 2.0768)$ and Condition (H) holds. In fact,

$$\begin{cases} \frac{r_1 r_2}{K_1 K_2} (2ahu^* - ahK_1 + 1) + \frac{ea^2}{(1+ahu^*)^2} = 0.1302 > 0, \\ 2ahu^* - ahK_1 + 1 = -3.8132 < 0. \end{cases}$$

Also, we have

$$N_1(u^*) = \frac{u^*}{1 + ah u^*} \left[ea + \frac{r_1}{K_1} (2ahu^* - ahK_1 + 1) \right] = 1.8719,$$

and $0.35 = d < N_1(u^*) + r_2 = 2.0719$. The critical value ρ of $\frac{d_2}{d_1}$ can be get by

$$\rho = \frac{1}{(j_{11})^2} \left(\sqrt{\text{Det}(J|_{E^*})} + \sqrt{-j_{12}j_{21}} \right)^2 = 7.8355.$$

Now, we consider the pattern formation on the effect of the varied $\frac{d_2}{d_1}$. Setting $d_1 = 0.028$ fixed.

First, we take $d_2 = 0.226$. Then $\frac{d_2}{d_1} = 8.0714 > \rho = 7.8355$. From Theorem 2.5, the positive constant steady state solution $E^* = (1.5934, 2.0768)$ of model (2) is Turing instability if $B(d_1, d_2) \cap S_p \neq \emptyset$, where $B(d_1, d_2) = \{\mu : \mu \geq 0, \mu^-(d_1, d_2) < \mu < \mu^+(d_1, d_2)\}$ and μ^-, μ^+ are the roots of the quadratic polynomial (10). For $(d_1, d_2) = (0.028, 0.226)$, we have

$$\mu^- = 3.8018, \mu^+ = 6.9054.$$

It is well known that the eigenvalue problem

$$\begin{cases} -\Delta\psi = \lambda\psi, (x, y) \in \Omega = (0, l\pi) \times (0, k\pi), \\ \frac{\partial\psi}{\partial n} = 0 \end{cases}$$

has eigenvalues $\lambda_{n,m} = \frac{n^2}{l^2} + \frac{m^2}{k^2}, m, n = 0, 1, 2, \dots$. From the choose of spatial domain, it is clear that $B(d_1, d_2) \cap S_p \neq \emptyset$. Thus, Theorem 2.5 implies that $E^* = (1.5934, 2.0768)$ is Turing instability and we obtain the stationary spots pattern, c.f., Fig.1.

In Fig.1, we show the time process of hot spots pattern formation of the prey u at $t = 0; 1000; 5000$ for the parameters as (32) and $(d_1, d_2) = (0.028, 0.226)$. It indicates that the prey population are driven by predators to a very high level in hot spots regions surrounded by areas of low prey densities.

Now, taking $d_2 = 0.27$ and keeping other parameters unchange. In this case, $\mu^- = 2.1499, \mu^+ = 10.2213$ and $B(d_1, d_2) \cap S_p \neq \emptyset$. By Theorem 2.5, Turing instability emerges. We obtain the stationary stripes pattern, c.f., Fig.2.

At last, we take $d_2 = 0.45$ and keep other parameters unchange. In this case, $\mu^- = 0.8846, \mu^+ = 14.9053$, system (2) present stationary spots-stripes pattern, c.f., Fig.3.

5. Conclusions. In this paper, we study the spatiotemporal dynamics of the reaction-diffusion predator-prey model with predator being generalist under the homogeneous Neumann boundary condition. Some basic dynamics including permanence(c.f., Theorem 2.2), non-persistnce(c.f., Theorem 2.3), the local and global stability of the nonnegative steady states of the model (2)(c.f., Theorem 2.4 and 2.6, respectively) are investigated. The conditions of Turing instability at positive constant steady states due to diffusion are given (c.f., Theorem 2.4, 2.5, and Corollary 1, respectively).

Under suitable conditions, we obtain a critical value ρ of Turing bifurcation such that if $\frac{d_2}{d_1} > \rho$, then Turing bifurcation would emerge at a positive steady state of (2); while if $\frac{d_2}{d_1} < \rho$, both reaction-diffusion system (2) and ODE system (1) are stability at the positive steady state. In particular, the large diffusion rate d_2 of predator or the small diffusion rate d_1 of prey will lead to the occurrence of Turing instability at the positive constant steady state of (2).

From Theorem 2.3 and 3.4, we know that system (2) has no positive non-constant steady state if one of cases

(1) $d > r_2 + \frac{eaK_1}{1+haK_1}$, in this case species v goes extinct regardless of the diffusion

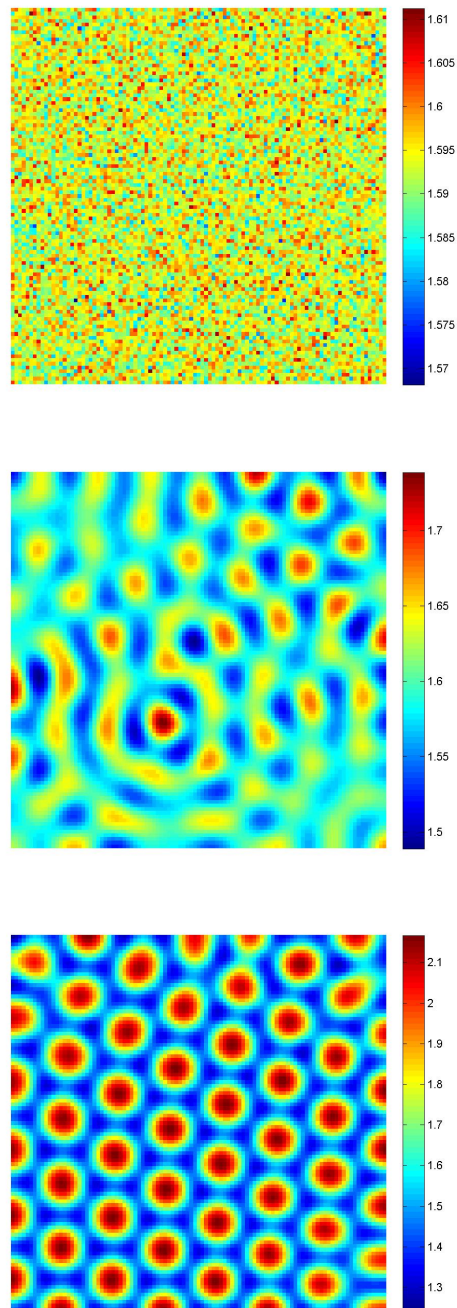


FIGURE 1. Stationary hot spots pattern in model (2). The parameter values are taken as (32) and $(d_1, d_2) = (0.028, 0.226)$. The zero-flux boundary condition is used and initial condition is small perturbation around the homogeneous steady-state $E^* = (1.5934, 2.0768)$.

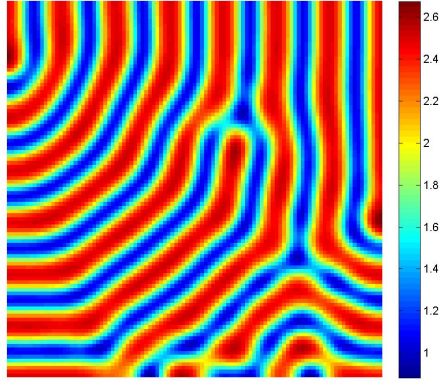


FIGURE 2. Stationary stripes pattern in model (2). The parameter values are taken as (32) and $(d_1, d_2) = (0.028, 0.27)$. The zero-flux boundary condition is used and initial condition is small perturbation around the homogeneous steady-state $E^* = (1.5934, 2.0768)$.

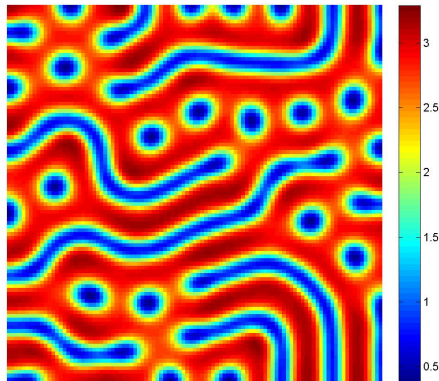


FIGURE 3. Stationary spots-stripes pattern in model (2). The parameter values are taken as (32) and $(d_1, d_2) = (0.028, 0.45)$. The zero-flux boundary condition is used and initial condition is small perturbation around the homogeneous steady-state $E^* = (1.5934, 2.0768)$.

coefficients;

(2) $d < r_2$ and either (i) $ahK_1 \leq 1$ and $\frac{r_1}{a} < \frac{K_2}{r_2}(r_2 - d)$, or (ii) $ahK_1 > 1$ and $\frac{r_1(1+ahK_1)^2}{4a^2hK_1} < \frac{K_2}{r_2}(r_2 - d)$, in this case species u goes extinct regardless of the diffusion coefficients;

(3) $r_2 < d < r_2 + \frac{eaK_1}{1+haK_1}$, $d_2 > \frac{1}{\mu_1} \left(r_2 - d + \frac{eaK_1}{1+haK_1} \right)$, and d_1 is large enough, which implies $\frac{d_2}{d_1}$ is small enough.

Thus, in order to guarantee the existence of positive non-constant steady state, it

is necessary that $r_2 < d < r_2 + \frac{eaK_1}{1+haK_1}$ and $\frac{d_2}{d_1}$ is large enough. In Theorem 3.6 and Corollary 2, this case is discussed under suitable conditions. These results indicate that the occurrence of Turing instability at a positive constant steady state of (2), along with other suitable conditions, implies the existence of non-constant positive steady state bifurcating from the constant solution.

By the numerical method, model (2) takes on some different stationary Turing patterns. For fixed $d_1 = 0.028$, as d_2 increases (i.e., as the ratio $\frac{d_2}{d_1}$ of diffusions of predator to prey increases), Turing patterns of model (2) change from spots pattern (i.e., Fig.1), stripes pattern (i.e., Fig.2) into spots-stripes pattern (i.e., Fig.3). It indicates that the pattern formation of the model (2) is rich and complex.

Acknowledgments. The research of J. Yu is supported by NSF of China (11631005) and PCSIRT of China (IRT1226). The research of D. Bai is partially supported by NSF of China (11771104). The research of Y. Kang is partially supported by NSF-DMS (1313312&1716802), NSF-IOS/DMS (1558127) and The James S. McDonnell Foundation 21st Century Science Initiative in Studying Complex Systems Scholar Award (220020472).

REFERENCES

- [1] J. Blat and K. J. Brown, [Global bifurcation of positive solutions in some systems of elliptic equation](#), *SIAM J. Math. Anal.*, **17** (1986), 1339–1353.
- [2] J. L. Brown, V. Morales and K. Summers, [Tactical reproductive parasitism via larval cannibalism in Peruvian poison frogs](#), *Biol. Lett.*, **5** (2009), 148–151.
- [3] Y. L. Cai, M. Banerjee, Y. Kang and W. M. Wang, [Spatiotemporal complexity in a predator-prey model with weak Allee effects](#), *Math. Biosci. Eng.*, **11** (2014), 1247–1274.
- [4] Y. L. Cai, Z. J. Gui, X. B. Zhang, H. B. Shi and W. M. Wang, [Bifurcations and pattern formation in a predator-prey model](#), *Internat. J. Bifur. Chaos Appl. Sci. Engrg.*, **28** (2018), 1850140, 17 pp.
- [5] S. Chakraborty, [The influence of generalist predators in spatially extended predator-prey systems](#), *Ecological Complexity*, **23** (2015), 50–60.
- [6] D. W. Crowder and W. E. Snyder, [Eating their way to the top? Mechanisms underlying the success of invasive generalist predators](#), *Biol. Invas.*, **12** (2010), 2857–2876.
- [7] Y. H. Du and J. P. Shi, [Allee effect and bistability in a spatially heterogeneous predator-prey model](#), *Tran. Amer. Math. Soc.*, **359** (2007), 4557–4593.
- [8] Y. H. Du and J. P. Shi, [A diffusive predator-prey model with a protection zone](#), *J. Differential Equations*, **229** (2006), 63–91.
- [9] A. Erbach, F. Lutscher and G. Seo, [Bistability and limit cycles in generalist predator-prey dynamics](#), *Ecological Complexity*, **14** (2014), 48–55.
- [10] Y.-H. Fan and W.-T. Li, [Global asymptotic stability of a ratio-dependent predator-prey system with diffusion](#), *J. Comput. Appl. Math.*, **188** (2006), 205–227.
- [11] D. Gilbarg and N. S. Trudinger, *Elliptic Partial Differential Equations of Second Order*, Second edition, Grundlehren der Mathematischen Wissenschaften, 224. Springer-Verlag, Berlin, 1983.
- [12] R. J. Han and B. X. Dai, [Spatiotemporal pattern formation and selection induced by nonlinear cross-diffusion in a toxic-phytoplankton-zooplankton model with Allee effect](#), *Nonlinear Anal. Real World Appl.*, **45** (2019), 822–853.
- [13] I. Hanski, L. Hansson and H. Henttonen, [Specialist predators, generalist predators, and the microtine rodent cycle](#), *J. Anim. Ecol.*, **60** (1991), 353–367.
- [14] M. P. Hassell, *The Dynamics of Arthropod Predator-Prey Systems*, Monographs in Population Biology, 13. Princeton University Press, Princeton, N.J., 1978..
- [15] X. He and S. N. Zheng, [Protection zone in a diffusive predator-prey model with Beddington-DeAngelis functional response](#), *J. Math. Biol.*, **75** (2017), 239–257.
- [16] D. Henry, *Geometric Theory of Semilinear Parabolic Equations*, Lecture Notes in Mathematics, 840. Springer-Verlag, Berlin-New York, 1981.

- [17] T. Kadota and K. Kuto, [Positive steady states for a prey-predator model with some nonlinear diffusion terms](#), *J. Math. Anal. Appl.*, **323** (2006), 1387–1401.
- [18] Y. Kang and J. H. Fewell, [Co-evolutionary dynamics of a social parasite-host interaction model: obligate versus facultative social parasitism](#), *Nat. Resour. Model.*, **28** (2015), 398–455.
- [19] Y. Kang and L. Wedekin, [Dynamics of an intraguild predation model with generalist or specialist predator](#), *J. Math. Biol.*, **67** (2013), 1227–1259.
- [20] X. L. Li, G. P. Hu and Z. S. Feng, [Pattern dynamics in a spatial predator-prey model with nonmonotonic response function](#), *Internat. J. Bifur. Chaos Appl. Sci. Engrg.*, **28** (2018), 1850077, 17 pp.
- [21] C.-S. Lin, W.-M. Ni and I. Takagi, [Large amplitude stationary solutions to a chemotaxis system](#), *J. Differential Equations*, **72** (1988), 1–27.
- [22] Y. Lou and W.-M. Ni, [Diffusion, self-diffusion and cross-diffusion](#), *J. Differential Equations*, **131** (1996), 79–131.
- [23] S. Madec, J. Casas, G. Barles and C. Suppo, [Bistability induced by generalist natural enemies can reverse pest invasions](#), *J. Math. Biol.*, **75** (2017), 543–575.
- [24] C. Magal, C. Cosner, S. G. Ruan and J. Casas, [Control of invasive hosts by generalist parasitoids](#), *Math. Med. Biol.*, **25** (2008), 1–20.
- [25] Z. Mei, [Numerical Bifurcation Analysis for Reaction-Diffusion Equations](#), Springer Series in Computational Mathematics, 28. Springer-Verlag, Berlin, 2000.
- [26] 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), 919–942.
- [27] R. Peng and J. P. Shi, [Non-existence of non-constant positive steady states of two Holling type-II predator-prey systems: Strong interaction case](#), *J. Differential Equations*, **247** (2009), 866–886.
- [28] R. Peng, M. X. Wang and M. Yang, [Positive solutions of a diffusive prey-predator model in a heterogeneous environment](#), *Math. Comput. Modelling*, **46** (2007), 1410–1418.
- [29] J. A. Rosenheim, H. K. Kaya, L. E. Ehler, J. J. Marois and B. A. Jaffee, [Intraguild predation among biological control agents: Theory and evidence](#), *Biol. Control*, **5** (1995), 303–335.
- [30] S. I. Rothstein, [Evolutionary rates and host defenses against avian brood parasitism](#), *The American Naturalist*, **109** (1975), 161–176.
- [31] W. E. Snyder and A. R. Ives, [Interactions between specialist and generalist natural enemies: parasitoids, predators, and pea aphid biocontrol](#), *Ecology*, **84** (2003), 91–107.
- [32] Y. L. Song, H. P. Jiang, Q.-X. Liu and Y. Yuan, [Spatiotemporal dynamics of the diffusive Mussel-Algae model near Turing-Hopf bifurcation](#), *SIAM J. Appl. Dyn. Syst.*, **16** (2017), 2030–2062.
- [33] M. D. Sorenson, [Effects of intra- and interspecific brood parasitism on a precocial host, the canvasback, *Aythya valisineria*](#), *Behavioral Ecology*, **8** (1997), 153–161.
- [34] C. N. Spottiswoode, R. M. Kilner and N. B. Davies, [Brood Parasitism](#), The Evolution of Parental Care, Oxford University Press, Oxford, 2012.
- [35] W. O. C. Symondson, K. D. Sunderland and M. H. Greenstone, [Can generalist predators be effective biocontrol agents?](#), *Annu. Rev. Entomol.*, **47** (2002), 561–594.
- [36] Q. Wang, C. Y. Gai and J. D. Yan, [Qualitative analysis of a Lotka-Volterra competition system with advection](#), *Discrete Contin. Dyn. Syst.*, **35** (2015), 1239–1284.
- [37] W. M. Wang, X. Y. Gao, Y. L. Cai, H. B. Shi and S. M. Fu, [Turing patterns in a diffusive epidemic model with saturated infection force](#), *J. Franklin Inst.*, **355** (2018), 7226–7245.
- [38] S. H. Wu and Y. L. Song, [Stability and spatiotemporal dynamics in a diffusive predator-prey model with nonlocal prey competition](#), *Nonlinear Anal. Real World Appl.*, **48** (2019), 12–39.

Received December 2018; revised February 2019.

E-mail address: baidy@gzhu.edu.cn

E-mail address: jsyu@gzhu.edu.cn

E-mail address: Yun.Kang@asu.edu