

Temporal and spatial patterns in a diffusive ratio-dependent predator-prey system with linear stocking rate of prey species

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Abstract. The ratio-dependent predator-prey model exhibits rich interesting dynamics due to the singularity of the origin. It is one of prototypical pattern formation models. Stocking in ratio-dependent predator-prey models is relatively an important research subject from both ecological and mathematical points of view. In this paper, we study the temporal, spatial patterns of a ratio-dependent predator-prey diffusive model with linear stocking rate of prey species. For the spatially homogeneous model, we derive conditions for determining the direction of Hopf bifurcation and the stability of the bifurcating periodic solution by the center manifold and the normal form theory. For the reaction-diffusion model, firstly it is shown that Turing (diffusion-driven) instability occurs, which induces spatial inhomogeneous patterns. Then it is demonstrated that the model exhibits Hopf bifurcation which produces temporal inhomogeneous patterns. Finally, the non-existence and existence of positive non-constant steady-state solutions are established. We can see spatial inhomogeneous patterns via Turing instability, temporal periodic patterns via Hopf bifurcation and spatial patterns via the existence of positive non-constant steady state. Moreover, numerical simulations are performed to visualize the complex dynamic behavior.

Keywords: ratio-dependent, stocking rate, Hopf bifurcation, Turing instability, steadystate, pattern.

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1 Introduction

One of important ecological fields is the dynamics between predators and prey. Since the first differential equation model of predator-prey type was found by Lotka [18] and Volterra [27] in 1920s, various kinds of predator-prey models have been proposed and studied. Some of these models are those with Holling types I, II, III and IV functional responses and have

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been intensively investigated, for example in [6,13,23,30]. The Holling type II (or Michaelis–Menten) model is of the form

$$\frac{du}{dt} = ru\left(1 - \frac{u}{K}\right) - \frac{c_1 uv}{m + u},$$

$$\frac{dv}{dt} = v\left(-d + \frac{c_2 u}{m + u}\right),$$
(1.1)

where u, v stand for prey and predator density, respectively. r, K, c_1, m, c_2, d are positive constants that stand for prey intrinsic growth rate, carrying capacity, capturing rate, half capturing saturation constant, conversion rate, predator death rate, respectively. While many of the mathematicians working in mathematical biology may regard these as important contributions that mathematics had for ecology, they are very controversial among ecologists up to this day. Indeed, some ecologists may simply view it as a problem [2,4], because they are not in line with many field observations [2,3,12].

Recently there is a growing evidences [3, 5, 10] that in some situations, especially when predator have to search for food (and therefore have to share or compete for food), a more suitable general predator–prey theory should be based on the so called ratio-dependent theory, which can be roughly stated as that the per capita predator growth rate should be a function of the ratio of prey to predator abundance. This is supported by numerous field and laboratory experiments and observations [2, 3]. Compared with Holling type functional responses, the ratio-dependent type functional response is more suitable to describe the interaction between the predator and prey.

The ratio-dependent predator–prey model have been studied by many researchers and very rich dynamics have been observed, see [1,9,24,26,32] and references therein. Now, we focus our attention on the following ratio-dependent predator–prey model

$$\frac{du}{dt} = ru\left(1 - \frac{u}{K}\right) - \frac{c_1 uv}{mv + u'},$$

$$\frac{dv}{dt} = v\left(-d + \frac{c_2 u}{mv + u}\right).$$
(1.2)

The term $\frac{c_1u}{mv+u}$ is called the ratio-dependent Holling type II functional response, and is derived from p(u/v), where *p* is the Holling type II prey-dependent functional response defined by

$$p(u) = \frac{c_1 u}{m+u}.\tag{1.3}$$

We refer to [11] and the references therein for the study of the predator–prey system (1.1). However, more realistic and suitable predator–prey systems should rely on the ratio-dependent functional responses. Roughly speaking, the per capita predator growth rate should be a function of the ratio of prey to predator abundance. Hence, the prey-dependent functional response p(u) given in (1.3) would be replaced by the ratio-dependent functional response p(u/v).

The dynamics of the model (1.2) has been studied extensively [7, 14, 29, 31]. These researches on the ratio-dependent predator–prey model (1.2) revealed rich interesting dynamics such as deterministic extinction, existence of multiple attractors, and existence of a stable limit cycle. Especially, it was shown in [7], [14], and [29] that the model (1.2) has very complicated dynamics close to the origin: There exist numerous kinds of topological structures in a neighborhood of the origin, including parabolic orbits, elliptic orbits, hyperbolic orbits, and any combination thereof, depending on the different values of parameters. In realistic ecology, the activities of harvesting or stocking often occur in fishery, forestry, and wildlife management. For example, certain number of animals are removed per year by hunting. It leads one to add harvesting rates or stocking rates into some models, see [8,20,33].

In this paper, we insert a linear stocking rate δ of prey into the first equation (1.2) and study the bifurcation dynamics of the following ratio-dependent predator–prey system with linear stocking rate

$$\frac{du}{dt} = ru\left(1 - \frac{u}{K}\right) - \frac{c_1 uv}{mv + u} + \delta u,$$

$$\frac{dv}{dt} = v\left(-d + \frac{c_2 u}{mv + u}\right).$$
(1.4)

In [19], M. Lei investigated the permanence of a class of Holling III-Tanner predator–prey diffusion system with stocking rate and time delay, the existence of positive periodic solution by using comparability theorem, coincidence degree theory. They obtained the sufficient conditions which guarantee permanent of the system and existence of the positive periodic solution of the periodic system. In [28], Z. Wang et al. considered a nonautonomous predator–prey system with Holling III functional responses and stocking rate. They proved that the system is uniformly permanent under suitable condition. Furthermore, sufficient criteria are established for existence, uniqueness and global asymptotic stability of periodic solution by establishing Lyapunov function. Anorexia predator–prey system under constant stocking rate of prey is discussed. The local behaviour and global behaviour of feasible equilibrium points were studied and the conditions of the existence and non-existence of limit cycle are obtained.

For simplicity, using the scaling: $u \rightarrow u/K$, $v \rightarrow mv/K$, $t \rightarrow rt$, one can change the model (1.4) into the following equivalent system

$$\frac{du}{dt} = u(1-u) - \frac{\alpha uv}{u+v} + hu,$$

$$\frac{dv}{dt} = v\left(-\gamma + \frac{\beta u}{u+v}\right),$$
(1.5)

where $\alpha = c_1/(rm)$, $\beta = c_2/r$, $\gamma = d/r$, $h = \delta/r$.

When the densities of the prey and predator are spatially inhomogeneous in a bounded domain, and the prey and predator move randomly-described as Brownian random motion, we need consider the following reaction-diffusion model corresponding model (1.5). In this paper, we investigate the temporal, spatial and temporospatial patterns of the following diffusive ratio-dependent predator–prey model with prey stocking

$$\frac{\partial u}{\partial t} - d_1 \triangle u = u(1-u) - \frac{\alpha u v}{u+v} + hu, \qquad x \in \Omega, \ t > 0,$$

$$\frac{\partial v}{\partial t} - d_2 \triangle v = v \left(-\gamma + \frac{\beta u}{u+v} \right), \qquad x \in \Omega, \ t > 0,$$

$$\frac{\partial u}{\partial v} = \frac{\partial v}{\partial v} = 0, \qquad x \in \partial\Omega, \ t > 0,$$

$$u(x,0) = u_0(x), \ v(x,0) = v_0(x), \qquad x \in \Omega,$$
(1.6)

where $\Omega \subset \mathbb{R}^n (n \ge 1)$ is a smooth bounded domain, ν is the outward unit normal vector on $\partial \Omega$. $d_1, d_2, \alpha, \beta, \gamma, h$ are all positive constants. $u_0(x)$ and $v_0(x)$ are nonnegative smooth functions and $u_0(x) + v_0(x) > 0$. To study the stationary patterns, we need consider the steady-state problem associated with (1.6)

$$-d_{1} \triangle u = u(1-u) - \frac{\alpha uv}{u+v} + hu, \qquad x \in \Omega,$$

$$-d_{2} \triangle v = v \left(-\gamma + \frac{\beta u}{u+v}\right), \qquad x \in \Omega,$$

$$\frac{\partial u}{\partial v} = \frac{\partial v}{\partial v} = 0, \qquad x \in \partial\Omega.$$
(1.7)

This paper is organized as follows. In Section 2, we investigate the existence, direction and stability of the Hopf bifurcation for the model (1.5) by applying the Poincaré–Andronov–Hopf bifurcation theorem. In Section 3, we first consider the Turing (diffusion-driven) instability of the reaction-diffusion model (1.6) when the spatial domain is a bounded interval, which will produce spatial inhomogeneous patterns. Then we study the existence and direction of Hopf bifurcation and the stability of the bifurcating periodic solution, which is a spatially inhomogeneous periodic solution of (1.6). In Section 4, we first give a priori estimates for the positive steady-state solutions of the model (1.7). Moreover, numerical simulations are presented to verify and illustrate the above theoretical results. The paper ends with a brief discussion.

2 Dynamics of the ODE model

Let

(

$$f_1(u,v) = u(1-u) - \frac{\alpha uv}{u+v} + hu, \quad f_2(u,v) = v\left(-\gamma + \frac{\beta u}{u+v}\right)$$

It is easy to know that model (1.5) has a free equilibrium (1 + h, 0) and the unique positive equilibrium $U^* = (u^*, v^*) = \left(\frac{\alpha\gamma + \beta(1+h-\alpha)}{\beta}, \left(\frac{\beta-\gamma}{\gamma}\right)u^*\right)$ if and only if

$$\mathbf{H}_{1}) \qquad \qquad \beta > \gamma, \quad h > \max\left\{0, \alpha - 1 - \frac{\alpha \gamma}{\beta}\right\}.$$

In this section, we mainly discuss the existence, direction and stability of the Hopf bifurcation in the model (1.5). The Jacobian matrix of model (1.5) at U^* as follows

$$J = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix},$$

where

$$a_{11} = \frac{(\alpha - h - 1)\beta^2 - \alpha\gamma^2}{\beta^2}, \qquad a_{12} = -\frac{\alpha\gamma^2}{\beta^2} < 0,$$
$$a_{21} = \frac{(\gamma - \beta)^2}{\beta} > 0, \qquad \qquad a_{22} = \frac{(\gamma - \beta)\gamma}{\beta} < 0$$

The characteristic polynomial is

$$P(\lambda) = \lambda^2 - Y\lambda + \Theta,$$

where

$$Y = \alpha - \gamma - h - 1 + \frac{\gamma^2}{\beta^2}(\beta - \alpha), \quad \Theta = \frac{\gamma(\beta - \gamma)(\alpha\gamma + \beta(1 + h - \alpha))}{\beta^2}.$$

For the Jacobian matrix *J*, we have the following conclusions.

Lemma 2.1.

- (1) $\Theta > 0$ if $(\mathbf{H_1})$ holds.
- (2) $a_{11} > 0$ if the following assumption holds

$$(\mathbf{H_2}) h < \alpha - 1 - \frac{\alpha \gamma^2}{\beta^2}.$$

By the standard linearization method, we can easily prove the following theorem.

Theorem 2.2. *Free equilibrium* (1 + h, 0) *of* (1.5) *is locally asymptotically stable if* $\beta < \gamma$ *and is unstable if* $\beta > \gamma$.

Theorem 2.3. Suppose that (H_1) holds. The unique positive equilibrium U^* of (1.5) is locally asymptotically stable if

(**H**₃₁)
$$h > \alpha - \gamma - 1 + \frac{\gamma^2}{\beta^2}(\beta - \alpha) \triangleq h_0$$

and is unstable if

 $(\mathbf{H}_{32}) h < h_0.$

To analyze the Hopf bifurcation of (1.5) occurring at U^* , we take *h* as the bifurcation parameter. In fact, *h* plays an important role in determining the stability of the interior equilibrium and the existence of Hopf bifurcation. Clearly, $h_0 > 0$ if and only if

$$(\mathbf{H}_4) \qquad \qquad (\gamma+1)\beta^2 + \alpha\gamma^2 < \alpha\beta^2 + \beta\gamma^2).$$

Let $\lambda(h) = \phi(h) \pm i\phi(h)$ be a pair of complex roots of $P(\lambda) = 0$ when *h* near h_0 . Then

$$\phi(h) = \frac{Y}{2}, \quad \phi(h) = \frac{1}{2}\sqrt{-4a_{12}a_{21} - (a_{11} - a_{22})^2}.$$

Furthermore, we can verify

$$\phi(h_0) = 0, \quad \phi'(h_0) = -\frac{1}{2} < 0.$$

This means that the transversality condition holds. By the Poincaré–Andronov–Hopf bifurcation theorem [17], we know that (1.5) undergoes a Hopf bifurcation at U^* as h passes through the h_0 .

To understand the detailed property of the Hopf bifurcation, we need a further analysis for the normal form of the model (1.5). Being more specific, we use the framework [16] to analysis the direction and stability of the Hopf bifurcation of the model (1.5).

We translate the positive equilibrium U^* to the origin by the transformation $\tilde{u} = u - u^*$, $\tilde{v} = v - v^*$. For the sake of convenience, we still denote \tilde{u} and \tilde{v} by u and v. Thus, the local system (1.5) is transformed into

$$\frac{du}{dt} = (u+u^*)(1-(u+u^*)) - \frac{\alpha(u+u^*)(v+v^*)}{(u+u^*) + (v+v^*)} + h(u+u^*),$$

$$\frac{dv}{dt} = (v+v^*)\left(-\gamma + \frac{\beta(u+u^*)}{(u+u^*) + (v+v^*)}\right).$$
(2.1)

Rewrite the system (2.1) as

$$\begin{pmatrix} \frac{du}{dt} \\ \frac{dv}{dt} \\ \frac{dv}{dt} \end{pmatrix} = J \begin{pmatrix} u \\ v \end{pmatrix} + \begin{pmatrix} f(u, v, \delta) \\ g(u, v, \delta) \end{pmatrix},$$
(2.2)

where

$$f(u, v, \delta) = a_1 u^2 + a_2 u v + a_3 v^2 + a_4 u^3 + a_5 u^2 v + a_6 u v^2 + a_7 v^3 + \cdots,$$

$$g(u, v, \delta) = b_1 u^2 + b_2 u v + b_3 v^2 + b_4 u^3 + b_5 u^2 v + b_6 u v^2 + b_7 v^3 + \cdots,$$

and

$$\begin{aligned} a_{1} &= -1 + \frac{\alpha v^{*2}}{(u^{*} + v^{*})^{3}}, \qquad a_{2} &= -\frac{2\alpha u^{*}v^{*}}{(u^{*} + v^{*})^{3}}, \qquad a_{3} &= \frac{\alpha u^{*2}}{(u^{*} + v^{*})^{3}}, \qquad a_{4} &= -\frac{\alpha v^{*2}}{(u^{*} + v^{*})^{4}}, \\ a_{5} &= \frac{2\alpha u^{*}v^{*} - \alpha v^{*2}}{(u^{*} + v^{*})^{4}}, \qquad a_{6} &= \frac{2\alpha u^{*}v^{*} - \alpha u^{*2}}{(u^{*} + v^{*})^{4}}, \qquad a_{7} &= -\frac{\alpha u^{*2}}{(u^{*} + v^{*})^{4}}, \\ b_{1} &= -\frac{\beta v^{*2}}{(u^{*} + v^{*})^{3}}, \qquad b_{2} &= \frac{2\beta u^{*}v^{*}}{(u^{*} + v^{*})^{3}}, \qquad b_{3} &= -\frac{\beta u^{*2}}{(u^{*} + v^{*})^{3}}, \qquad b_{4} &= \frac{\beta v^{*2}}{(u^{*} + v^{*})^{4}}, \\ b_{5} &= \frac{\beta v^{*2} - 2\beta u^{*}v^{*}}{(u^{*} + v^{*})^{4}}, \qquad b_{6} &= \frac{\beta u^{*2} - 2\beta u^{*}v^{*}}{(u^{*} + v^{*})^{4}}, \qquad b_{7} &= \frac{\beta u^{*2}}{(u^{*} + v^{*})^{4}}. \end{aligned}$$

Set the matrix

$$P:=\begin{pmatrix}N&1\\M&0\end{pmatrix},$$

where $M = -\frac{a_{21}}{\varphi}$, $N = \frac{a_{22}-a_{11}}{2\varphi}$. It is easy to obtain that

$$P^{-1}JP = \Phi(h) := \begin{pmatrix} \phi(h) & -\phi(h) \\ \phi(h) & \phi(h) \end{pmatrix}.$$

Let

$$M_0 := M|_{h=h_0}, \quad N_0 := N|_{h=h_0}, \quad \varphi_0 := \varphi(h_0).$$
 (2.3)

By the transformation $(u, v)^T = P(x, y)^T$, the system (2.2) becomes

$$\begin{pmatrix} \frac{dx}{dt} \\ \frac{dy}{dt} \end{pmatrix} = \Phi(h) \begin{pmatrix} x \\ y \end{pmatrix} + \begin{pmatrix} f^1(x, y, h) \\ g^1(x, y, h) \end{pmatrix},$$
(2.4)

where

$$f^{1}(x,y,h) = \frac{1}{M}g(Nx+y,Mx,h)$$

= $\left(\frac{N^{2}}{M}b_{1}+Nb_{2}+Mb_{3}\right)x^{2} + \left(\frac{2N}{M}b_{1}+b_{2}\right)xy + \frac{b_{1}}{M}y^{2}$
+ $\left(\frac{N^{3}}{M}b_{4}+N^{2}b_{5}+NMb_{6}+M^{2}b_{7}\right)x^{3} + \left(\frac{3N^{2}}{M}b_{4}+2Nb_{5}+Mb_{6}\right)x^{2}y$
+ $\left(\frac{3N}{M}b_{4}+b_{5}\right)xy^{2} + \frac{b_{4}}{M}y^{3} + \cdots,$

$$g^{1}(x,y,h) = f(Nx + y, Mx, h) - \frac{N}{M}g(Nx + y, Mx, h)$$

$$= \left(N^{2}a_{1} + NMa_{2} + M^{2}a_{3} - \frac{N^{3}}{M}b_{1} - N^{2}b_{2} - NMb_{3}\right)x^{2}$$

$$+ \left(2Na_{1} + Ma_{2} - \frac{2N^{2}}{M}b_{1} - Nb_{2}\right)xy + \left(a_{1} - \frac{N}{M}b_{1}\right)y^{2}$$

$$+ \left(N^{3}a_{4} + M^{3}a_{7} + N^{2}Ma_{5} + NM^{2}a_{6} - \frac{N^{4}}{M}b_{4} - N^{3}b_{5} - MN^{2}b_{6} + NM^{2}b_{7}\right)x^{3}$$

$$+ \left(3N^{2}a_{4} + 2NMa_{5} + M^{2}a_{6} - \frac{3N^{3}}{M}b_{4} - 2N^{2}b_{5} - NMb_{6}\right)x^{2}y$$

$$+ \left(3Na_{4} + Ma_{5} - \frac{3N^{2}}{M}b_{4} - Nb_{5}\right)xy^{2} + \left(a_{4} - \frac{N}{M}b_{4}\right)y^{3} + \cdots$$

The polar coordinates form of (2.4) is as the following

$$\dot{\tau} = \phi(h)\tau + a(h)\tau^3 + \cdots,$$

$$\dot{\theta} = \phi(h) + c(h)\tau^2 + \cdots,$$
(2.5)

then it follows from the Taylor expansion of (2.5) at $\delta = \delta_0$ that

$$\begin{aligned} \dot{\tau} &= \phi'(h_0)(h - h_0)\tau + a(h_0)\tau^3 + o((h - h_0)^2\tau, \ (h - h_0)\tau^3, \ \tau^5), \\ \dot{\theta} &= \varphi(h_0) + \varphi'(h_0)(h - h_0) + c(h_0)\tau^2 + o((h - h_0)^2, \ (h - h_0)\tau^2, \ \tau^4). \end{aligned}$$
(2.6)

In order to determine the stability of the Hopf bifurcation periodic solution, we need to calculate the sign of the coefficient $a(h_0)$, which is given by

$$a(h_0) = \frac{1}{16} \left(f_{xxx}^1 + f_{xyy}^1 + g_{xxy}^1 + g_{yyy}^1 \right) + \frac{1}{16\varphi_0} \left[f_{xy}^1 (f_{xx}^1 + f_{yy}^1) - g_{xy}^1 (g_{xx}^1 + g_{yy}^1) - f_{xx}^1 g_{xx}^1 + f_{yy}^1 g_{yy}^1 \right],$$
(2.7)

where all partial derivatives are evaluated at the bifurcation point $(x, y, h) = (0, 0, h_0)$, and

$$\begin{split} f^1_{xxx}(0,0,h_0) &= 6 \left(\frac{N_0^3}{M_0} b_4 + N_0^2 b_5 + N_0 M_0 b_6 + M_0^2 b_7 \right), \quad f^1_{xyy}(0,0,h_0) = 2 \left(\frac{3N_0}{M_0} b_4 + b_5 \right), \\ g^1_{xxy}(0,0,h_0) &= 2 \left(3N_0^2 a_4 + 2N_0 M_0 a_5 + M_0^2 a_6 - \frac{3N_0^3}{M_0} b_4 - 2N_0^2 b_5 - N_0 M_0 b_6 \right), \\ g^1_{yyy}(0,0,h_0) &= 6 \left(a_4 - \frac{N_0}{M_0} b_4 \right), \quad f^1_{xx}(0,0,h_0) = 2 \left(\frac{N_0^2}{M_0} b_1 + N_0 b_2 + M_0 b_3 \right), \\ f^1_{xy}(0,0,h_0) &= \frac{2N_0}{M_0} b_1 + b_2, \quad f^1_{yy}(0,0,h_0) = \frac{2}{M_0} b_1, \\ g^1_{xx}(0,0,h_0) &= 2 \left(N_0^2 a_1 + N_0 M_0 a_2 + M_0^2 a_3 - \frac{N_0^3}{M_0} b_1 - N_0^2 b_2 - N_0 M_0 b_3 \right), \\ g^1_{xy}(0,0,h_0) &= 2N_0 a_1 + M_0 a_2 - \frac{2N_0^2}{M_0} b_1 - N_0 b_2, \quad g^1_{yy}(0,0,h_0) = 2 \left(a_1 - \frac{N_0}{M_0} b_1 \right). \end{split}$$

Thus, we can determine the value and sign of $a(h_0)$ in (2.7).

Recall that $\sigma_2 = -\frac{a(h_0)}{\phi'(h_0)}$ and $\phi'(h_0) = -\frac{1}{2} < 0$, form the Poincaré–Andronov–Hopf bifurcation theorem, we can summarize our results as follows.

Theorem 2.4. Suppose that (H_1) and (H_4) hold. Then model (1.5) undergoes a Hopf bifurcation at U^* when $h = h_0$.

- (1) The direction of the Hopf bifurcation is subcritical and the bifurcated periodic solutions are orbitally asymptotically stable if $a(h_0) < 0$;
- (2) The direction of the Hopf bifurcation is supercritical and the bifurcated periodic solutions are unstable if $a(h_0) > 0$.

To illustrate Theorem 2.4, we give some simple numerical examples.

Example 2.5. (1) We choose the coefficients in the system (1.5) as follows

$$\alpha = 4, \ \beta = 1, \ \gamma = 0.5.$$
 (2.8)

It is easy to see that (**H**₄) holds and the critical point $h_0 = 1.75$. Set h = 1.5, then $U^* = (0.5, 0.5)$, Y = 0.25 > 0, $\Theta = 0.125 > 0$, i.e. (**H**₁), (**H**₃₂) hold and so U^* is unstable.

Set h = 2.5 and the parameters in (2.8) satisfy (**H**₁). Then $U^* = (1.5, 1.5)$, Y = -0.75 < 0, $\Theta = 0.375 > 0$, by Theorem 2.3, U^* is locally asymptotically stable. Besides, $a(h_0) \approx -1.407 < 0$ and $\sigma_2 \approx -1.407 < 0$. By Theorem 2.4, Hopf bifurcation occurs at $h = h_0$, the Hopf bifurcation is subcritical and the bifurcating periodic solutions are stable.

(2) If we choose

$$\alpha = 1.7, \ \beta = 1, \ \gamma = 0.4.$$
 (2.9)

It is easy to see that (**H**₄) holds and the critical point $h_0 = 0.188$, $U^* = (0.168, 0.252)$, $a(\delta_0) \approx 0.227 > 0$ and $\sigma_2 \approx 0.227 > 0$. By Theorem 2.4, Hopf bifurcation occurs at $h = h_0$, the Hopf bifurcation is supercritical and the bifurcating periodic solutions are unstable.

3 Turing instability and bifurcations in the reaction-diffusion model

In this section, we mainly discuss the stability of positive equilibrium and the existence, stability and direction of the Hopf bifurcation for the reaction diffusion system (1.6). For simplicity, we shall take the spatial domain Ω as the one-dimensional interval $\Omega = (0, \pi)$, and consider

$$u_{t} - d_{1}u_{xx} = u(1 - u) - \frac{\alpha uv}{u + v} + hu, \qquad x \in (0, \pi), \ t > 0,$$

$$v_{t} - d_{2}v_{xx} = v\left(-\gamma + \frac{\beta u}{u + v}\right), \qquad x \in (0, \pi), \ t > 0,$$

$$u_{x}(0, t) = u_{x}(\pi, t) = v_{x}(0, t) = v_{x}(\pi, t) = 0, \qquad t > 0,$$

$$u(x, 0) = u_{0}(x), \ v(x, 0) = v_{0}(x), \qquad x \in (0, \pi).$$

(3.1)

It is well known that the operator $u \rightarrow -u_{xx}$ with no-flux boundary condition has eigenvalues and eigenfunctions as follows:

$$\mu_0 = 0$$
, $\phi_0 = \sqrt{\frac{1}{\pi}}$, $\mu_i = i^2$, $\phi_i(x) = \sqrt{\frac{2}{\pi}} \cos ix$, for $i = 1, 2, 3, ...$

Diffusive effects on the interior equilibrium point 3.1

Theorem 3.1. Assume that the conditions $(\mathbf{H_1})$ and $h > \alpha - 1 - \frac{\alpha \gamma^2}{\beta^2}$ hold. Then the unique positive equilibrium U^* in (3.1) is uniformly asymptotically stable.

Proof. Let $D = \text{diag}(d_1, d_2)$, U = (u, v), $L = D \triangle + J_U(U^*)$. Then the linearized system of (3.1) at U^* is

$$U_t = LU, (3.2)$$

and the eigenvalues of the operator *L* are the eigenvalues of the matrix $-\mu_i D + J_U(U^*), \forall i \ge 1$. The characteristic equation of $-\mu_i D + J_U(U^*)$ is

$$\varphi_i(\lambda) \triangleq |\lambda I + \mu_i D - J_U(U^*)| = \lambda^2 + A_i \lambda + B_i = 0,$$

where

$$A_i = \mu_i(d_1 + d_2) - Y, \quad B_i = \mu_i^2 d_1 d_2 - a_{11} \mu_i d_2 - a_{22} \mu_i d_1 + \Theta,$$

and Y, Θ be defined as in the Section 2.

If $h > \alpha - 1 - \frac{\alpha \gamma^2}{\beta^2}$, then $a_{11} < 0$, $A_i > 0$ and $B_i > 0$. The roots $\lambda_{i,1}$ and $\lambda_{i,2}$ of $\varphi_i(\lambda) = 0$ all have negative real parts.

We claim that there exists a positive constant $\bar{\delta}$ such that

$$\operatorname{Re}\{\lambda_{i,1}\}, \operatorname{Re}\{\lambda_{i,2}\} \le -\bar{\delta}, \quad \forall i \ge 1.$$
(3.3)

In fact, let $\lambda = \mu_i \zeta$, then

$$\varphi_i(\lambda) = \mu_i^2 \zeta^2 + A_i \mu_i \zeta + B_i \triangleq \overline{\varphi_i}(\zeta),$$

and

$$\lim_{i o\infty} rac{\overline{arphi_i}(\zeta)}{\mu_i^2} = \zeta^2 + (d_1+d_2)\zeta + d_1d_2 riangleq \overline{arphi}(\zeta).$$

Notice that $\overline{\varphi}(\zeta) = 0$ has two negative roots $-d_1$ and $-d_2$. Thus, $\operatorname{Re}\{\zeta_1\}, \operatorname{Re}\{\zeta_2\} \leq -\overline{d} =$ $-\min\{d_1, d_2\}$. By continuity, there exists an i_0 such that the two roots $\zeta_{i,1}, \zeta_{i,2}$ of $\overline{\varphi}_i(\zeta) = 0$ satisfy $\operatorname{Re}{\zeta_{i,1}}$, $\operatorname{Re}{\zeta_{i,2}} \leq -\overline{d}/2$, $\forall i \geq i_0$. In turn, $\operatorname{Re}{\lambda_{i,1}}$, $\operatorname{Re}{\lambda_{i,2}} \leq -\overline{d}/2$, $\forall i \geq i_0$. Let

$$\max\{\operatorname{Re}\{\lambda_{i,1}\},\operatorname{Re}\{\lambda_{i,2}\}\}=-\eta$$

Then $\eta > 0$, and (3.3) holds for $\overline{\delta} = \min\{\eta, \overline{d}/2\}$.

This implies that the spectrum of L, which consists of eigenvalues, lies in $\{\text{Re}\lambda \leq -\bar{\delta}\}$, and uniform stability of U^* follows [15]. This completes the proof.

From Lemma 2.1 and Theorem 2.3, we know that the interior equilibrium U^* of the ODE model (1.5) is locally asymptotically stable if (H_{31}) holds, that is, Y < 0. To investigate the Turing instability of the spatially homogeneous equilibrium U^* of the diffusive model (3.1), we need look for the condition of diffusion-driven instability under the assumption (H_{31}) . It is well known that the positive equilibrium U^* of (3.1) is unstable if $\varphi_i(\lambda) = 0$ has at least one root with positive real part.

For the sake of convenience, define

$$\phi(\mu_i) := B_i = \mu_i^2 d_1 d_2 - (a_{11}d_2 + a_{22}d_1)\mu_i + \Theta_i$$

which is a quadratic polynomial with respect to μ_i . It is necessary to determine the sign of $\phi(\mu_i)$. Clearly, if $\phi(\mu_i) < 0$, then $\varphi_i(\lambda) = 0$ has two real roots in which one is positive and the other is negative. Notice that if

$$G(d_1, d_2) := a_{11}d_2 + a_{22}d_1 > 0,$$

then $\phi(\mu_i)$ will take the minimum value

$$\min_{\mu_i} \phi(\mu_i) = \Theta - \frac{(a_{11}d_2 + a_{22}d_1)^2}{4d_1d_2} < 0$$

at the critical value $\mu^* > 0$, where $\mu^* = \frac{a_{11}d_2 + a_{22}d_1}{2d_1d_2}$.

Define the ratio $\rho = d_2/d_1$ and

$$\Lambda(d_1, d_2) = (a_{11}d_2 + a_{22}d_1)^2 - 4d_1d_2\Theta$$

= $a_{11}^2d_2^2 + 2(2a_{12}a_{21} - a_{11}a_{22})d_1d_2 + a_{22}^2d_1^2$.

Then

$$\begin{split} \Lambda(d_1, d_2) &= 0 \Leftrightarrow a_{11}^2 \rho^2 + 2(2a_{12}a_{21} - a_{11}a_{22})\rho + a_{22}^2 = 0, \\ G(d_1, d_2) &= 0 \Leftrightarrow \rho = -\frac{a_{22}}{a_{11}} \equiv \rho^*. \end{split}$$

Recall that $\Theta > 0$ and $a_{12} < 0$, $a_{21} > 0$, we have

$$4(2a_{12}a_{21}-a_{11}a_{22})^2-4a_{11}^2a_{22}^2=16a_{12}a_{21}(a_{12}a_{21}-a_{11}a_{22})>0.$$

Therefore, $\Lambda(d_1, d_2) = 0$ has two positive real roots

$$\rho_{1} = \frac{-(2a_{12}a_{21} - a_{11}a_{22}) + 2\sqrt{a_{12}a_{21}(a_{12}a_{21} - a_{11}a_{22})}}{a_{11}^{2}},$$

$$\rho_{2} = \frac{-(2a_{12}a_{21} - a_{11}a_{22}) - 2\sqrt{a_{12}a_{21}(a_{12}a_{21} - a_{11}a_{22})}}{a_{11}^{2}},$$

and $0 < \rho_2 < \rho^* < \rho_1$. Moreover, if $d_2/d_1 > \rho_1$, then min $\phi(\mu_i) < 0$, $G(d_1, d_2) < 0$, and U^* is unstable. It follows from Theorem 2.4 that the Turing instability occurs. Based on the above analyze, we have the following Turing instability result.

Theorem 3.2. Assume that the conditions (H_1) and (H_{31}) hold(in the case U^* is stable with respect to the local model (1.5)). Then there exists an unbounded region

$$T := \{ (d_1, d_2) : d_1 > 0, \ d_2 > 0, \ d_2 > \rho_1 d_1 \}$$

for $\rho_1 > 0$, such that, for any $(d_1, d_2) \in T$, U^* is unstable with respect to the reaction-diffusion model (3.1), that is, Turing instability occurs.

Example 3.3. (1) We choose the coefficients of the model (3.1) as follows

$$\alpha = 1.5, \quad \beta = 1, \quad \gamma = 0.35, \quad h = 0.2, \quad d_1 = 0.015, \quad d_2 = 0.25.$$
 (3.4)

It is easy to see that the parameters in (3.4) satisfy (\mathbf{H}_1) and Y = -0.11125 < 0, i.e. (\mathbf{H}_{31}) holds. The unique positive equilibrium point $U^* \approx (0.225, 0.4179)$ in (1.5) is locally

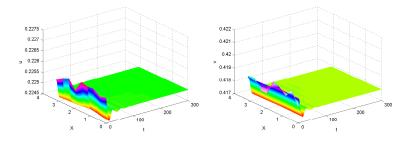


Figure 3.1: Stable behaviour with $d_1 = 0.015$, $d_2 = 0.25$ for the model (3.1).

asymptotically stable. Furthermore, $\rho_1 \approx 18.86$ and $d_2 - \rho_1 d_1 \approx -0.0329 < 0$, so U^* in (3.1) is uniformly asymptotically stable (see Fig. 3.1).

(2) Choose

 $\alpha = 1.5, \quad \beta = 1, \quad \gamma = 0.35, \quad h = 0.2, \quad d_1 = 0.015, \quad d_2 = 0.5.$ (3.5)

In (3.5), we only change a diffusion coefficient compared with (3.4). In the case, $\rho_1 \approx 18.862$ and $d_2 - \rho_1 d_1 \approx 0.217 > 0$. By Theorems 2.3, 3.2, we know that $U^* \approx (0.225, 0.4179)$ is stable with respect to the local model (1.5), and unstable for the diffusive system (3.1). This means that the Turing instability occurs in (3.1) (see Fig. 3.2).

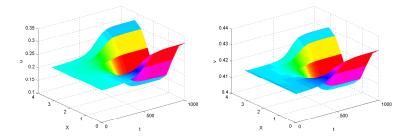


Figure 3.2: Turing instability with $d_1 = 0.015$, $d_2 = 0.5$ for the model (3.1).

(3) Choose

$$\alpha = 1.7, \quad \beta = 3, \quad \gamma = 1.2, \quad h = 0.2, \quad d_1 = 0.01, \quad d_2 = 0.5.$$
 (3.6)

In (3.6), all coefficients are changed but satisfy (**H**₁) and (**H**₃₁). Thus, $U^* = (0.18, 0.27)$ in (1.5) is locally stable. In this case, $\rho_1 \approx 15.65$ and $d_2 - \rho_1 d_1 \approx 0.3435 > 0$. By Theorem 3.2, Turing instability occurs in the diffusive system (3.1) (see Fig. 3.3).

Remark 3.4. Via numerical simulations, we can see that the model exhibits spatiotemporal complexity of pattern formation, including stripe, stripe-hole and hole Turing patterns.

For example, in (3.1), fix

$$\alpha = 1.5, \quad \beta = 1, \quad \gamma = 0.35, \quad h = 0.2, \quad d_1 = 0.01, \quad d_2 = 0.62.$$
 (3.7)

By numerical simulation results, we can observe the stripe-hole pattern of u in the model (3.1) (see Fig. 3.4). Changing the diffusion coefficients $d_1 = 0.015$, $d_2 = 0.3$ in (3.7), hole pattern can be obtained (see Fig. 3.5).

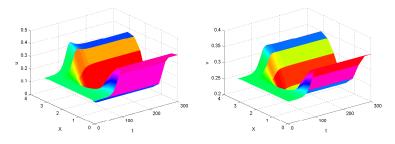


Figure 3.3: Turing instability with $d_1 = 0.01$, $d_2 = 0.5$ for the model (3.1).

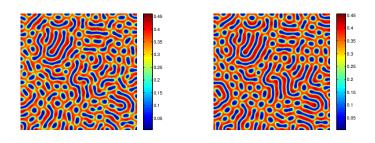


Figure 3.4: Stripe-hole pattern of u in the model (3.1).

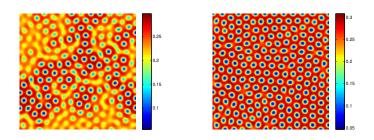


Figure 3.5: Hole pattern of u in the model (3.1).

If we fix

$$\alpha = 3$$
, $\beta = 1.3$, $\gamma = 0.2$, $h = 1.8$, $d_1 = 0.01$,

we can see that pattern with $d_1 = 0.25$ is similar to the one with $d_1 = 0.45$, they are all stripe patterns in (Fig. 3.6). Fig. 3.6 (a) consists of blue stripe on a red background, i.e., the prey is isolated zones with low population density. While (b) consists of red stripe on a blue background, i.e., the prey is isolated zones with high population density.

3.2 Diffusive effects on the bifurcation limit cycle

In this subsection, we seek for the related Hopf bifurcation points and consider the stability of the bifurcating periodic solutions of model (3.1) with spatial domain $(0, \pi)$. In order to use framework of the Hopf bifurcation theory [16], we need to complete the following three steps. **Step 1**. Linearization analysis.

For (3.1), we introduce the perturbation $u = \hat{u} + u^*$, $v = \hat{v} + v^*$, and still denote (\hat{u}, \hat{v}) by

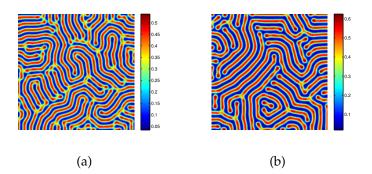


Figure 3.6: Stripe pattern of u in the model (3.1).

(*u*, *v*). Then

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$$u_{t} - d_{1}u_{xx} = (u + u^{*})(1 - (u + u^{*})) - \frac{\alpha(u + u^{*})(v + v^{*})}{(u + u^{*}) + (v + v^{*})} + h(u + u^{*}), \qquad x \in (0, \pi), \ t > 0,$$

$$v_{t} - d_{2}v_{xx} = (v + v^{*})\left(-\gamma + \frac{\beta(u + u^{*})}{(u + u^{*}) + (v + v^{*})}\right), \qquad x \in (0, \pi), \ t > 0,$$

$$u_{x}(0, t) = u_{x}(\pi, t) = v_{x}(0, t) = v_{x}(\pi, t) = 0, \qquad t > 0,$$

$$u(x, 0) = u_{0}(x) - u^{*}, \ v(x, 0) = v_{0}(x) - u^{*}, \qquad x \in (0, \pi).$$

(3.8)

Consider the linearization matrix of (3.8) at (0,0)

$$L(h) := \begin{pmatrix} d_1 \frac{d^2}{dx^2} + A(h) & B(h) \\ C(h) & d_2 \frac{d^2}{dx^2} + D(h) \end{pmatrix} \text{ and } L_i(h) := \begin{pmatrix} A(h) - d_1 i^2 & B(h) \\ C(h) & D(h) - d_2 i^2 \end{pmatrix},$$

where

$$A(h) = \frac{(\alpha - h - 1)\beta^2 - \alpha\gamma^2}{\beta^2}, \quad B(h) = -\frac{\alpha\gamma^2}{\beta^2}, \quad C(h) = \frac{(\gamma - \beta)^2}{\beta}, \quad D(h) = \frac{(\gamma - \beta)\gamma}{\beta}.$$

The characteristic equation of $L_i(h)$ is

$$\lambda^2 - \lambda T_i(h) + D_i(h) = 0, \quad i = 0, 1, 2, \dots,$$
(3.9)

where

$$\begin{cases} T_i(h) = A(h) + D(h) - i^2(d_1 + d_2), \\ D_i(h) = d_1 d_2 i^4 - (A(h)d_2 + D(h)d_1)i^2 + A(h)D(h) - B(h)C(h), \end{cases}$$
(3.10)

the eigenvalues are determined by $\lambda(h) = \frac{T_i(h) \pm \sqrt{T_i(h)^2 - 4D_i(h)}}{2}$, i = 0, 1, 2, ...

Step 2. Identify possible Hopf bifurcation values and verify transversality conditions.

To seek for the Hopf bifurcation values h_k , we need the following necessary and sufficient conditions from [16]:

(**H**₅) There exists $i \ge 0$ such that

$$T_i(h_k) = 0, \quad D_i(h_k) > 0, \quad T_j(h_k) \neq 0, \quad D_j(h_k) \neq 0 \quad \text{for} \quad j \neq i$$
 (3.11)

and for the unique pair of complex eigenvalues near the imaginary axis $\phi(h) \pm i\phi(h)$,

$$\phi'(h_k) \neq 0. \tag{3.12}$$

Let $\lambda(h) = \phi(h) \pm \phi(h)$ be the roots of (3.9). Obviously, $\phi(h) = T_i(h)/2$. If there exist some i = 0, 1, 2, ... such that

$$(d_1 + d_2)i^2 < A(h), (3.13)$$

letting h_i^k be the roots of $T_i(h) = 0$, then we have

$$T_i(h_i^k) = 0$$
, $\phi'(h_i^k) = -\frac{1}{2} < 0$ and $T_j(h_i^k) \neq 0$ for $j \neq i$.

The transversality condition (3.12) is satisfied. We only need to verify whether $D_j(h_i^k) \neq 0$ for i = 0, 1, 2, ... Here, we obtain a condition on the parameters so that $D_i(h_i^k) > 0$. In fact, if the following inequality

$$d_1 > -\frac{A(h_i^k)d_2}{D(h_i^k)}$$
(3.14)

holds, then

$$D_i(h_i^k) \ge i^4 d_1 d_2 - i^2 (A(h_i^k) d_2 + D(h_i^k) d_1) > 0.$$
(3.15)

Hence, the condition (**H**₅) is satisfied, which implies that (3.1) undergoes a Hopf bifurcation at $h = h_i^k$. Clearly, $h = h_0^k (= h_0)$ is always the unique value for the Hopf bifurcation of spatially homogeneous periodic solution to (3.1).

Theorem 3.5. Assume (\mathbf{H}_1) , (\mathbf{H}_4) and (3.14) hold. Then the model (3.1) undergoes Hopf bifurcations at $h_i^k (i \ge 1)$ and h_0 .

Step 3. Verify the sign of the $\text{Re}(c_1(h_0))$ which is defined by (3.20) later.

Notice that $\phi'(h_0) < 0$, adopting the work in [16], we know that if $\text{Re}(c_1(h_0)) < 0$ (resp. > 0), then the bifurcation periodic solution is stable (resp. unstable) and the bifurcation is subcritical (resp. supercritical).

With the condition of Theorem 3.5, it is easy to obtain that all other eigenvalues of $L(h_0)$ have negative real parts and any $L(h_i^k)$, $i \ge 1$, has at least one eigenvalues whose real part is positive. So the bifurcation periodic solutions bifurcating from $(0, 0, h_i^k)$ are unstable.

In order to get the stability and the bifurcation direction of the bifurcation periodic solution bifurcating from $(0, 0, h_0)$, we need to make a further consideration for the bifurcation solution, where the complex variable calculation will play a critical role.

Let L^* be the conjugate operator of *L* defined as (3.2),

$$L^*U := D\Delta U + J^*U, \tag{3.16}$$

where $J^* = J^T$ with the domain $D_L^* = X_C$. Let

$$q := \begin{pmatrix} q_1 \\ q_2 \end{pmatrix} = \begin{pmatrix} 1 \\ -\frac{s_1}{s_2} + \frac{\varphi_0}{s_2}i \end{pmatrix},$$

where $s_1 = \frac{\gamma(\beta - \gamma)}{\beta}$, $s_2 = -\frac{\alpha \gamma^2}{\beta^2}$, and

$$q^* := \begin{pmatrix} q_1^* \\ q_2^* \end{pmatrix} = \frac{s_2}{2\pi\varphi_0} \begin{pmatrix} \frac{\varphi_0}{s_2} + \frac{s_1}{s_2}i \\ i \end{pmatrix}$$

For any $\xi \in D_L^*$, $\eta \in D_L$, it is not difficult to verify that $\langle L^*\xi, \eta \rangle = \langle \xi, L\eta \rangle$, $L(h_0)q = i\varphi_0 q$, $L^*(h_0)q^* = -i\varphi_0 q^*$, $\langle q^*, \overline{q} \rangle = 0$, $\langle q^*, q \rangle = 1$, where $\langle \xi, \eta \rangle = \int_0^\pi \overline{\xi}^T \eta dx$ denotes the inner

product in $L^2[(0,\pi)] \times L^2[(0,\pi)]$. According to [16], we decompose $X = X^C \oplus X^S$ with $X^C = \{zq + \bar{z}\bar{q} : z \in \mathbb{C}\}$ and $X^S = \{\omega \in X : \langle q^*, \omega \rangle = 0\}$.

For any $(u, v) \in X$, there exist $z \in \mathbb{C}$ and $\omega = (\omega_1, \omega_2) \in X^S$ such that

$$(u,v)^T = zq + \overline{z}\overline{q} + (\omega_1,\omega_2)^T, \quad z = \langle q^*, (u,v)^T \rangle.$$

Thus

$$\begin{cases} u = z + \overline{z} + \omega_1, \\ v = z \left(-\frac{s_1}{s_2} + \frac{\varphi_0}{s_2} i \right) + \overline{z} \left(-\frac{s_1}{s_2} - \frac{\varphi_0}{s_2} i \right) + \omega_2 \end{cases}$$

The model (3.1) is reduced to the following system in (z, ω) coordinates:

$$\begin{cases} \frac{dz}{dt} = i\varphi_0 z + \langle q^*, \tilde{h} \rangle, \\ \frac{d\omega}{dt} = L\omega + H(z, \bar{z}, \omega), \end{cases}$$
(3.17)

where

$$\tilde{h} = \tilde{h}(zq + \bar{z}\bar{q} + \omega), \quad H(z,\bar{z},\omega) = \tilde{h} - \langle q^*, \tilde{h} \rangle q - \langle \bar{q}^*, \tilde{h} \rangle \bar{q}$$

As in [16], we write \tilde{h} in the form

$$\tilde{h}(U) = \frac{1}{2}Q(U,U) + \frac{1}{6}C(U,U,U) + O(|U|^4),$$

where *Q*, *C* are symmetric multi-linear forms and

$$\begin{split} \tilde{h} &= \frac{1}{2}Q(q,q)z^2 + Q(q,\bar{q})z\bar{z} + \frac{1}{2}Q(\bar{q},\bar{q})\bar{z}^2 + O(|z|^3,|z|\cdot|\omega|,|\omega|^2), \\ \langle q^*,\tilde{h} \rangle &= \frac{1}{2}\langle q^*,Q(q,q) \rangle z^2 + \langle q^*,Q(q,\bar{q}) \rangle z\bar{z} + \frac{1}{2}\langle q^*,Q(\bar{q},\bar{q}) \rangle \bar{z}^2 + O(|z|^3,|z|\cdot|\omega|,|\omega|^2), \\ \langle \bar{q}^*,\tilde{h} \rangle &= \frac{1}{2}\langle \bar{q}^*,Q(q,q) \rangle z^2 + \langle \bar{q}^*,Q(q,\bar{q}) \rangle z\bar{z} + \frac{1}{2}\langle \bar{q}^*,Q(\bar{q},\bar{q}) \rangle \bar{z}^2 + O(|z|^3,|z|\cdot|\omega|,|\omega|^2), \end{split}$$

so

$$H(z,\bar{z},\omega) = \frac{H_{20}}{2}z^2 + H_{11}z\bar{z} + \frac{H_{02}}{2}\bar{z}^2 + O(|z|^3, |z| \cdot |\omega|, |\omega|^2).$$

where

$$H_{20} = Q(q,q) - \langle q^*, Q(q,q) \rangle q - \langle \bar{q}^*, Q(q,q) \rangle \bar{q},$$

$$H_{11} = Q(q,\bar{q}) - \langle q^*, Q(q,\bar{q}) \rangle q - \langle \bar{q}^*, Q(q,\bar{q}) \rangle \bar{q},$$

$$H_{02} = Q(\bar{q},\bar{q}) - \langle q^*, Q(\bar{q},\bar{q}) \rangle q - \langle \bar{q}^*, Q(\bar{q},\bar{q}) \rangle \bar{q}.$$
(3.18)

Furthermore, $H_{20} = H_{11} = H_{02} = (0,0)^T$, and $H(z, \bar{z}, \omega) = O(|z|^3, |z| \cdot |\omega|, |\omega|^2)$. It follows from Appendix A in [16] that the model (3.17) possesses a center manifold, and then we can write ω in the form

$$\omega = \frac{\omega_{20}}{2}z^2 + \omega_{11}z\bar{z} + \frac{\omega_{02}}{2}\bar{z}^2 + o(|z|^3).$$

Thus,

$$\begin{cases}
\omega_{20} = (2i\varphi_0 I - L)^{-1} H_{20}, \\
\omega_{11} = (-L)^{-1} H_{11}, \\
\omega_{02} = \bar{\omega}_{20}.
\end{cases}$$
(3.19)

This implies that $\omega_{20} = \omega_{02} = \omega_{11} = 0$.

For later uses, define

$$\begin{split} c_{0} &:= f_{uu}q_{1}^{2} + 2f_{uv}q_{1}q_{2} + f_{vv}q_{2}^{2} = 2a_{1} + 2a_{2}q_{2} + 2a_{3}q_{2}^{2}, \\ d_{0} &:= g_{uu}q_{1}^{2} + 2g_{uv}q_{1}q_{2} + g_{vv}q_{2}^{2} = 2b_{1} + 2b_{2}q_{2} + 2b_{3}q_{2}^{2}, \\ e_{0} &:= f_{uu}|q_{1}|^{2} + f_{uv}(q_{1}\bar{q}_{2} + \bar{q}_{1}q_{2}) + f_{vv}|q_{2}|^{2} = 2a_{1} + a_{2}(q_{2} + \bar{q}_{2}) + 2a_{3}|q_{2}|^{2}, \\ f_{0} &:= g_{uu}|q_{1}|^{2} + g_{uv}(q_{1}\bar{q}_{2} + \bar{q}_{1}q_{2}) + g_{vv}|q_{2}|^{2} = 2b_{1} + b_{2}(q_{2} + \bar{q}_{2}) + 2b_{3}|q_{2}|^{2}, \\ g_{0} &:= f_{uuu}|q_{1}|^{2}q_{1} + f_{uuv}(2|q_{1}|^{2}q_{2} + q_{1}^{2}\bar{q}_{2}) + f_{uvv}(2q_{1}|q_{2}|^{2} + \bar{q}_{1}q_{2}^{2}) + f_{vvv}|q_{2}|^{2}q_{2} \\ &= 6a_{4} + 2a_{5}(2q_{2} + \bar{q}_{2}) + 2a_{6}(2|q_{2}|^{2} + q_{2}^{2}) + 6a_{7}|q_{2}|^{2}q_{2}, \\ j_{0} &:= g_{uuu}|q_{1}|^{2}q_{1} + g_{uuv}(2|q_{1}|^{2}q_{2} + q_{1}^{2}\bar{q}_{2}) + g_{uvv}(2q_{1}|q_{2}|^{2} + \bar{q}_{1}q_{2}^{2}) + g_{vvv}|q_{2}|^{2}q_{2} \\ &= 6b_{4} + 2b_{5}(2q_{2} + \bar{q}_{2}) + 2b_{6}(2|q_{2}|^{2} + q_{2}^{2}) + 6b_{7}|q_{2}|^{2}q_{2}, \end{split}$$

with all the partial derivatives evaluated at the point $(u, v, \delta) = (0, 0, h_0)$. Therefore, the reaction diffusion system restricted to the center manifold in z, \bar{z} coordinates is given by

$$\frac{dz}{dt} = i\varphi_0 z + \frac{1}{2}\phi_{20}z^2 + \phi_{11}z\bar{z} + \frac{1}{2}\phi_{02}\bar{z}^2 + \frac{1}{2}\phi_{21}z^2\bar{z} + o(|z|^4),$$

where

$$\phi_{20} = \langle q^*, (c_0, d_0)^T \rangle, \quad \phi_{11} = \langle q^*, (e_0, f_0)^T \rangle, \quad \phi_{21} = \langle q^*, (g_0, j_0)^T \rangle.$$

Then some tedious calculations show that

$$\begin{split} \phi_{20} &= \frac{s_2}{2\varphi_0} \left[\left(\frac{\varphi_0}{s_2} - \frac{s_1}{s_2} i \right) c_0 - i d_0 \right] \\ &= a_1 + b_2 - \frac{2b_3 s_1}{s_2} - \frac{a_3 (s_1^2 + \varphi_0^2)}{s_2^2} \\ &\quad + \frac{i}{\varphi_0} \left(b_2 s_1 - a_1 s_1 - b_1 s_2 + \frac{a_2 (\varphi_0^2 + s_1^2) - b_3 (s_1^2 - \varphi_0^2)}{s_2} - \frac{a_3 s_1 (s_1^2 + \varphi_0^2)}{s_2^2} \right), \\ \phi_{11} &= \frac{s_2}{2\varphi_0} \left[\left(\frac{\varphi_0}{s_2} - \frac{s_1}{s_2} i \right) e_0 - i f_0 \right] \\ &= a_1 - \frac{a_2 s_1}{s_2} + \frac{a_3 (s_1^2 + \varphi_0^2)}{s_2^2} \\ &\quad + \frac{i}{\varphi_0} \left(b_2 s_1 - a_1 s_1 - b_1 s_2 + \frac{a_2 s_1^2 - b_3 (s_1^2 + \varphi_0^2)}{s_2} - \frac{a_3 s_1 (s_1^2 + \varphi_0^2)}{s_2^2} \right), \end{split}$$

and

$$\begin{split} \phi_{21} &= \frac{s_2}{2\beta_0} \left[\left(\frac{\beta_0}{s_2} - \frac{s_1}{s_2} i \right) g_0 - i h_0 \right] \\ &= 3a_4 + b_5 - \frac{2s_1(a_5 + b_6)}{s_2} + \frac{(a_6 + 3b_7)(s_1^2 + \beta_0^2)}{s_2^2} \\ &+ \frac{i}{\beta_0} \left(3b_5 s_1 - 3b_4 s_2 - 3a_4 s_1 + \frac{(a_5 - b_6)(3s_1^2 + \beta_0^2)}{s_2} \right) \\ &- \frac{3s_1(a_6 + b_7)(s_1^2 + \beta_0^2)}{s_2^2} + \frac{3a_7(\beta_0^2 + s_1^2)^2}{s_2^3} \right). \end{split}$$

Furthermore,

$$\operatorname{Re}(c_{1}(h_{0}) = \operatorname{Re}\left\{\frac{i}{2\varphi_{0}}\left(\phi_{20}\phi_{11} - 2|\phi_{11}|^{2} - \frac{1}{3}|\phi_{02}|^{2}\right) + \frac{1}{2}\phi_{21}\right\}$$

$$= -\frac{1}{2\varphi_{0}}[\operatorname{Re}(\phi_{20})\operatorname{Im}(\phi_{11}) + \operatorname{Im}(\phi_{20})\operatorname{Re}(\phi_{11})] + \frac{1}{2}\operatorname{Re}(\phi_{21}).$$
(3.20)

Based the above analyze and the expression of $\text{Re}(c_1(h_0))$, we give our main results in this subsection.

Theorem 3.6. Suppose that (H_1) , (H_4) and (3.14) hold. Then model (3.1) undergoes a Hopf bifurcation at $h = h_0$.

- (a) The direction of the Hopf bifurcation is subcritical and the bifurcated periodic solutions are orbitally asymptotically stable if $\operatorname{Re}(c_1(h_0)) < 0$.
- (b) The direction of the Hopf bifurcation is supercritical and the bifurcated periodic solutions are unstable if $\operatorname{Re}(c_1(h_0)) > 0$.

To illustrate Theorem 3.6, we give two simple numerical examples.

Example 3.7. We choose the coefficients of the system (3.1) as follows

$$\alpha = 5, \quad \beta = 3.5, \quad \gamma = 0.4, \quad d_1 = 0.7, \quad d_2 = 0.5.$$
 (3.21)

We can see that $h_0 \approx 3.5804$ and the parameters in (3.21) satisfy (**H**₁), (**H**₄). Then $d_1 + \frac{A(h_0)d_2}{D(h_0)} \approx 0.2 > 0$, Re $(c_1(h_0)) \approx 8.069 > 0$. By Theorem 3.6, the model (3.1) undergoes a supercritical Hopf bifurcation at $h = h_0$ and the bifurcated periodic solutions are unstable.

Choosing the following coefficients

$$\alpha = 4, \ \beta = 1, \ \gamma = 0.5, \ d_1 = 0.3, \ d_2 = 0.1.$$
 (3.22)

In this case $h_0 = 1.75$ and satisfy (**H**₁), (**H**₄). Then $d_1 + \frac{A(h_0)d_2}{D(h_0)} = 0.2 > 0$, Re $(c_1(h_0)) \approx -3.833 < 0$. By Theorem 3.6, the model (3.1) undergoes a subcritical Hopf bifurcation at $h = h_0$ and the bifurcated periodic solutions are stable.

4 Positive nonconstant steady states

In this section, we consider the nonexistence and existence of positive nonconstant steady states of (1.7).

Let $0 = \mu_0 < \mu_1 < \mu_2 < \cdots < \mu_i < \cdots$ be the eigenvalues of the operator $-\Delta$ on Ω with the homogeneous Neumann boundary condition, and $E(\mu_i)$ be the eigenspace corresponding to μ_i . Let $X = \{(u, v) \in [C^1(\overline{\Omega})]^2 : \partial u / \partial v = \partial v / \partial v = 0 \text{ on } \partial \Omega\}$, $\{\phi_{ij} : j = 1, 2, \dots, \dim E(\mu_i)\}$ be an orthonormal basis of $E(\mu_i)$ and $X_{ij} = \{c\phi_{ij} : c \in \mathbb{R}^2\}$. Then, we decompose X as

$$X = \oplus_{i=1}^{\infty} X_i, \qquad X_i = \oplus_{i=1}^{\dim E(\mu_i)} X_{ij}.$$

4.1 A priori estimates

In this subsection, by using maximum principle in Lou and Ni [22] and Harnack inequality in Lin et al. [21], we establish a priori estimates of positive solutions of (1.7).

Theorem 4.1. Assume that (H_1) holds. Let (u, v) be any positive solution of (1.7). Then

$$0 < u(x) < 1+h, \quad 0 < v(x) < \frac{\beta - \gamma}{\gamma}(1+h), \quad \forall x \in \overline{\Omega}.$$

If $h > \alpha - 1$, then

$$1+h-\alpha < u(x) < 1+h, \quad \frac{\beta-\gamma}{\gamma}(1+h-\alpha) < v(x) < \frac{\beta-\gamma}{\gamma}(1+h), \quad \forall x \in \bar{\Omega}.$$

Proof. Let (u, v) be a given positive solution of (1.7). First of all, it follows from Maximum principle in [22] that $0 < u(x) < 1 + h, \forall x \in \overline{\Omega}$. Set $v(z_0) = \max_{\overline{\Omega}} v(x)$. By virtue of maximum principle in [22] again, we have

$$-\gamma+rac{eta u(z_0)}{u(z_0)+v(z_0)}\geq 0.$$

Thus

$$0 < v(x) < \frac{\beta - \gamma}{\gamma}(1 + h).$$

Assume $h > \alpha - 1$ and denote

$$u(x_0) = \min u(x), \quad v(y_0) = \min v(x)$$

for some $x_0, y_0 \in \overline{\Omega}$. We obtain

$$1 - u(x_0) - \frac{\alpha v(x_0)}{u(x_0) + v(x_0)} + h \le 0,$$

and

$$-\gamma + \frac{\beta u(y_0)}{u(y_0) + v(y_0)} \le 0.$$

Then

$$1-u(x_0)+h$$

So if assumption $(\mathbf{H_1})$ and $h > \alpha - 1$ hold, then

$$u(x_0) > 1+h-\alpha > 0$$
, $v(y_0) > \frac{\beta-\gamma}{\gamma}(1+h-\alpha) > 0$.

From this and Harnack inequality, we derive the desired estimates. This completes the proof of the theorem. $\hfill \Box$

4.2 Nonexistence of positive nonconstant steady states

In this subsection, we apply the energy method to prove the nonexistence of nonconstant positive steady-state solutions to (1.7). For convenience, let **P** denote the set of positive parameters α , β , γ and h.

Theorem 4.2. Under the assumption (\mathbf{H}_1) , let D_2 be a fixed positive constant satisfying $D_2 > \frac{\beta - \gamma}{\mu_1}$. Then there exists a positive constant $D_1 = D_1(\mathbf{P}, D_2)$ such that the model (1.7) has no nonconstant positive solution provided that $d_1 \ge D_1$ and $d_2 \ge D_2$.

Proof. Denote

$$\overline{u} = \frac{1}{|\Omega|} \int_{\Omega} u(x) dx, \quad \overline{v} = \frac{1}{|\Omega|} \int_{\Omega} v(x) dx$$

Now we prove $(u, v) = (\bar{u}, \bar{v})$ is a unique positive solution of (1.7), i.e. $(u, v) = U^*$.

Multiplying the first equation of (1.7) by $(u - \overline{u})$ and integrating the obtained equation from Theorem 4.1, we have

$$\begin{split} d_1 \int_{\Omega} |\nabla(u-\overline{u})|^2 dx &= \int_{\Omega} (u-\overline{u})^2 \left[1 - (u+\overline{u}) + h - \frac{\alpha \overline{v}}{\overline{u} + \overline{v}} + \frac{\alpha u v}{(u+v)(\overline{u} + \overline{v})} \right] dx \\ &- \int_{\Omega} \frac{\alpha u^2}{(u+v)(\overline{u} + \overline{v})} (v-\overline{v})(u-\overline{u}) dx \\ &\leq (1+h+L_1) \int_{\Omega} (u-\overline{u})^2 dx + L_2 \int_{\Omega} |u-\overline{u}| |v-\overline{v}| dx. \end{split}$$

Similarly,

$$d_{2} \int_{\Omega} |\nabla(v-\overline{v})|^{2} dx = \int_{\Omega} (v-\overline{v})^{2} \left[\frac{\beta \overline{u}}{\overline{u}+\overline{v}} - \gamma - \frac{\beta u v}{(u+v)(\overline{u}+\overline{v})} \right] dx + \int_{\Omega} \frac{\beta v^{2}}{(u+v)(\overline{u}+\overline{v})} (v-\overline{v})(u-\overline{u}) dx \leq (\beta-\gamma) \int_{\Omega} (v-\overline{v})^{2} dx + L_{3} \int_{\Omega} |u-\overline{u}| |v-\overline{v}| dx,$$

where the positive constants L_1 , L_2 , L_3 dependent on the coefficients **P**.

Furthermore

$$\begin{split} d_1 \int_{\Omega} |\nabla(u-\bar{u})|^2 dx + d_2 \int_{\Omega} |\nabla(v-\bar{v})|^2 dx \\ &\leq \int_{\Omega} [(1+h+L_1)(u-\bar{u})^2 + 2\vartheta |u-\bar{u}| |v-\bar{v}| + (\beta-\gamma)(v-\bar{v})^2] dx \\ &\leq \int_{\Omega} \bigg[(u-\bar{u})^2 \bigg(1+h+L_1 + \frac{\vartheta}{\epsilon} \bigg) + (v-\bar{v})^2 (\beta-\gamma+\vartheta\epsilon) \bigg] dx \end{split}$$

for $\vartheta = \frac{L_2 + L_3}{2}$ and an arbitrary small positive constant ϵ , in which the last inequality follows form the following fact

$$2\vartheta|u-\bar{u}||v-\bar{v}|=2\sqrt{\frac{\vartheta}{\epsilon}}|u-\bar{u}|\cdot\sqrt{\vartheta\epsilon}|v-\bar{v}|\leq \frac{\vartheta}{\epsilon}|u-\bar{u}|^2+\vartheta\epsilon|v-\bar{v}|^2.$$

By using the Poincaré inequality, we obtain

$$\int_{\Omega} \left\{ d_1 \mu_1 (u - \bar{u})^2 + d_2 \mu_1 (v - \bar{v})^2 \right\} dx$$

$$\leq \int_{\Omega} \left[|\nabla (u - \bar{u})|^2 \left(1 + h + L_1 + \frac{\vartheta}{\epsilon} \right) + |\nabla (v - \bar{v})|^2 (\beta - \gamma + \vartheta \epsilon) \right] dx.$$

Since $d_2\mu_1 > \beta - \gamma$, we can find a sufficiently small $\epsilon_0 > 0$ such that $d_2\mu_1 \ge \beta - \gamma + \vartheta\epsilon_0$. Finally, by taking $D_1 = \frac{1}{\mu_1} (1 + h + L_1 + \frac{\vartheta}{\epsilon_0})$, we can conclude that $u = \bar{u}$ and $v = \bar{v}$. This completes the proof.

4.3 Existence of positive nonconstant steady states

In this subsection, by using the Leray–Schauder degree theory, we discuss the existence of positive nonconstant solutions to (1.7) when the diffusion coefficients d_1 and d_2 vary while the parameters α , β , γ , h keep fixed.

For simplicity, define $F = (f_1, f_2)^T$ $(f_1, f_2$ be defined as in the Section 2). Thus, $J = F_U(U^*)$ and the model (1.7) can be written as follows

$$\begin{cases} -\Delta U = D^{-1}F(U), & x \in \Omega, \\ \frac{\partial U}{\partial \nu} = 0, & x \in \partial\Omega, \end{cases}$$
(4.1)

where $D = \text{diag}(d_1, d_2)$. Therefore, U solves (4.1) if and only if it satisfies

$$\widehat{f}(d_1, d_2, U) := U - (I - \Delta)^{-1} \{ D^{-1} F(U) + U \} = 0 \text{ on } X,$$
(4.2)

where *I* is the identity matrix, $(I - \Delta)^{-1}$ represents the inverse of $I - \Delta$ with homogeneous Neumann boundary condition.

A straightforward computation reveals

$$D_U \hat{f}(d_1, d_2, U^*) = I - (I - \Delta)^{-1} (D^{-1} J + I).$$

For each X_i , ξ is an eigenvalue of $D_U \hat{f}(d_1, d_2, U^*)$ on X_i if and only if $\xi(1 + \mu_i)$ is an eigenvalue of the matrix

$$M_i := \mu_i I - D^{-1} J = \begin{pmatrix} \mu_i - d_1^{-1} a_{11} & -d_1^{-1} a_{12} \\ -d_2^{-1} a_{21} & \mu_i - d_2^{-1} a_{22} \end{pmatrix}$$

Clearly,

$$\det M_i = d_1^{-1} d_2^{-1} [d_1 d_2 \mu_i^2 + (-d_1 a_{22} - d_2 a_{11}) \mu_i + a_{11} a_{22} - a_{12} a_{21}],$$

and

tr
$$M_i = 2\mu_i - d_1^{-1}a_{11} - d_2^{-1}a_{22}$$
.

Define

$$\widehat{g}(d_1, d_2, \mu) := d_1 d_2 \mu^2 + (-d_1 a_{22} - d_2 a_{11}) \mu + a_{11} a_{22} - a_{12} a_{21}.$$

Then $\widehat{g}(d_1, d_2, \mu_i) = d_1 d_2 \det M_i$. If

$$d_1a_{22} + d_2a_{11} > 2\sqrt{d_1d_2(a_{11}a_{22} - a_{12}a_{21})},$$
 (4.3)

then $\widehat{g}(d_1, d_2, \mu) = 0$ has two real roots

$$\mu_{+}(d_{1}, d_{2}) = \frac{d_{1}a_{22} + d_{2}a_{11} + \sqrt{(d_{1}a_{22} + d_{2}a_{11})^{2} - 4d_{1}d_{2}(a_{11}a_{22} - a_{12}a_{21})}}{2d_{1}d_{2}}$$
$$\mu_{-}(d_{1}, d_{2}) = \frac{d_{1}a_{22} + d_{2}a_{11} - \sqrt{(d_{1}a_{22} + d_{2}a_{11})^{2} - 4d_{1}d_{2}(a_{11}a_{22} - a_{12}a_{21})}}{2d_{1}d_{2}}$$

Let

$$A = A(d_1, d_2) = \{\mu : \mu \ge 0, \mu_-(d_1, d_2) < \mu < \mu_+(d_1, d_2)\},\$$

$$S_p = \{\mu_0, \mu_1, \mu_2, \dots\},\$$

and let $m(\mu_i)$ be multiplicity of μ_i . In order to calculate the index of $\hat{f}(d_1, d_2, \cdot)$ at U^* , we need the following lemma in [25].

Lemma 4.3. Suppose $\widehat{g}(d_1, d_2, \mu_i) \neq 0$ for all $\mu_i \in S_p$. Then

$$\operatorname{index}(\widehat{f}(d_1, d_2, \cdot), U^*) = (-1)^{\sigma},$$

where

$$\sigma = \begin{cases} \sum_{\mu_i \in A \cap S_p} m(\mu_i), & A \cap S_p \neq \emptyset, \\ 0, & A \cap S_p = \emptyset. \end{cases}$$

In particular, $\sigma = 0$ if $\widehat{g}(d_1, d_2, \mu_i) > 0$ for all $\mu_i \ge 0$.

Form Lemma 4.3, in order to calculate the index of $\hat{f}(d_1, d_2, \cdot)$ at U^* , we need to determine the range of μ for which $\hat{g}(d_1, d_2, \mu) < 0$.

Theorem 4.4. Suppose that $(\mathbf{H_1})$ and $(\mathbf{H_2})$ hold. If $\frac{a_{11}}{d_1} \in (\mu_k, \mu_{k+1})$ for some $k \ge 1$, and $\sigma_k = \sum_{i=1}^k m(\mu_i)$ is odd, then there exists a positive constant D^* such that for all $d_2 \ge D^*$, the model (1.7) has at least one positive nonconstant solution.

Proof. Since (**H**₂) holds, that is $a_{11} > 0$, it follows that if d_2 is large enough, then (4.3) holds and $\mu_+(d_1, d_2) > \mu_-(d_1, d_2) > 0$. Furthermore,

$$\lim_{d_2 \to \infty} \mu_+(d_1, d_2) = \frac{a_{11}}{d_1}, \quad \lim_{d_2 \to \infty} \mu_-(d_1, d_2) = 0.$$

As $\frac{a_{11}}{d_1} \in (\mu_k, \mu_{k+1})$, there exists $d_0 \gg 1$ such that

$$\mu_+(d_1, d_2) \in (\mu_k, \mu_{k+1}), \quad 0 < \mu_-(d_1, d_2) < \mu_1 \quad \forall d_2 \ge d_0.$$
 (4.4)

Form Theorem 4.2, we know that there exists $d > d_0$ such that (1.7) with $d_1 = d$ and $d_2 \ge d$ has no positive nonconstant solution. Let d > 0 be large enough such that $\frac{a_{11}}{d_1} < \mu_1$. Then there exists $D^* > d$ such that

$$0 < \mu_{-}(d_{1}, d_{2}) < \mu_{+}(d_{1}, d_{2}) < \mu_{1} \quad \text{for all } d_{2} \ge D^{*}.$$

$$(4.5)$$

Now we prove that, for any $d_2 \ge D^*$, (1.7) has at least one positive nonconstant solution. By way of contradiction, assume that the assertion is not true for some $D_2^* \ge D^*$. By using the homotopy argument, we can derive a contradiction in the sequel. Fixing $d_2 = D_2^*$, for $\tau \in [0, 1]$, we define

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

and consider the following problem

$$\begin{cases} -\triangle U = D^{-1}(\tau)F(U), & x \in \Omega, \\ \frac{\partial U}{\partial \nu} = 0, & x \in \partial\Omega. \end{cases}$$
(4.6)

Thus, *U* is a positive nonconstant solution of (1.7) if and only if it solves (4.6) with $\tau = 1$. Evidently, U^* is the unique positive constant solution of (4.6). For any $\tau \in [0,1]$, *U* is a positive nonconstant solution of (4.6) if and only if

$$h(U,\tau) = U - (I - \Delta)^{-1} \{ D^{-1}(\tau) F(U) + U \} = 0 \quad \text{on } X.$$
(4.7)

Form the discussion above, we know that (4.7) has no positive nonconstant solution when $\tau = 0$, and we have assumed that there is no such solution for $\tau = 1$ at $d_2 = D_2^*$. Clearly, $h(U,1) = \hat{f}(d_1, d_2, U), h(U,0) = \hat{f}(d, D^*, U)$ and

$$D_U \hat{f}(d_1, d_2, U^*) = I - (I - \Delta)^{-1} (D^{-1} J + I),$$

$$D_U \hat{f}(d, D^*, U^*) = I - (I - \Delta)^{-1} (\widetilde{D}^{-1} J + I),$$

where $\widehat{f}(\cdot, \cdot, \cdot)$ is as given in (4.2) and $\widetilde{D} = \text{diag}(d, D^*)$. From (4.4) and (4.5), we have $A(d_1, d_2) \cap S_p = \{\mu_1, \mu_2, \dots, \mu_k\}$ and $A(d, D^*) \cap S_p = \emptyset$. Since σ_k is odd, Lemma 4.3 yields

index
$$(h(\cdot, 1), U^*)$$
 = index $(\hat{f}(d_1, d_2, \cdot), U^*)$ = $(-1)^{\sigma_k}$ = -1,
index $(h(\cdot, 0), U^*)$ = index $(\hat{f}(d, D^*, \cdot), U^*)$ = $(-1)^0$ = 1.

From Theorem 4.1, there exist positive constants $\underline{C} = \underline{C}(d, d_1, D^*, D_2^*, \mathbf{P})$ and $\overline{C} = \overline{C}(d, D^*, \mathbf{P})$ such that the positive solutions of (4.7) satisfy $\underline{C} < u(x), v(x) < \overline{C}$ on $\overline{\Omega}$ for all $\tau \in [0, 1]$.

Define $\Sigma = \{(u, v)^T \in C^1(\overline{\Omega}, \mathbb{R}^2) : \underline{C} < u(x), v(x) < \overline{C}, x \in \overline{\Omega}\}$. Then $h(U, \tau) \neq 0$ for all $U \in \partial \Sigma$ and $\tau \in [0, 1]$. By virtue of the homotopy invariance of the Leray–Schauder degree, we have

$$\deg(h(\cdot,0),\Sigma,0) = \deg(h(\cdot,1),\Sigma,0). \tag{4.8}$$

Notice that both equations h(U, 0) = 0 and h(U, 1) = 0 have a unique positive solution U^* in Σ , and we obtain

$$deg(h(\cdot, 0), \Sigma, 0) = index(h(\cdot, 0), U^*) = 1,deg(h(\cdot, 1), \Sigma, 0) = index(h(\cdot, 1), U^*) = -1,$$

which contradicts (4.8). The proof is complete.

Pattern formation in ecological systems has been an important and fundamental topic in ecology. The development processes of such patterns are complex. The ratio-dependent predator– prey model exhibits rich interesting dynamics due to the singularity of the origin. To understand the underlying mechanism for patterns of plants and animals, we study the diffusive ratio-dependent predator–prey model (1.6) with prey stocking rate under Neumann boundary conditions. In particular, the existence, direction and stability of temporal patterns in (1.6) and the existence of spatial patterns in (1.6) are established. In virtue of our investigation, we may hope to reveal some interesting phenomena of pattern formations in ratio-dependent predator–prey models.

In this paper, we provided detailed analyses on the temporal and spatial patterns in a ratio-dependent predator-prey diffusive model (1.6) with linear stocking rate of prey species through qualitative analysis, such as stability theory, normal form and bifurcation technique. By the condition of (H_1) , we see that if one considers the model (1.5) with the prey stocking

rates, then the prey capturing rate α is allowed to be greater than the value $\beta/(\beta - \gamma)$ but the stocking rate on prey h cannot be too small and must be greater than $\alpha - 1 - \alpha \gamma / \beta > 0$. Biologically, if predators eat less prey, then more preys would be stocked to ensure that the system has the positive interior equilibrium or the predators and prey can coexist. Noticing that $\frac{du^*}{dh} = \frac{dv^*}{dh} = \beta > 0$, it is easy to see that u^* and v^* are both the strictly increasing function of h, that is, increasing the stock rate of prey species leads to the increasing of the density of both prey and predator species. The h > 0 in model (1.6) stabilisation the local asymptotic stability region of the positive equilibrium point at h = 0, and h has a stabilizing effect (see Theorem 2.3 and Theorem 3.1). Spatial and temporal patterns could occur in the reaction-diffusion model (1.6) via Turing instability, Hopf bifurcation and positive non-constant steady state. (1) We studied diffusion-induced Turing instability of the positive equilibrium U^* when the spatial domain is a bounded interval, it is found that under some conditions Turing instability will happen in the system, which produces spatial inhomogeneous patterns (see Theorem 3.2); (2) We also considered the existence and direction of Hopf bifurcation and the stability of the bifurcating periodic solution in (1.6), which exhibits temporal periodic patterns (see Theorem 3.6); (3) We established the existence of positive non-constant steady states which also corresponds to the spatial patterns. Moreover, numerical simulations are also carried out to illustrate theoretical analysis, from which the theoretical results are verified and patterns are expected to appear in the model. More interesting and complex behavior (for example, stripe, stripe-hole and hole Turing patterns on Fig. 3.4, 3.5, 3.6) about such model will further

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References

be explored.

- P. A. ABRAMS, L. R. GINZBURG, The nature of predation: Prey dependent, ratio dependent or neither? *Trends Ecol. Evol.* 15(2000), No. 8, 337–341. https://doi.org/10.1016/S0169-5347(00)01908-X
- [2] R. ARDITI, L. R. GINZBURG, Coupling in predator-prey dynamics: Ratio dependence, J. Theor. Biol. 139(1989), No. 3, 311–326. https://doi.org/10.1016/S0022-5193(89) 80211-5
- [3] R. ARDITI, L. R. GINZBURG, H. R. AKCAKAYA, Variation in plankton densities among lakes: A case for ratio dependent predation models, *Am. Nat.* 138(1991), No. 5, 1287– 1296. https://doi.org/10.1086/285286
- [4] R. ARDITI, H. SAIAH, Empirical evidence of the role of heterogeneity in ratio dependent consumption, *Ecology* **73**(1993), No. 5, 1544–1551. https://doi.org/10.2307/1940846
- [5] H. R. AKCAKAYA, R. ARDITI, L. R. GINZBURG, Ratio dependent predation: An abstraction that works, *Ecology* 76(1995), No. 3, 995–1004. https://doi.org/10.2307/1939362

- [6] P. A. BRAZA, The bifurcation structure of the Holling–Tanner model for predator–prey interaction using twotiming, SIAM J. Appl. Math. 63(2003), No. 3, 889–904. https://doi. org/10.2307/3648800; MR1969680
- [7] F. BEREZOVSKAYA, G. KAREV, R. ARDITI, Parametric analysis of the ratio-dependent predator-prey model, J. Math. Biol. 43(2001), No. 3, 221–246. https://doi.org/10.1007/ s002850000078; MR1868215; Zbl 0995.92043
- [8] F. BRAUER, A. C. SOUDACK, Coexistence properties of some predator-prey systems under constant rate harvesting and stocking, J. Math. Biol. 12(1981), 101–114. https://doi.org/ 10.1007/BF00275206; Zbl 0482.92015
- [9] M. BANERJEE, S. BANERJEE, Turing instabilities and spatio-temporal chaos in ratiodependent Holling–Tanner model, *Math. Biosci.* 236(2012), No. 1, 64–76. https://doi. org/10.1016/j.mbs.2011.12.005; MR2902111; Zbl 1375.92077
- [10] C. COSNER, D. L. DEANGELIS, J. S. AULT, D. B. OLSON, Effects of spatial grouping on the functional response of predators, *Theor. Popul. Biol.* 56(1999), No. 1, 65–75. https: //doi.org/10.1006/tpbi.1999.1414; Zbl 0928.92031
- [11] H. I. FREEDMAN, Deterministic mathematical model in population ecology, Monographs and Textbooks in Pure and Applied Mathematics, Vol. 57, Marcel Dekker, Inc., New York, 1980. https://doi.org/10.2307/2530090; MR0586941
- [12] L. R. GINZBURG, H. R. AKAKAYA, Consequences of ratio dependent predation for steady state properties of ecosystems, *Ecology* 73(1992), No. 5, 1536–1543. https://doi.org/10. 2307/1940006
- S. B. HSU, S. P. HUBBELL, P. WALTMAN, Competing predators, SIAM J. Appl. Math. 35(1978), No. 4, 617–625. https://doi.org/10.2307/2100978; MR0512172; Zbl 0394.92025
- [14] S. B. Hsu, T. W. HWANG, Y. KUANG, Global analysis of the Michaelis–Menten-type ratiodependent predator-prey system, J. Math. Biol. 42(2001), No. 6, 489–506. https://doi. org/10.1007/s002850100079; MR1845589; Zbl 0984.92035
- [15] D. HENRY, Geometric theory of semilinear parabolic equations, Lecture Notes in Mathematics, Vol. 840, Springer-Verlag, Berlin-New York, 1981. https://doi.org/10.1007/ BFb0089647; MR0610244
- [16] B. D. HASSARD, N. D. KAZARINOFF, Y. H. WAN, Theory and applications of Hopf bifurcation, London Mathematical Society Lecture Note Series, Vol. 41, Cambridge University Press, Cambridge-New York, 1981. https://doi.org/10.1090/conm/445; MR0603442; Zbl 0474.34002
- [17] J. K. HALE, H. KOÇAK, Dynamics and bifurcations, Texts in Applied Mathematics, Vol. 3, Springer-Verlag, New York, 1991. https://doi.org/10.1007/978-1-4612-4426-4; MR1138981; Zbl 0745.58002
- [18] A. J. LOTKA, The elements of physical biology, Williams and Wilkins, Baltimore, Williams Wilkins Co.; London, Baillière, Tindall Cox (1925). https://doi.org/10.1038/116461b0; Zbl 51.0416.06

- [19] M. LEI, Permanence and periodicity of a Holling III–Tanner system with stocking rate and diffusion, in: 2012 Fifth International Conference on Information and Computing Science, 2012, pp. 194–197. https://doi.org/10.1109/ICIC.2012.38
- [20] K. Q. LAN, C. R. ZHU, Phase portraits of predator-prey systems with harvesting rates, Discrete Contin. Dyn. Syst. A 32(2012), No. 3, 901–933. https://doi.org/10.3934/dcds. 2012.32.901; MR2851884; Zbl 1252.34052
- [21] C. S. LIN, W. M. NI, I. TAKAGI, Large amplitude stationary solutions to a chemotaxis system, J. Differential Equations 72(1988), No. 1, 1–27. https://doi.org/10.1016/ 0022-0396(88)90147-7; MR0929196; Zbl 0676.35030
- [22] Y. LOU, W. M. NI, Diffusion vs cross-diffusion: An elliptic approach, J. Differential Equations 154(1999), No. 1, 157–190. https://doi.org/10.1006/jdeq.1998.3559; MR1685622; Zbl 0934.35040
- [23] R. M. MAY, Stability and complexity in model ecosystems. With a new introduction by the author. 2nd ed., Princeton Landmarks in Biology. Princeton, NJ: Princeton University Press, Vol. 265, 2001. https://doi.org/10.1109/TSMC.1978.4309856; Zbl 1044.92047
- [24] R. PENG, M. X. WANG, Qualitative analysis on a diffusive prey-predator model with ratio-dependent functional response, *Sci. China Ser. A* 51(2008), No. 11, 2043–2058. https: //doi.org/10.1007/s11425-008-0037-8; MR2447429; Zbl 1181.35298
- [25] H. B. SHI, S. G. RUAN, Spatial, temporal and spatiotemporal patterns of diffusive predator-prey models with mutual interference, *IMA J. Appl. Math.* 80(2015), No. 5, 1534– 1568. https://doi.org/10.1093/imamat/hxv006; MR3403990; Zbl 1327.35376
- [26] T. SAHA, C. CHAKRABARTI, Dynamical analysis of a delayed ratio-dependent Holling– Tanner predator–prey model, J. Math. Anal. Appl. 358(2009), No. 2, 389–402. https:// doi.org/10.1016/j.jmaa.2009.03.072; MR2532515; Zbl 1177.34103
- [27] V. VOLTERRA, Variazionii e fluttuazioni del numero d'individui in specie animali conviventi (in Italian), *Mem. Acad. Lincei.* **2**(1926), 31–113.
- [28] Z. G. WANG, J. R. CHEN, Permanence and periodic solutions for predator-prey system with Holling III functional responses and stocking rate, *Math. Prac. Theory* 2009, No. 14, 1–13. https://doi.org/10.1360/972009-1650
- [29] D. M. XIAO, S. G. RUAN, Global dynamics of a ratio-dependent predator-prey system, J. Math. Biol. 43(2001), No. 3, 268–290. https://doi.org/10.1007/s002850100097; MR1868217; Zbl 1007.34031
- [30] D. M. XIAO, H. P. ZHU, Multiple focus and Hopf bifurcations in a predator-prey system with nonmonotonic functional response, *IAM J. Appl. Math.* 66(2006), No. 3, 802–819. https://doi.org/10.1137/050623449; MR2216721; Zbl 1109.34034
- [31] K. YANG, E. BERETTA, Global qualitative analysis of a ratio-dependent predator-prey system, J. Math. Biol. 36(1998), No. 4, 389–406. https://doi.org/10.1007/s002850050105; MR1624192; Zbl 0895.92032

- [32] X. Z. ZENG, J. C. ZHANG, Y. G. GU, Uniqueness and stability of positive steady state solutions for a ratio-dependent predator-prey system with a crowding term in the prey equation, *Nonlinear Anal. Real World Appl.* 24(2015), 163–174. https://doi.org/10.1016/ j.nonrwa.2015.02.005; MR3332888; Zbl 1327.35160
- [33] C. R. ZHU, K. Q. LAN, Phase portraits, Hopf bifurcations and limit cycles of Leslie-Gower predator-prey systems with harvesting rates, *Discrete Contin. Dyn. Syst. Ser. B* 14(2010), No. 1, 289–306. https://doi.org/10.3934/dcdsb.2010.14.289; MR2644265; Zbl 1201.34065