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Dynamics analysis of a diffusive prey-taxis system with memory and maturation delays

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Abstract. In this paper, a diffusive predator-prey system considering prey-taxis term with memory and maturation delays under Neumann boundary conditions is investigated. Firstly, the existence and stability of equilibria, especially the existence, uniqueness and stability of the positive equilibrium, are studied. Secondly, we prove that: (i) there is no spatially homogeneous steady state bifurcation as the eigenvalue of the negative Laplace operator is zero; (ii) as this system is only with memory delay τ_1, the the spatially nonhomogeneous Hopf bifurcation appears; (iii) when the model is only with maturation delay τ_2, the system has spatially homogeneous and nonhomogeneous periodic solutions; (iv) for the case of two delays, the system has rich dynamics, for example, stability switches, whose curves have four forms. Finally, some numerical simulations are produced to verify and support the theoretical results.

Keywords: diffusive system, fear effect, prey-taxis, memory delay, maturation delay.

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1 Introduction

The predator-prey dynamics is of great significance for developing the mathematical ecology and has been investigated by many scholars [5, 9, 10, 15, 18, 19]. That the prey population is also affected by the fear of predators not only the direct killing has been found [18]. On the basis of the experiment of Zanette [18], Wang et al. originally introduced the fear effect into the predator-prey model. The results showed that the incorporation of fear effect into the predator-prey model with Holling-II functional response can affect the stability of equilibrium [15]. With further research, for the various biological factors, Holling-II functional response of the predator-prey model with fear effect is modified differently, such as Allee effect [5], Leslie–Gower term [9] and prey refuge [19].

It is well known that in the spatial predator-prey model, predator and prey are usually considered to move randomly and are modeled by the reaction-diffusion equation. However, species also move towards certain directions due to the attraction or repulsion of some

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chemical signals, which is commonly called chemotactic movement [16]. In biology, predator population tends to move to the area where the density of the prey population is higher, which is termed prey-taxis [6,16]. This phenomenon was first noticed in a regional experiment about individual ladybugs and aphids by Karevia and Odell [7]. They derived a predator-prey model by considering prey-taxis as biased random walks, which is as follows

$$\begin{cases} \dfrac{\partial u(x,t)}{\partial t} = \Delta u - \nabla \cdot (u\rho(u,v)\nabla v) + G_1(u,v), \\ \dfrac{\partial v(x,t)}{\partial t} = D\Delta v + G_2(u,v), \end{cases} \tag{1.1}$$

where $u(x,t)$ and $v(x,t)$ represent separately the density of the prey and predator at time $t > 0$ and space location x; $-\nabla \cdot (u\rho(u,v)\nabla v)$ stands for the prey-taxis term, and $\rho(u,v)$ is a coefficient that may rely on $u(x,t)$ or $v(x,t)$ and D represents the diffusion rate; $G_1(u,v)$ and $G_2(u,v)$ describe the functional response functions.

Considering that the ability to perceive danger is also related to the memory of animals, Fagan pointed out that it is vital to incorporate spatial memory into models of animal movements [3]. Namely, combining the reaction-diffusion equation with the memory delay term, form the spatial memory model or the memory-based diffusion system, which has attracted many researchers [1, 12, 13]. For example, Aly [1] studied bifurcations of a memory-based diffusive predator-prey system. Shi et al. [12] showed the wellposedness of the memory-based diffusive system; Song [13] investigated Hopf bifurcation caused by memory delay for a memory-based diffusive system. Recently, some scholars have considered to combine memory delay with fear effect into diffusion system [2, 17]. For example, Debnath et al. [2] explored the role of memory and fear effect on prey-predator dynamics. Yang et al. [17] considered memory delay and fear effect into a predator-prey model with diffusion. They proved that the fear effect has both the stabilizing and the destabilizing effect on the coexisting equilibrium under different conditions.

After the predator gets its food, it does not immediately respond to a change in the number of population, but requires a period of digestion or pregnancy. Namely, there is a time delay to allow the predator to reach maturity. Therefore, it is necessary to introduce the maturation or digestion delay into the model. For example, Liu et al. [8] introduced the digestion delay into a predator-prey model with fear effect. They showed that the occurrence of stability switches and Hopf bifurcations as the digestion delay passes through a series of critical values. Shi et al. [11] studied a model incorporating memory-based diffusion and maturation delay. They proved that the proper association of two delay mechanisms can cause the appearance of the spatially inhomogeneous time-periodic patterns. Wang et al. [14] investigated the model collecting the spatial memory, maturation effect, prey-taxis and fear effect, which is as follows

$$\begin{cases} \dfrac{\partial u}{\partial t} = d_1\Delta u + \alpha\nabla(u\nabla v_{\tau_1}) + \dfrac{r_0 u}{1+kv_{\tau_2}} - du - au^2 - \dfrac{puv}{1+cu}, \ x \in \Omega, \ t > 0, \\ \dfrac{\partial v}{\partial t} = d_2\Delta v - mv^2 + \dfrac{quv}{1+cu}, \ x \in \Omega, \ t > 0, \\ \dfrac{\partial u}{\partial \nu} = \dfrac{\partial v}{\partial \nu} = 0, \ x \in \partial\Omega, \ t > 0, \\ u(x,t) = u_0(x) \geq 0, v(x,t) = v_0(x) \geq 0, \ x \in \Omega, \ t \in (-\max\{\tau_1,\tau_2\}, 0], \end{cases} \tag{1.2}$$

where the meanings of $u(x,t)$, $v(x,t)$ are the same to those of model (1.1); $v_{\tau_1} = v(x,t-\tau_1)$,

$v_{\tau_2} = v(x, t - \tau_2)$; τ_1 is the memory delay; τ_2 represents the maturation delay; d_1 and d_2 are self-diffusion coefficients; r_0 and d stand for separately prey's growth rate and natural death rate without considering fear cost; a and m are on behalf of the death rates for prey's and predator's intra-special competition, respectively; $\frac{1}{1+kv}$ denotes the fear factor; $\alpha\nabla(u\nabla v_{\tau_1})$ stands for the prey-taxis term; $\frac{uv}{1+cu}$ is the Holling-II functional response; Ω is a bounded domain in $\mathbb{R}^N$, $N \geq 1$, with a smooth boundary $\partial\Omega$; $\partial\nu$ is the outer flux; Δ and ∇ are Laplace and gradient operator defined in Ω. All of the parameters are positive. They showed that the model can exhibit rich dynamics, such as Turing instability, Hopf bifurcation and spatially nonhomogeneous (homogeneous) periodic distribution. They considered the spatial memory, pregnancy effect and fear effect for prey into a diffusive prey-taxis model with Holling-II functional response function. Motivated by this, we interest the system that the spatial memory and maturation effect in predator and fear effect in prey are incorporated in a diffusive prey-taxis model with the modified Leslie–Gower term and are curious about what dynamic behaviors for this complex model occur. In this paper, we aim to study the diffusive prey-taxis system considering fear effect with memory and maturation delays as follows,

$$\begin{cases} \dfrac{\partial u(x,t)}{\partial t} = d_1\Delta u + \dfrac{r_0 u}{1+av} - du - cu^2 - \dfrac{puv}{u+kv}, \ x \in \Omega, \ t > 0, \\ \dfrac{\partial v(x,t)}{\partial t} = d_2\Delta v - \chi\nabla(v\nabla u_{\tau_1}) + sv\left(1 - \dfrac{qv}{u_{\tau_2}+m}\right), \ x \in \Omega, \ t > 0, \\ \dfrac{\partial u(x,t)}{\partial \nu} = \dfrac{\partial v(x,t)}{\partial \nu} = 0, \ x \in \partial\Omega, \ t > 0, \\ u(x,t) = u_0(x) \geq 0, v(x,t) = v_0(x) \geq 0, \ x \in \Omega, \ t \in (-\max\{\tau_1,\tau_2\}, 0], \end{cases} \tag{1.3}$$

where $u_{\tau_1} = u(x, t - \tau_1)$; $u_{\tau_2} = u(x, t - \tau_2)$; $\frac{1}{1+av}$ is the fear factor; c represents the birth rate of prey; $-\chi\nabla(v\nabla u)$ stands for prey-taxis term; χ is prey-taxis coefficient; $\chi > 0$ (< 0) is called attractive (repulsive) prey-taxis; s is the intrinsic growth rate of predator; $\frac{puv}{u+kv}$ is the Holling-II functional response; $\frac{qv}{u+m}$ is the modified Leslie–Gower term. Keep the meanings and qualities of other parameters and functions be the same to system (1.2).

The remainder of this paper is structured as follows. In Sect. 2, we not only discuss the number and stability of equilibria, but also give the conditions for the existence and stability of the unique positive equilibrium. In Sect. 3, we analyze the existence of the spatially homogeneous and nonhomogeneous steady states and Hopf bifurcation, and exhibit the dynamics of the model with the cases of $\tau_1 > 0$, $\tau_2 = 0$; $\tau_1 = 0$, $\tau_2 > 0$; $\tau_1 > 0$, $\tau_2 > 0$. At the end, numerical simulations are given to substantiate the theoretical findings.

2 The existence and stability of equilibria

First, we discuss the existence and stability of the equilibria for the following ordinary differential equation of system (1.3)

$$\begin{cases} \dfrac{\mathrm{d}u}{\mathrm{d}t} = \dfrac{r_0 u}{1+av} - du - cu^2 - \dfrac{puv}{u+kv}, \\ \dfrac{\mathrm{d}v}{\mathrm{d}t} = sv\left(1 - \dfrac{qv}{u+m}\right). \end{cases} \tag{2.1}$$

Clearly, system (2.1) always has the trivial equilibrium $(0,\ 0)$ and a semi-trivial equilibrium $e_{01}(0, \frac{m}{q})$; as $r_0 > d$, the semi-trivial equilibrium $e_{10}(\frac{r_0-d}{c}, 0)$ exists; as

$$r_0 > r_0^* \triangleq (dk+p)(q+am)/kq, \tag{2.2}$$

system (2.1) has the unique positive solution $e_2(\bar{u}, \bar{v})$ with $\bar{v} = \frac{\bar{u}+m}{q}$, and $\bar{u}$ is the positive root of the equation

$$\frac{r_0 q}{a\bar{u} + am + q} - d - c\bar{u} - \frac{p(\bar{u}+m)}{(q+k)\bar{u} + km} = 0.$$

For each nonnegative equilibrium $e_2(\bar{u}, \bar{v})$, the Jacobi matrix can be expressed by

$$J_{(u,v)} := \begin{pmatrix} \dfrac{r_0}{1+av} - d - 2cu - \dfrac{pkv^2}{(u+kv)^2} & -\dfrac{ar_0 u}{(1+av)^2} - \dfrac{pu^2}{(u+kv)^2} \\ \dfrac{qsv^2}{(u+m)^2} & s - \dfrac{2qsv}{u+m} \end{pmatrix}. \tag{2.3}$$

For $(0,0)$ and $e_{10}(\frac{r_0-d}{c}, 0)$, they are always unstable because $\lambda_2 = s > 0$; for $e_{01}(0, \frac{m}{q})$, the eigenvalues of the Jacobi matrix are $\lambda_1 = \frac{r_0 q}{q+am} - d - \frac{p}{k}$, $\lambda_2 = -s < 0$, then e_{01} is locally asymptotically stable (unstable) if $r_0 < r_0^*$($r_0 > r_0^*$); the corresponding characteristic equation at the positive equilibrium $e_2(\bar{u}, \bar{v})$ is

$$\lambda^2 - (A_{11} - s)\lambda + \left(-sA_{11} - \frac{s}{q}A_{12}\right) = 0,$$

where

$$A_{11} = \frac{r_0}{1+a\bar{v}} - d - 2c\bar{u} - \frac{pk\bar{v}^2}{(\bar{u}+k\bar{v})^2},$$
$$A_{12} = -\frac{p\bar{u}}{(\bar{u}+k\bar{v})^2} - \frac{ar_0\bar{u}}{(1+a\bar{v})^2}.$$

Hence, if

$$A_{11} - s < 0, \qquad qA_{11} + A_{12} < 0, \tag{2.4}$$

then the positive equilibrium $e_2(\bar{u}, \bar{v})$ is locally asymptotically stable.

Summarizing the above works, we have the following theorem.

Theorem 2.1. *Model (2.1) always has an unstable trivial equilibrium $(0,0)$; if $r_0 > d$, then system (2.1) has a saddle $e_{10}(\frac{r_0-d}{c}, 0)$; the semi-trivial equilibrium $e_{01}(0, \frac{m}{q})$ is locally asymptotically stable when $r_0 < (dk+p)(q+am)/kq$ and unstable when $r_0 > (dk+p)(q+am)/kq$; suppose that condition (2.2) holds, then model (2.1) has the unique positive equilibrium $e_2(\bar{u}, \bar{v})$, and it is locally asymptotically stable as (2.4) are satisfied.*

Remark 2.2. Notice that (2.2) is not only the condition for the existence of positive equilibrium e_2, but also the change situation of the stability of equilibrium e_{01}. In other words, the appearance of the positive equilibrium e_2 leads to the instability of the boundary equilibrium e_{01}. Moreover, the condition for the existence of the equilibrium e_{10} is also contained in (2.2).

3 Stability analysis

In this section, we are going to analyse the stability of the positive equilibrium on one-dimension $\Omega = (0, \ell\pi)$. The linearized system of model (1.3) at $e_2(\bar{u}, \bar{v})$ is

$$\begin{cases} \dfrac{\partial u(x,t)}{\partial t} = d_1 \Delta u(x,t) + A_{11} u(x,t) + A_{12} v(x,t), & x \in \Omega, t > 0, \\ \dfrac{\partial v(x,t)}{\partial t} = d_2 \Delta v(x,t) - \chi \bar{v} \Delta u_{\tau_1} + \dfrac{s}{q} u_{\tau_2} - s v(x,t), & x \in \Omega, t > 0, \\ \dfrac{\partial u(x,t)}{\partial v} = 0, \dfrac{\partial v(x,t)}{\partial v} = 0, & x \in \partial\Omega, t > 0, \\ u(x,t) = u_0(x) \geq 0, v(x,t) = v_0(x) \geq 0, & x \in \Omega, t \in (-\max\{\tau_1, \tau_2\}, 0]. \end{cases} \tag{3.1}$$

The characteristic equation of model (3.1) at $e_2(\bar{u}, \bar{v})$ is

$$\Delta_n := \lambda^2 + A_n \lambda + B_n + C_n e^{-\lambda \tau_1} + D_n e^{-\lambda \tau_2} = 0, \qquad n \in \mathbb{N}, \tag{3.2}$$

where

$$\begin{aligned} A_n &= (d_1 + d_2) \frac{n^2}{l^2} - (A_{11} - s) > 0, & B_n &= \left(d_1 \frac{n^2}{l^2} - A_{11} \right) \left(d_2 \frac{n^2}{l^2} + s \right), \\ C_n &= -A_{12} \chi \bar{v} \frac{n^2}{l^2} > 0, & D_n &= -\frac{s}{q} A_{12} > 0. \end{aligned} \tag{3.3}$$

First, we discuss the existence of the steady states of model (1.3). Assume that $\lambda = 0$, then the characteristic equation (3.2) becomes

$$B_n + C_n + D_n = 0. \tag{3.4}$$

Note that there is no delay in equation (3.4), which is equivalent to, $\tau_1 = \tau_2 = 0$.

3.1 Steady states

If $n = 0$, one can deduce that $C_0 = 0$, then equation (3.4) can be rewritten as

$$B_0 + D_0 = -s A_{11} - \frac{s}{q} A_{12} = 0,$$

which is a contradiction with condition (2.4), therefore, there is no spatially homogeneous steady state bifurcation.

As $n \neq 0$, equation (3.4) becomes

$$d_1 d_2 \frac{n^4}{\ell^4} - (A_{11} d_2 - s d_1 + \chi A_{12} \bar{v}) \frac{n^2}{\ell^2} - \left(s A_{11} + \frac{s}{q} A_{12} \right) = 0. \tag{3.5}$$

Regard χ as a function of n^2, if

$$A_{11} d_2 - s d_1 > 0, \quad q (A_{11} d_2 + s d_1)^2 + 4 d_1 d_2 s A_{12} > 0, \tag{3.6}$$

then there is

$$\chi(n^2) = \frac{d_1 d_2 n^4 - (A_{11} d_2 - s d_1) l^2 n^2 - \left(sA_{11} + \frac{s}{q} A_{12}\right) l^4}{A_{12} \bar{v} l^2 n^2} > 0.$$

Taking the derivative of $\chi(n^2)$, there is

$$\chi'(n^2) = \frac{d_1 d_2 n^4 + \left(sA_{11} + \frac{s}{q} A_{12}\right) l^4}{A_{12} \bar{v} l^2 n^4}.$$

If $n < n_T$, one can deduce that $\chi'(n^2) > 0$, then $\chi(n^2)$ is increasing with n^2; if $n > n_T$, then $\chi'(n^2) < 0$, and $\chi(n^2)$ is decreasing with n^2 , where

$$n_T^2 = \ell^2 \sqrt{\frac{-(qsA_{11} + sA_{12})}{q d_1 d_2}}.$$

In order to ensure n^* is a positive integer, let

$$n^* = \begin{cases} [n_T], & \text{if } \chi([n_T]^2) > \chi\left(([n_T]+1)^2\right), \\ [n_T]+1, & \text{if } \chi([n_T]^2) < \chi\left(([n_T]+1)^2\right), \end{cases}$$

and $\chi^* = \chi(n^*)$, if $\chi > \chi^*$, then $B_n + C_n + D_n > 0$; if $\chi < \chi^*$, then there is $n \in \mathbb{N}_+$ satisfying $B_n + C_n + D_n = 0$.

To sum up, we have the following theorem.

Theorem 3.1. *Suppose that conditions (2.2), (2.4) and (3.6) hold. Let $n = 0$, then $e_2(\bar{u}, \bar{v})$ is always stable and there is no spatially homogeneous steady state bifurcation. Let $n \in \mathbb{N}_+$, if $\chi > \chi^*$, then $e_2(\bar{u}, \bar{v})$ is asymptotically stable; if $\chi < \chi^*$, then the spatially homogeneous steady state occurs.*

Remark 3.2. According to Theorem 3.1, the stability of positive equilibrium $e_2(\bar{u}, \bar{v})$ is affected by χ for the predator-prey system without delay ($\tau_1 = \tau_2 = 0$). That is to say, fast memory diffusion ($\chi > \chi^*$) remains the stability of the system, while slow memory diffusion ($\chi < \chi^*$) causes the system to be unstable. Moreover, if $A_{11} d_2 - s d_1 < 0$, $\chi(n^2) < 0$ for each $n \in \mathbb{N}_+$, then $e_2(\bar{u}, \bar{v})$ is asymptotically stable for $\chi > 0$. That is, for a sufficiently large self-diffusion d_1, there is no spatially homogeneous steady state bifurcation.

3.2 Hopf bifurcations

In this subsection, we always assume $\chi > \chi^*$ to analyze the Hopf bifurcation of model (1.3).

Let $\lambda = i\omega (\omega > 0)$, then the characteristic equation (3.2) becomes

$$-\omega^2 + B_n + C_n \cos(\omega\tau_1) + D_n \cos(\omega\tau_2) + i\big(A_n\omega - C_n \sin(\omega\tau_1) - D_n \sin(\omega\tau_2)\big) = 0. \quad (3.7)$$

As $n = 0$, equation (3.7) becomes

$$-\omega^2 + B_0 + D_0 \cos(\omega\tau_2) + i\left(A_0\omega - D_0 \sin(\omega\tau_2)\right) = 0, \quad (3.8)$$

which only contains pregnancy delay τ_2. By equation (3.8), we have

$$\sin(\omega\tau_2) = \frac{A_0\omega}{D_0} > 0, \qquad \cos(\omega\tau_2) = \frac{\omega^2 - B_0}{D_0},$$

and

$$\omega^4 + \left(A_0^2 - 2B_0\right)\omega^2 + B_0^2 - D_0^2 = 0. \tag{3.9}$$

By condition (2.4), one can obtain $B_0 + D_0 > 0$, $A_0^2 - 2B_0 > 0$, $\left(A_0^2 - 2B_0\right)^2 - 4(B_0^2 - D_0^2) > 0$. So we consider equation (3.9) from several different cases.

1) $qA_{11} < A_{12}$, there are no positive real roots of equation (3.9), so the system is always stable;

2) $qA_{11} > A_{12}$, for this case, equation (3.9) has only one positive root satisfying

$$\omega_{2,0}^{+} = \sqrt{\frac{-q\left(A_{11}^2 + s^2\right) + \sqrt{q^2\left(A_{11}^2 - s^2\right)^2 + 4s^2A_{12}^2}}{2q}}, \tag{3.10}$$

and the transversality condition

$$\left(\frac{\mathrm{d}\Re(\lambda)}{\mathrm{d}\tau_2}\right)^{-1}\Bigg|_{\tau_2=\tau_{2,0}^{j+}} = \frac{\sqrt{q^4(1+4sA_{11})(s-A_{11})^2 + 4q^2s^2A_{12}^2}}{s^2A_{12}^2} > 0, \tag{3.11}$$

where $\tau_{2,0}^{j+}$ is a sequence as follows

$$\tau_{2,0}^{j+} = \frac{1}{\omega_{2,0}^{+}}\left(\arccos\frac{q\omega_{2,0}^{+2} + qsA_{11}}{-sA_{12}} + 2j\pi\right), \qquad j = 0, 1, 2, \ldots \tag{3.12}$$

The sequence $\{\tau_{2,0}^{j+}\}_{j=0}^{\infty}$ is an increasing sequence for j, thus $\tau_2^* = \tau_{2,0}^{0+} = \min_{j\in\mathbb{N}} \tau_{2,0}^{j+}$. If $0 < \tau_2 < \tau_2^*$, all the real parts of the roots of equation (3.2) are negative; if $\tau_2 = \tau_{2,0}^{j+}$, equation (3.2) has a pair of pure imaginary roots; if $\tau_2 > \tau_2^*$, at least, one of the roots of equation (3.2) is positive.

Theorem 3.3. *Suppose that conditions (2.2) and (2.4) hold. When $n = 0$, for $\tau_1 = 0$, we have the following statements.*

(1) If $qA_{11} < A_{12}$ or $qA_{11} > A_{12}$, $\tau_2 < \tau_2^*$, then e_2 is asymptotically stable;

(2) if $qA_{11} > A_{12}$, $\tau_2 > \tau_2^*$, then e_2 is unstable;

(3) if $qA_{11} > A_{12}$, $\tau_2 = \tau_{2,0}^{j+}$ $(j = 0, 1, 2, \ldots)$, then the spatially homogeneous Hopf bifurcation occurs.

Remark 3.4. From the above discussion, we can see that model (1.3) does not undergo the spatially homogeneous Hopf bifurcation as it only has the spatial memory delay τ_1, and for this case, memory diffusion χ has no effect on the stability of the positive equilibrium $(\bar{u}, \bar{v})$ of system (1.3).

Next, we assume $n \neq 0$, and consider the two cases (1) $\tau_1 > 0$, $\tau_2 = 0$; or $\tau_1 = 0$, $\tau_2 > 0$; (2) $\tau_1 > 0$, $\tau_2 > 0$.

Case 1. $\tau_1 = 0$, $\tau_2 > 0$ or $\tau_1 > 0$, $\tau_2 = 0$.

When $\tau_1 = 0$, $\tau_2 > 0$, equation (3.7) can be simplified as

$$-\omega^2 + B_n + C_n + D_n \cos(\omega\tau_2) + i\left(A_n\omega - D_n \sin(\omega\tau_2)\right) = 0. \tag{3.13}$$

Solving equation (3.13), we obtain

$$\sin(\omega\tau_2) = \frac{A_n\omega}{D_n} > 0, \qquad \cos(\omega\tau_2) = \frac{\omega^2 - (B_n + C_n)}{D_n},$$

and

$$\omega^4 + \left(A_n^2 - 2(B_n + C_n)\right)\omega^2 + (B_n + C_n)^2 - D_n^2 = 0, \tag{3.14}$$

where for $\forall n \in \mathbb{N}_+$, $(B_n + C_n)^2 - D_n^2 \neq 0$.

1). There exists at least a $n \in \mathbb{N}_+$ satisfying the condition

$$|B_n + C_n| < D_n, \tag{3.15}$$

or

$$|B_n + C_n| > D_n, \quad A_n^2 = 2\left((B_n + C_n) - \sqrt{(B_n + C_n)^2 - D_n^2}\right), \tag{3.16}$$

such that equation (3.14) has a unique positive root

$$\omega_{2,n}^{+} = \sqrt{\frac{-\left(A_n^2 - 2(B_n + D_n)\right) + \sqrt{A_n^4 - 4(B_n + C_n)A_n^2 + 4D_n^2}}{2}},$$

and the corresponding τ_2 is

$$\tau_{2,n}^{j+} = \frac{1}{\omega_{2,n}^{+}}\left(\arccos\frac{\omega_{2,n}^{+2} - (B_n + C_n)}{D_n} + 2j\pi\right), \qquad j = 0, 1, 2, \ldots$$

For each fixed n, $\{\tau_{2,n}^{j+}\}_{j=0}^{\infty}$ is an increasing sequence with the variable j. Denote

$$\tau_2^* := \tau_{2,n_c}^{0+} = \min_{n\in\mathbb{N}_+}\left\{\tau_{2,n}^{0+}\right\},$$

and τ_2^* is the minimum value of the sequence of $\left\{\tau_{2,n}^{j+}\right\}_{j=0}^{\infty}$, $n \in \mathbb{N}_+$. The transversality condition is

$$\left(\frac{\mathrm{d}\Re(\lambda)}{\mathrm{d}\tau_2}\right)^{-1}\Bigg|_{\tau_2=\tau_{2,0}^{j+}} = \frac{2\left(\omega_{2,0}^{+2} - B_0\right) + A_0^2}{\left(\omega_{2,0}^{+2} - B_0\right)^2 + A_0^2\omega_{2,0}^{+2}} > 0. \tag{3.17}$$

That is, if $\tau_2 < \tau_2^*$, then all the real parts of the roots of equation (3.2) are negative; if $\tau_2 = \tau_2^*$, then equation (3.2) has a pair of pure imaginary roots; if $\tau_2 > \tau_2^*$, then there is at least a root of equation (3.2) that has positive real part.

2). There exists a $n \in \mathbb{N}_+$ satisfying

$$|B_n + C_n| > D_n, \quad A_n^2 < 2\left((B_n + C_n) - \sqrt{(B_n + C_n)^2 - D_n^2}\right), \tag{3.18}$$

such that, equation (3.13) has two positive roots,

$$\omega_{2,n}^{\pm} = \sqrt{\frac{-\left(A_n^2 - 2\left(B_n + C_n\right)\right) \pm \sqrt{A_n^4 - 4\left(B_n + C_n\right) A_n^2 + 4D_n^2}}{2}},$$

and the corresponding τ_2 are

$$\tau_{2,n}^{j\pm} = \frac{1}{\omega_{2,n}^{\pm}} \left(\arccos \frac{\omega_{2,n}^{\pm 2} - \left(B_n + C_n\right)}{D_n} + 2j\pi \right), \qquad j = 0, 1, 2, \ldots$$

The transversality condition is

$$\left(\frac{\mathrm{d}\Re(\lambda)}{\mathrm{d}\tau_2}\right)^{-1}\Bigg|_{\tau_2 = \tau_{2,n}^{j+}} = \frac{\sqrt{A_n^4 - 4\left(B_n + C_n\right) A_n^2 + 4D_n^2}}{\left(\omega_{2,n}^{+2} - B_n\right)^2 + A_n^2 \omega_{2,n}^{+2}} > 0,$$
$$\left(\frac{\mathrm{d}\Re(\lambda)}{\mathrm{d}\tau_2}\right)^{-1}\Bigg|_{\tau_2 = \tau_{2,n}^{j-}} = -\frac{\sqrt{A_n^4 - 4\left(B_n + C_n\right) A_n^2 + 4D_n^2}}{\left(\omega_{2,n}^{-2} - B_n\right)^2 + A_n^2 \omega_{2,n}^{-2}} < 0.$$

For each fixed $n \in \mathbb{N}_+$, $\{\tau_{2,n}^{j+}\}_{j=0}^{\infty}$, $\{\tau_{2,n}^{j-}\}_{j=0}^{\infty}$ are increasing sequences with j, and $\tau_{2,n}^{j+} < \tau_{2,n}^{j-}$ due to $\omega_{2,n}^{j+} > \omega_{2,n}^{j-}$. Reorder $\{\tau_{2,n}^{j+}\}_{j=0}^{\infty}$, $\{\tau_{2,n}^{j-}\}_{j=0}^{\infty}$ as increasing subsequences and denote as $\{\tau_2^{S+}\}_{S=1}^{\infty}$,$\{\tau_2^{S-}\}_{S=1}^{\infty}$, respectively, and $\tau_2^* = \tau_2^{0+}$ is the minimum value. There exists a $K_2 \in \mathbb{N}$, such that all the real parts of the roots of model (3.13) are negative for

$$\tau_2 \in \left(0, \tau_2^{0+}\right) \bigcup \left(\tau_2^{0-}, \tau_2^{1+}\right) \bigcup \cdots \bigcup \left(\tau_2^{(K_2-1)-}, \tau_2^{K_2+}\right);$$

at least one root of model (3.13) has positive real part for

$$\tau_2 \in \left(\tau_2^{0+}, \tau_2^{0-}\right) \bigcup \left(\tau_2^{1+}, \tau_2^{1-}\right) \bigcup \cdots \bigcup \left(\tau_2^{K_2+}, \infty\right).$$

3). For each $n \in \mathbb{N}_+$ satisfying

$$|B_n + C_n| > D_n, \quad A_n^2 > 2\left(\left(B_n + C_n\right) - \sqrt{\left(B_n + C_n\right)^2 - D_n^2}\right), \tag{3.19}$$

(3.13) has no positive root.

Theorem 3.5. *Suppose that (2.2), (2.4) and $\chi < \chi^*$ hold. When $\tau_1 = 0$, for $n \neq 0$, we have the results.*

1. The positive equilibrium $e_2(\bar{u}, \bar{v})$ is asymptotically stable if one of the following conditions is satisfied:

- *(1) $\exists n \in \mathbb{N}_+$, (3.15) or (3.16), $\tau_2 < \tau_2^*$;*
- *(2) $\exists n \in \mathbb{N}_+$, (3.18), $\tau_2 \in \left(0, \tau_2^{0+}\right) \cup \cdots \cup \left(\tau_2^{(K_2-1)-}, \tau_2^{K_2+}\right)$, $K_2 \geq 0$;*
- *(3) $\forall n \in \mathbb{N}_+$, (3.19).*

2. The positive equilibrium $e_2(\bar{u}, \bar{v})$ is unstable if one of the following conditions holds:

(1) $\exists n \in \mathbb{N}_+$, (3.15) *or* (3.16) , $\tau_2 > \tau_2^*$;

(2) $\exists n \in \mathbb{N}_+$, (3.18) *holds*, $\tau_2 \in \left(\tau_2^{0+}, \tau_2^{0-}\right) \cup \cdots \cup \left(\tau_2^{K_2+}, +\infty\right)$, $K_2 \geq 0$.

3. System (1.3) undergoes the spatially nonhomogeneous Hopf bifurcation if one of the following conditions is met:

(1) $\exists n \in \mathbb{N}_+$, (3.15) *or* (3.16) *holds*, $\tau_2 = \tau_{2,n}^{j+}$ $(j = 0, 1, 2, \ldots)$;

(2) $\exists n \in \mathbb{N}_+$, (3.18) *holds*, $\tau_2 = \tau_2^{S\pm}$ $(S = 0, 1, 2, \ldots)$.

When $\tau_1 > 0$ and $\tau_2 = 0$, the discussion process is the same as above. Denote

$$\omega_{1,n}^{\pm} = \sqrt{\frac{-\left(A_n^2 - 2\left(B_n + D_n\right)\right) \pm \sqrt{A_n^4 - 4\left(B_n + D_n\right) A_n^2 + 4C_n^2}}{2}}, \tag{3.20}$$

and the corresponding delay τ_1 are

$$\tau_{1,n}^{j\pm} = \frac{1}{\omega_{1,n}^{\pm}}\left(\arccos \frac{\omega_{1,n}^{\pm 2} - \left(B_n + D_n\right)}{C_n} + 2j\pi\right), \qquad j = 0, 1, 2, \ldots \tag{3.21}$$

Let

$$\tau_1^* := \tau_1^{0+} = \min_{n \in \mathbb{N}_+} \left\{\tau_{1,n}^{0+}\right\}. \tag{3.22}$$

We have the following statements.

Theorem 3.6. *Suppose that* (2.2), (2.4) *and* $\chi < \chi^*$ *hold. When* $\tau_2 = 0$, *for* $n \neq 0$, *the following statements hold.*

1. The positive equilibrium $(\bar{u}, \bar{v})$ *is asymptotically stable if the parameters satisfy one of the following conditions:*

(1) $\exists n \in \mathbb{N}_+$, $|B_n + D_n| < C_n$ *or* $|B_n + D_n| > C_n$, $A_n^2 = 2\left(\left(B_n + D_n\right) - \sqrt{\left(B_n + D_n\right)^2 - C_n^2}\right)$ *hold*, $\tau_1 < \tau_1^*$;

(2) $\exists n \in \mathbb{N}_+$, $|B_n + D_n| > C_n$, $A_n^2 < 2\left(\left(B_n + D_n\right) - \sqrt{\left(B_n + D_n\right)^2 - C_n^2}\right)$ *hold*, $\tau_1 \in \left(0, \tau_1^{0+}\right) \cup \cdots \cup \left(\tau_1^{(K_1-1)-}, \tau_2^{K_1+}\right)$, $K_1 \geq 0$;

(3) $\forall n \in \mathbb{N}_+$, $|B_n + D_n| > C_n$, $A_n^2 > 2\left(\left(B_n + D_n\right) - \sqrt{\left(B_n + D_n\right)^2 - C_n^2}\right)$ *hold.*

2. The positive equilibrium $(\bar{u}, \bar{v})$ *is unstable if the parameters meet one of the following conditions:*

(1) $\exists n \in \mathbb{N}_+$, $|B_n + D_n| < C_n$ *or* $|B_n + D_n| > C_n$, $A_n^2 = 2\left(\left(B_n + D_n\right) - \sqrt{\left(B_n + D_n\right)^2 - C_n^2}\right)$ *hold*, $\tau_1 > \tau_1^*$;

(2) $\exists n \in \mathbb{N}_+$, $|B_n + D_n| > C_n$, $A_n^2 < 2\left(\left(B_n + D_n\right) - \sqrt{\left(B_n + D_n\right)^2 - C_n^2}\right)$ *hold*, $\tau_1 \in \left(\tau_1^{0+}, \tau_1^{0-}\right) \cup \cdots \cup \left(\tau_1^{K_1+}, +\infty\right)$, $K_1 \geq 0$;

3. System (1.3) undergoes the spatially nonhomogeneous Hopf bifurcation if the parameters fulfill one of the following conditions:

(1) $\exists n \in \mathbb{N}_+$, $|B_n + D_n| < C_n$ *or* $|B_n + D_n| > C_n$, $A_n^2 = 2\Big((B_n + D_n) - \sqrt{(B_n + D_n)^2 - C_n^2}\Big)$ *hold,* $\tau_1 = \tau_{1,n}^{j+}$ $(j = 0, 1, 2, \dots)$;

(2) $\exists n \in \mathbb{N}_+$, $|B_n + D_n| > C_n$, $A_n^2 < 2\Big((B_n + D_n) - \sqrt{(B_n + D_n)^2 - C_n^2}\Big)$ *hold,* $\tau_1 = \tau_{1,n}^{S+}$ $(S = 0, 1, 2, \dots)$.

Case 2. $\tau_1, \tau_2 > 0$

We rewrite (3.2) with $\tau_1 > 0$ and $\tau_2 > 0$ as

$$D_n(\lambda, \tau_1, \tau_2) := P_{0,n}(\lambda) + P_{1,n}(\lambda)e^{-\lambda\tau_1} + P_{2,n}(\lambda)e^{-\lambda\tau_2} = 0, \tag{3.23}$$

where

$$P_{0,n}(\lambda) = \lambda^2 + A_n\lambda + B_n, \qquad P_{1,n}(\lambda) = C_n, \qquad P_{2,n}(\lambda) = D_n, \tag{3.24}$$

A_n, B_n, C_n and D_n are defined in (3.3). $\forall n \in \mathbb{N}_+$, $P_{S,n}(\lambda)$ $(S = 0, 1, 2)$ satisfy

(I) $\deg P_{0,n}(\lambda) \geq \max\{\deg P_{1,n}(\lambda), \deg P_{2,n}(\lambda)\}$;

(II) $P_{0,n}(0) + P_{1,n}(0) + P_{2,n}(0) = B_n + C_n + D_n \neq 0$;

(III) $P_{0,n}(\lambda)$, $P_{1,n}(\lambda)$, $P_{2,n}(\lambda)$ has no common zeros;

(IV) $\lim_{\lambda\to\infty}\left(\left|\frac{P_{1,n}(\lambda)}{P_{0,n}(\lambda)}\right| + \left|\frac{P_{2,n}(\lambda)}{P_{0,n}(\lambda)}\right|\right) < 1$.

Notice that $\lambda = 0$ is the solution of (3.23), thus we assume that the root of (3.23) is $\lambda = i\omega$ $(\omega > 0)$, and for $\forall\omega > 0$, $P_{j,n}(i\omega) \neq 0$ $(j = 0, 1, 2)$. According to [4], $\lambda = i\omega$ $(\omega > 0)$ is a solution of (3.23) if and only if Ω_n is nonempty. Ω_n is defined as,

$$\Omega_n = \left\{\omega \in \mathbb{R}_+ : |P_{1,n}(i\omega)| + |P_{2,n}(i\omega)| \geq |P_{0,n}(i\omega)|, \big||P_{1,n}(i\omega)| - |P_{2,n}(i\omega)|\big| \leq |P_{0,n}(i\omega)|\right\}. \tag{3.25}$$

If Ω_n is nonempty, then we denote the delays (τ_1, τ_2) satisfying (3.25) as

$$\begin{aligned} \tau_{1,n,K_1}^{\pm}(\omega) &= \frac{\angle\arg\dfrac{P_{1,n}(i\omega)}{P_{0,n}(i\omega)} + (2K_1 - 1)\pi \pm \theta_{1,n}(\omega)}{\omega}, \quad K_1 = K_{1,n}^{\pm}, K_{1,n}^{\pm} + 1, K_{1,n}^{\pm} + 2, \dots, \\ \tau_{2,n,K_2}^{\pm}(\omega) &= \frac{\angle\arg\dfrac{P_{2,n}(i\omega)}{P_{0,n}(i\omega)} + (2K_2 - 1)\pi \mp \theta_{2,n}(\omega)}{\omega}, \quad K_2 = K_{2,n}^{\pm}, K_{2,n}^{\pm} + 1, K_{2,n}^{\pm} + 2, \dots, \end{aligned} \tag{3.26}$$

where

$$\begin{aligned} \theta_{1,n}(\omega) &= \arccos\left(\frac{|P_{0,n}(i\omega)|^2 + |P_{1,n}(i\omega)|^2 - |P_{2,n}(i\omega)|^2}{2|P_{0,n}(i\omega)||P_{1,n}(i\omega)|}\right), \\ \theta_{2,n}(\omega) &= \arccos\left(\frac{|P_{0,n}(i\omega)|^2 - |P_{1,n}(i\omega)|^2 + |P_{2,n}(i\omega)|^2}{2|P_{0,n}(i\omega)||P_{2,n}(i\omega)|}\right). \end{aligned} \tag{3.27}$$

$K_{1,n}^{\pm}$ and $K_{2,n}^{\pm}$ is the smallest integers to ensure $\tau_{1,n,K_1}^{\pm}$, $\tau_{2,n,K_2}^{\pm}$ are positive. Furthermore, the mode-n stability switching curves (3.23) are

$$\mathcal{T}_n = \bigcup_{K=1}^{N} \left\{ \bigcup_{K_1=-\infty}^{+\infty} \bigcup_{K_2=-\infty}^{+\infty} \left(\mathcal{T}_{n,K_1,K_2}^{+K}, \mathcal{T}_{n,K_1,K_2}^{-K} \right) \bigcap \mathbb{R}_+^2 \right\},$$

where

$$\mathcal{T}_{n,K_1,K_2}^{\pm K} = \left\{ \left(\tau_{1,n,K_1}^{\pm}(\omega), \tau_{2,n,K_2}^{\mp}(\omega) \right) : \omega \in \Omega_n \right\}.$$

By [4, Proposition 4.5], we have the following conclusion about $\mathcal{T}_n$ and Ω_n.

Theorem 3.7. *The mode-n stability switching curves $\mathcal{T}_n$ and the crossing set Ω_n have the following structures with $\forall n \in \mathbb{N}_+$,*

(1) $\mathcal{T}_n$ is a series of spiral-like curves

(1a) for $\Omega_n = [\omega_{2,n}^r, \omega_{1,n}^r]$, if $|B_n| < |C_n - D_n|$;

(1b) for $\Omega_n = [\omega_{1,n}^l, \omega_{2,n}^l] \bigcup [\omega_{2,n}^r, \omega_{1,n}^r]$, if

$$C_n + D_n < |B_n|, \quad A_n^2 < 2\left(B_n - \sqrt{B_n^2 - (C_n - D_n)^2} \right);$$

(2) $\mathcal{T}_n$ contains a series of open ended curves and a series of spiral-like curves for $\Omega_n = (0, \omega_{2,n}^l] \bigcup [\omega_{2,n}^r, \omega_{1,n}^r]$, if

$$|C_n - D_n| < |B_n| < C_n + D_n, \quad A_n^2 < 2\left(B_n - \sqrt{B_n^2 - (C_n - D_n)^2} \right);$$

(3) $\mathcal{T}_n$ is a series of open ended curves for $\Omega_n = \left(0, \omega_{1,n}^r\right]$, if

$$|C_n - D_n| < |B_n| < C_n + D_n, \quad A_n^2 > 2\left(B_n - \sqrt{B_n^2 - (C_n - D_n)^2} \right);$$

(4) $\mathcal{T}_n$ is a series of closed curves for $\Omega_n = [\omega_{1,n}^l, \omega_{1,n}^r]$, if

$$C_n + D_n < |B_n|, \quad 2\left(B_n - \sqrt{B_n^2 - (C_n - D_n)^2} \right) < A_n^2 < 2\left(B_n - \sqrt{B_n^2 - (C_n + D_n)^2} \right),$$

where

$$\omega_{1,n}^l = \sqrt{\frac{-\left(A_n^2 - 2B_n\right) - \sqrt{\Delta_1}}{2}}, \qquad \omega_{1,n}^r = \sqrt{\frac{-\left(A_n^2 - 2B_n\right) + \sqrt{\Delta_1}}{2}},$$

$$\omega_{2,n}^l = \sqrt{\frac{-\left(A_n^2 - 2B_n\right) - \sqrt{\Delta_2}}{2}}, \qquad \omega_{2,n}^r = \sqrt{\frac{-\left(A_n^2 - 2B_n\right) + \sqrt{\Delta_2}}{2}},$$

and

$$\Delta_1 = A_n^4 - 4B_n A_n^2 + 4\left(C_n + D_n\right)^2,$$
$$\Delta_2 = A_n^4 - 4B_n A_n^2 + 4\left(C_n - D_n\right)^2.$$

Proof. By (3.25) and (3.24), $|P_{1,n}(i\omega)| + |P_{2,n}(i\omega)| = |P_{0,n}(i\omega)|$ can be rewritten as

$$\omega^4 + \left(A_n^2 - 2B_n\right)\omega^2 + B_n^2 - \left(C_n + D_n\right)^2 = 0. \tag{3.28}$$

We have the cases:

- when $C_n + D_n < |B_n|$, if $A_n^2 > 2\left(B_n - \sqrt{B_n^2 - (C_n + D_n)^2}\right)$, for $\forall\omega > 0$, then $|P_{1,n}(i\omega)| + |P_{2,n}(i\omega)| < |P_{0,n}(i\omega)|$, thus $\Omega_n = \emptyset$; if $A_n^2 < 2\left(B_n - \sqrt{B_n^2 - (C_n + D_n)^2}\right)$, for $\omega \in \left[\omega_{1,n}^l, \omega_{1,n}^r\right]$, then $|P_{1,n}(i\omega)| + |P_{2,n}(i\omega)| \geq |P_{0,n}(i\omega)|$;
- when $C_n + D_n > |B_n|$, $|P_{1,n}(i\omega)| + |P_{2,n}(i\omega)| \geq |P_{0,n}(i\omega)|$ for $\omega \in \left(0, \omega_{1,n}^r\right]$.

Similarly, $\left||P_{1,n}(i\omega)| - |P_{2,n}(i\omega)|\right| = |P_{0,n}(i\omega)|$ can expressed as

$$\omega^4 + \left(A_n^2 - 2B_n\right)\omega^2 + B_n^2 - \left(C_n - D_n\right)^2 = 0. \tag{3.29}$$

For the same discussion, we also have:

- when $|C_n - D_n| < |B_n|$, $\Omega_n = (0, \infty)$ for $A_n^2 < 2\left(B_n - \sqrt{B_n^2 - (C_n - D)^2}\right)$; $\Omega_n = \left(0, \omega_{2,n}^l\right] \cup \left[\omega_{2,n}^r, +\infty\right)$ for $A_n^2 > 2\left(B_n - \sqrt{B_n^2 - (C_n - D)^2}\right)$;
- when $|C_n - D_n| > |B_n|$, $\Omega_n = \left[\omega_{2,n}^r, +\infty\right)$.

Particularly, $\omega_{1,n}^l < \omega_{2,n}^l$, $\omega_{2,n}^r < \omega_{1,n}^r$ due to $\Delta_1 > \Delta_2$. □

Remark 3.8. In addition, $\Omega_n = \emptyset$ for

$$C_n + D_n < |B_n|, A_n^2 > 2\left(B_n - \sqrt{B_n^2 - (C_n - D_n)^2}\right),$$

the conditions are continue holding for $n \to \infty$.

Let $\lambda = \sigma + i\omega$, and view τ_1, τ_2 as functions $\tau_1(\sigma, \omega)$, $\tau_2(\sigma, \omega)$. Calculating from (3.23), we have

$$\begin{aligned}
\frac{P_{1,n}(i\omega)}{P_{0,n}(i\omega)}e^{-i\omega\tau_1} = & \frac{C_n}{\omega^4 + (A_n^2 - 2B_n)\omega^2 + B_n^2}\left(\left(-\omega^2 + B_n\right)\cos(\omega\tau_1) - A_n\omega\sin(\omega\tau_1)\right) \\
& + \frac{-C_n i}{\omega^4 + (A_n^2 - 2B_n)\omega^2 + B_n^2}\left(\left(-\omega^2 + B_n\right)\sin(\omega\tau_1) + A_n\omega\cos(\omega\tau_1)\right), \\
\frac{P_{2,n}(i\omega)}{P_{0,n}(i\omega)}e^{-i\omega\tau_2} = & \frac{D_n i}{\omega^4 + (A_n^2 - 2B_n)\omega^2 + B_n^2}\left(\left(-\omega^2 + B_n\right)\cos(\omega\tau_2) - A_n\omega\sin(\omega\tau_2)\right) \\
& + \frac{-D_n i}{\omega^4 + (A_n^2 - 2B_n)\omega^2 + B_n^2}\left(\left(-\omega^2 + B_n\right)\sin(\omega\tau_2) + A_n\omega\cos(\omega\tau_2)\right),
\end{aligned}$$

and

$$\begin{aligned}
R_1 &= \mathrm{Re}\left(\frac{P_{1,n}(i\omega)}{P_{0,n}(i\omega)}e^{-i\omega\tau_1}\right), \qquad I_1 = \mathrm{Im}\left(\frac{P_{1,n}(i\omega)}{P_{0,n}(i\omega)}e^{-i\omega\tau_1}\right), \\
R_2 &= \mathrm{Re}\left(\frac{P_{2,n}(i\omega)}{P_{0,n}(i\omega)}e^{-i\omega\tau_2}\right), \qquad I_2 = \mathrm{Im}\left(\frac{P_{2,n}(i\omega)}{P_{0,n}(i\omega)}e^{-i\omega\tau_2}\right).
\end{aligned}$$

Then

$$R_2 I_1 - R_1 I_2 = \frac{-C_n D_n}{\omega^4 + \left(A_n^2 - 2B_n\right)\omega^2 + B_n^2} \sin\left(\omega\left(\tau_1 - \tau_2\right)\right). \tag{3.30}$$

The sign of $R_2I_1 - R_1I_2$ is determined by $\sin\left(\omega\left(\tau_1 - \tau_2\right)\right)$ because $-C_nD_n < 0$, $\omega^4 + \left(A_n^2 - 2B_n\right)\omega^2 + B_n^2 > 0$, for $\forall\omega > 0$.

From [4, Proposition 6.1], we have the following lemma.

Lemma 3.9. *Let $\omega \in \Omega_n$, $(\tau_1, \tau_2) \in \mathcal{T}_n$ such that $i\omega$ is a simple root of (3.23). A pair of conjugate complex roots cross the imaginary axis to the right (left) for $\sin\left(\omega\left(\tau_1 - \tau_2\right)\right) < 0$ (> 0) as (τ_1, τ_2) moves from the region on the right to the left of $\mathcal{T}_n$.*

If the following conditions hold:

(1) when $n = 0$, $|B_0| > D_0$, $A_0^2 < 2\left(B_0 - \sqrt{B_0^2 - D_0^2}\right)$ or $|B_0| < D_0$;

(2) when $n \in \mathbb{N}_+$, $|B_n| > C_n + D_n$, $A_n^2 < 2\left(B_n - \sqrt{B_n^2 - (C_n + D_n)^2}\right)$ or $|B_n| < C_n + D_n$;

then there exists (τ_1^0, τ_2^0) such that (3.23) has the pure imaginary root $i\omega^0$. Moreover, when $\omega^0\left(\tau_1^0 - \tau_2^0\right) \neq k\pi$ ($k \in \mathbb{Z}$), there is a neighborhood U_1 of (τ_1^0, τ_2^0), the following results hold.

Theorem 3.10. *Denote that U_2 is the stable region enclosed by the stability curves $\mathcal{T}_n$ and $\tau_1 - \tau_2$, but not contain $\mathcal{T}_n$, then*

(1) when $(\tau_1, \tau_2) \in U_1 \cap U_2$, the positive equilibrium $(\bar{u}, \bar{v})$ is asymptotically stable;

(2) when $(\tau_1, \tau_2) \in U_1 \backslash \bar{U}_2$, the positive equilibrium $(\bar{u}, \bar{v})$ is unstable;

(3) when $(\tau_1, \tau_2) \in \mathcal{T}_n$, system (1.3) undergoes the spatially nonhomogeneous Hopf bifurcation at $(\bar{u}, \bar{v})$.

4 Numerical simulations

In this section, we give some numerical simulations to support the findings of this paper.

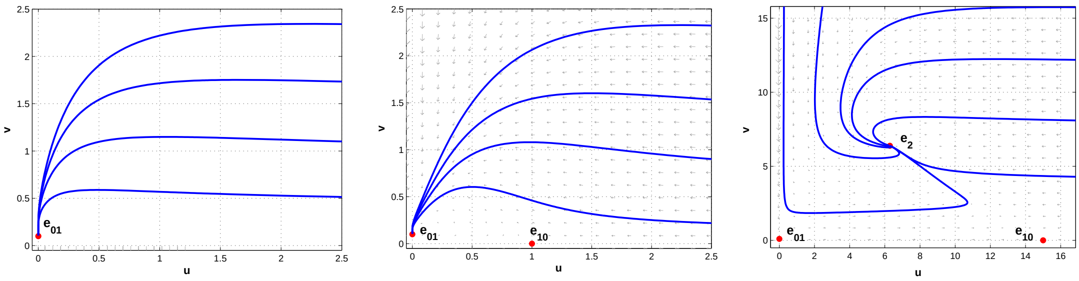
The parameters are chosen as $a = 0.1$, $c = 0.1$, $p = 0.1$, $k = 0.1$, $s = 0.1$, $m = 0.1$, $q = 1$, $d = 0.5$. Model (1.3) has only one non-negative stable solution $e_{01} = (0, 0.1)$ for $r_0 = 0.1 < d$ (see Fig. 4.1(a)); when $d < r_0 = 0.6 < (dk + p)(q + am)/kq$, model (1.3) has non-negative stable solution $e_{01} = (0, 0.1)$ and unstable solution $e_{10} = (1, 0)$ (see Fig. 4.1(b)); for $r_0 = 2 > (dk + p)(q + am)/kq$, model (1.3) has only one positive solution e_2, and non-negative solutions e_{01} and e_{10} are unstable (see Fig. 4.1(c)).

Taking the parameter values

$$r_0 = 80, \quad a = 2, \quad c = 3, \quad d = 2, \quad p = 18, \quad k = 1, \quad m = 1, \quad q = 1,$$

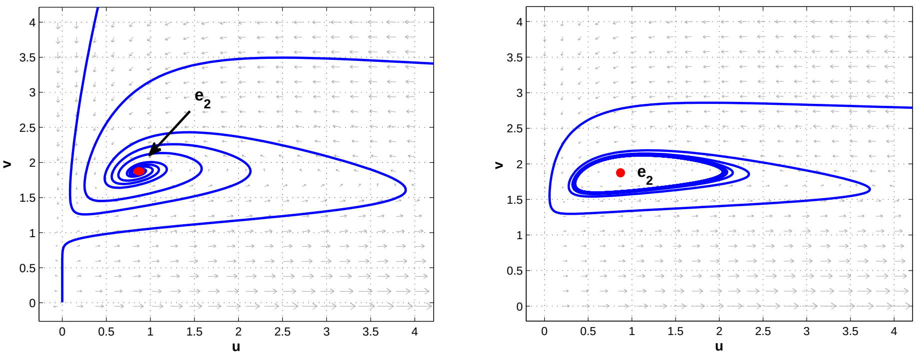
there are $(\bar{u}, \bar{v}) = (0.8678, 1.8678)$, $a_{11} = 1.292$, $a_{12} = -8.27$. According to condition (2.4), for $qa_{11} + a_{12} < 0$, the stability of $(\bar{u}, \bar{v}) = (0.8678, 1.8678)$ is determined by s. The positive equilibrium $(\bar{u}, \bar{v})$ is locally asymptotically stable when $s = 3 > 1.292$ (see Fig. 4.2(a)) and unstable when $s = 1 < 1.292$ (see Fig. 4.2(b)).

Assuming $d_1 = 0.01$, $d_2 = 10$, $\ell = 1$, $s = 1.5$, other parameters are the same as those of Fig. 4.2. Now $(\bar{u}, \bar{v}) = (0.8678, 1.8678)$, $A_{11} = 1.2952$, condition (3.6) is satisfied, $\chi^* = 0.7043$



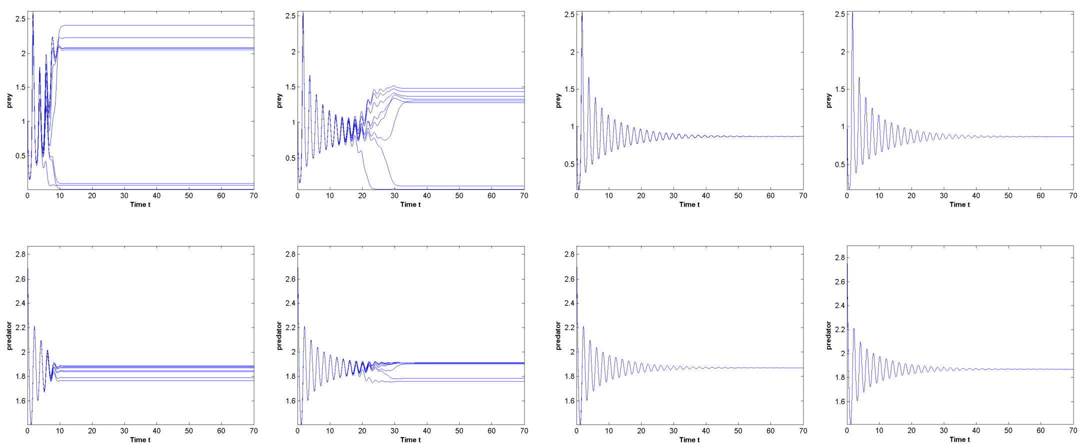
(a) $r_0 = 0.1$ (b) $r_0 = 0.6$ (c) $r_0 = 2$

Figure 4.1: The change of the number and stability of equilibrium points with the parameter r_0.



(a) $s = 3$ (b) $s = 1$

Figure 4.2: The relationship of the stability of $(\bar{u}, \bar{v})$ and s.

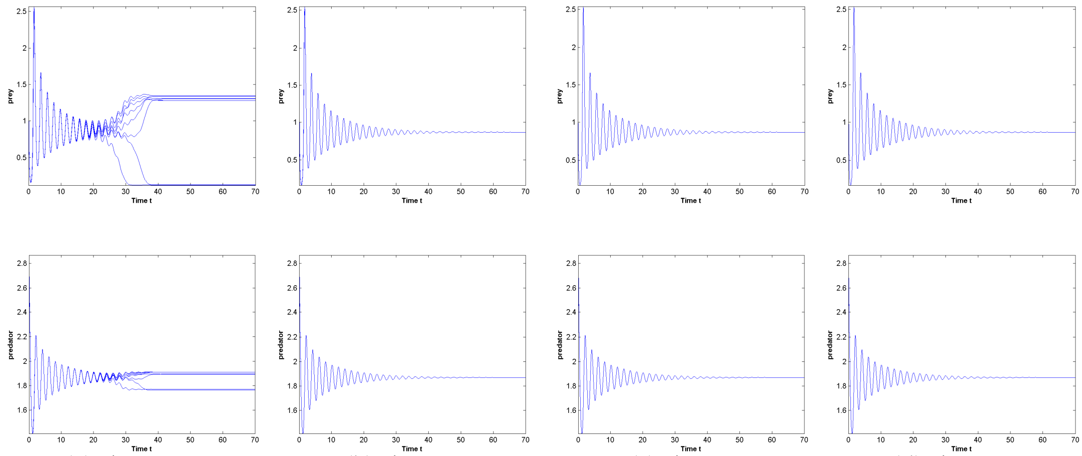


(a) $\chi = 0.01$ (b) $\chi = 0.5$ (c) $\chi = 1$ (d) $\chi = 10$

Figure 4.3: The first and second lines represent the populations of prey and predator, the stability of model (1.3) is controlled by χ, $(\bar{u}, \bar{v})$ is unstable for $\chi < \chi^*$ as (**a**) $\chi = 0.01$, (**b**) $\chi = 0.5$ and locally stable for $\chi > \chi^*$ as (**c**) $\chi = 1$, (**d**) $\chi = 10$.

for $n^* = 10$. Fig. 4.3 verifies Theorem 3.1, for $n \in \mathbb{N}_+$, $(\bar{u}, \bar{v})$ is asymptotically stable for $\chi > \chi^*$; when $\chi < \chi^*$, notice that $(\bar{u}, \bar{v})$ is unstable, Turing instability occurs (see Fig. 4.3(a)–(d)).

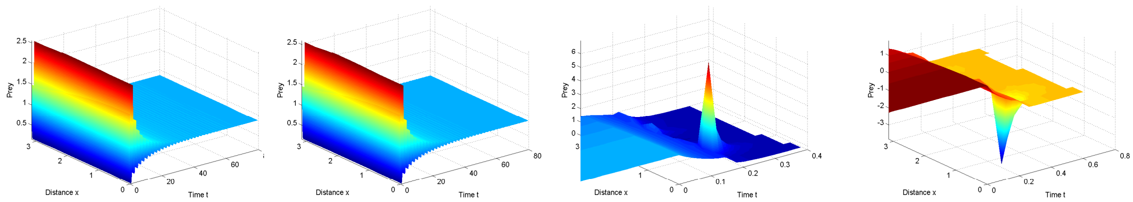
In addition, for the given χ, the stability of model (1.3) also affected by d_1. From Fig. 4.4, the spatiotemporal diagram of the prey is displayed in the figures of the first line and that of predator is showed in the figures of the second line for $\chi = 0.5$. Fig. 4.4 shows that, as the self-diffusion d_1 is big enough, there is no spatially or non-spatially homogeneous steady state bifurcation for the system.



(a) $d_1 = 0.02$ (b) $d_1 = 0.2$ (c) $d_1 = 2$ (d) $d_1 = 20$

Figure 4.4: The spatiotemporal diagram of the system. The value of d_1 is set as (**a**) $d_1 = 0.02$, (**b**) $d_1 = 0.2$, (**c**) $d_1 = 2$ and (**d**) $d_1 = 20$.

Next, we illustrate the influence of delay τ_1 and τ_2. For the delay τ_1, taking the parameter $\chi = 1 > \chi^*$, others are the same as those of Fig.4.3, then there exists $n \in \mathbb{N}_+$ satisfied $|B_n + D_n| < C_n$, and the critical values are $\omega_{1,0}^{3+} = 1.0828$ and $\tau_1^* = 0.7194$ for $n = 3$, so the positive equilibrium $(\bar{u}, \bar{v})$ is asymptotically stable for $\tau_1 < \tau_1^*$ (see Fig. 4.5(a)–(b)), and unstable for $\tau_1 > \tau_1^*$ (see Fig. 4.5(c)–(d)).

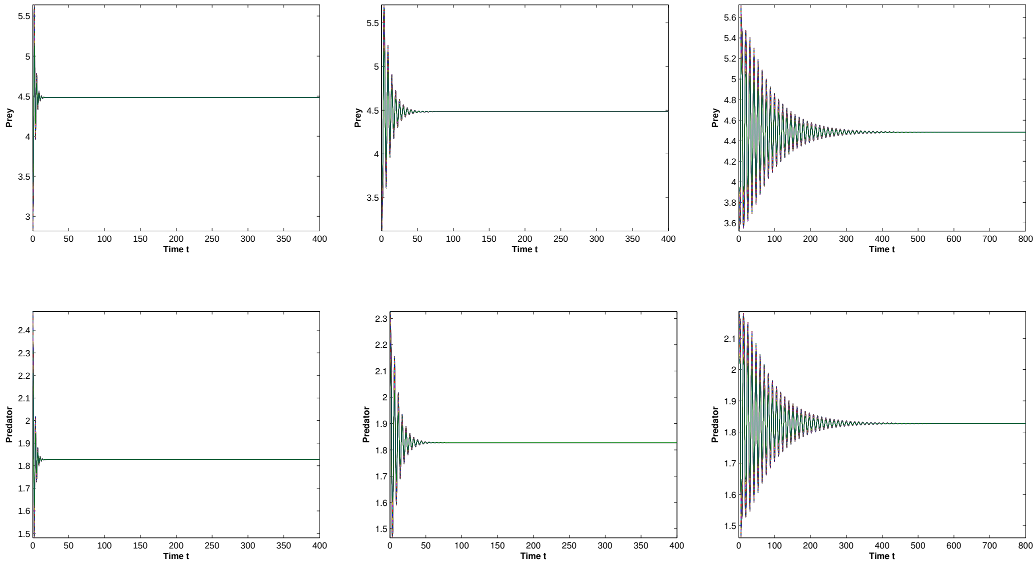


(a) $\tau_1 = 0.1$ (b) $\tau_1 = 0.2$ (c) $\tau_1 = 0.8$ (d) $\tau_1 = 1$

Figure 4.5: When $\tau_1 < \tau_1^*$, the system is always stable and unstable when $\tau_1 > \tau_1^*$, for the fixed value $\chi > \chi^*$.

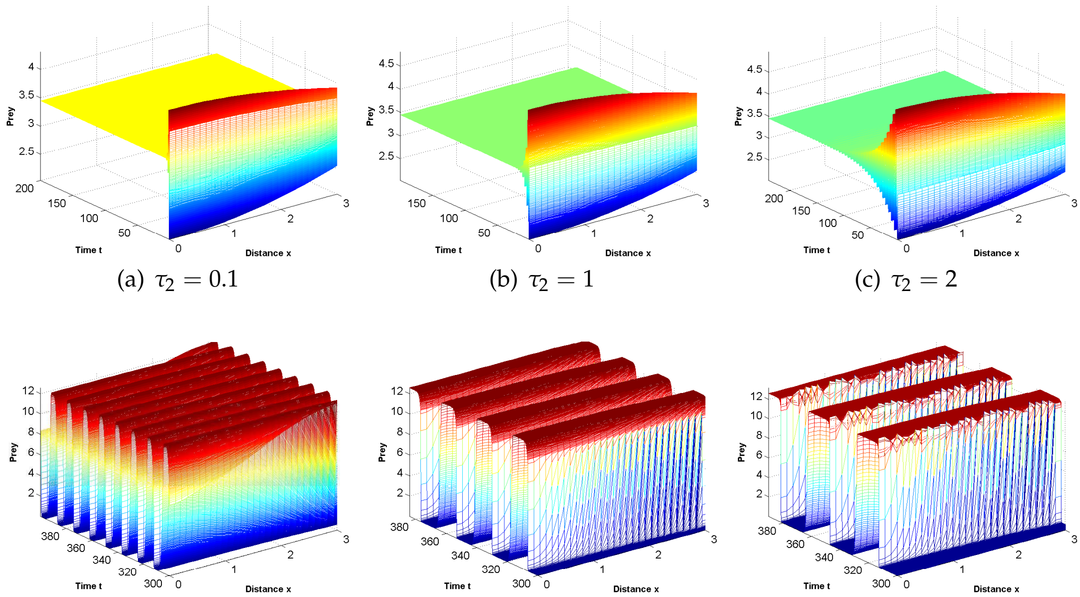
For delay τ_2 on the spatial distribution when $n = 0$, taking the parameter $q = 3$, model (1.3) has the unique positive equilibrium $(\bar{u}, \bar{v}) = (4.4826, 1.8275)$, the system is stable for $qA_{11} < A_{12}$ (see Fig. 4.6(a)–(c)).

While $q = 2$, $(\bar{u}, \bar{v}) = (3.4458, 2.2229)$, $qA_{11} > A_{12}$, we obtain the critical values $\omega_{2,0}^{0+} = 0.6008$ and $\tau_2^* = \tau_{2,0}^{0+} = 2.5366$. Taking $\tau_2 = 0.1, 1, 2 < \tau_2^*$ (see Fig. 4.7(a)–(c)), and $\tau_2 = 5, 10, 15 > \tau_2^*$ (see Fig. 4.7(d)–(f)) to verify the results of Theorem 3.3, the interval of the oscillation period becomes longer with the increasing of τ_2.



(a) $q = 3$, $\tau_2 = 1$ (b) $q = 3$, $\tau_2 = 2$ (c) $q = 3$, $\tau_2 = 5$

Figure 4.6: Spatiotemporal diagram of model (1.3). The system is always stable when $q = 3$ for any τ_2, due to $qA_{11} < A_{12}$.

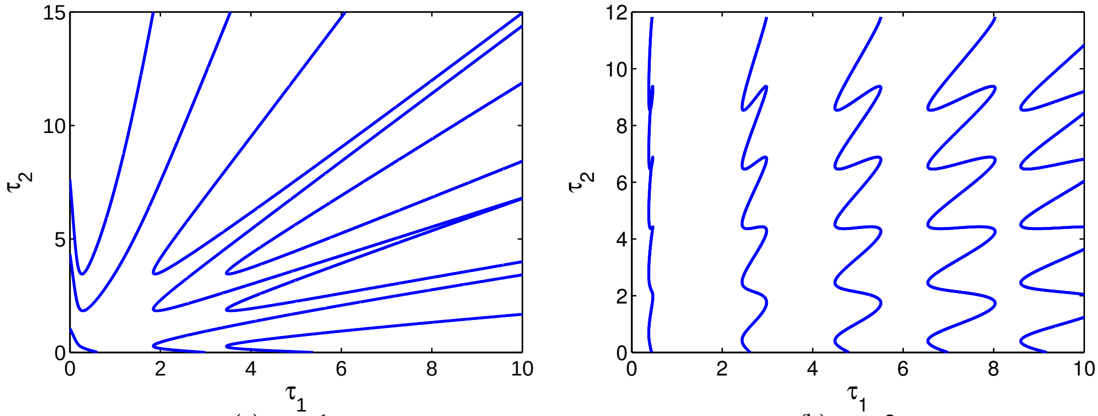


(a) $\tau_2 = 0.1$ (b) $\tau_2 = 1$ (c) $\tau_2 = 2$

(d) $\tau_2 = 5$ (e) $\tau_2 = 10$ (f) $\tau_2 = 15$

Figure 4.7: Spatiotemporal diagram of prey for model (1.3). The first line shows that the system is always stable for $\tau_2 < \tau_2^*$, and the second line shows that Hopf bifurcation occurs for $\tau_2 > \tau_2^*$.

For the model with two delay ($\tau_1, \tau_2 \neq 0$), when $s = 3$, $\ell = 1$ and other parameters are the same as those of Fig. 2, the positive equilibrium is $(0.8678, 1.8678)$. For $n = 1$, the crossing set is $\Omega_1 = (0, 3.9051]$, satisfying $|C_1 - D_1| < |B_1| < C_1 + D_1$, $A_1^2 > 2\big(B_1 - \sqrt{B_1^2 - (C_1 - D_1)^2}\big)$, then the stability switching curves are a series of open ended curves, so Theorem 3.7(3) is verified (see Fig. 4.8(a)); for $n = 3$, $\Omega_1 = [2.4861, 3.0613]$, satisfying $|B_2| < |C_2 - D_2|$, the stability switching curves are a series of spiral-like curves, and Theorem 3.7(1a) is verified (see Fig. 4.8(b)). Others can be got similarly.



(a) $n = 1$ (b) $n = 3$

Figure 4.8: The stability switching curves for $n = 1, 2$. (a) open ended curves for $n = 1$; (b) spiral-like curves for $n = 2$.

5 Conclusion

In the paper, we propose a diffusive predator-prey system with two delays. We introduce the modified Leslie–Gower term and fear effect to the system, and consider the stability of the model with the memory delay τ_1 and maturation delay τ_2, obtaining the following results.

(1) System (1.3) always has the semi-trivial equilibrium e_{01}, which is stable for $r_0 < (dk + p)(q + am)/kq$; when $r_0 > (dk + p)(q + am)/kq$, the equilibrium e_{01} loses stable; when $r_0 > d$, there exists semi-trivial equilibrium e_{10}, which is always unstable. Meanwhile, the model has the unique positive equilibrium e_2, which is locally asymptotically stable for $a_{11} - s < 0$, $qa_{11} + a_{12} < 0$. The number and stability of model (1.3) are determined by r_0.

(2) For $n = 0$, as conditions (2.2) and (2.4) hold, there is no spatially homogeneous steady state bifurcation. When $n \neq 0$ and condition (3.6) is satisfied, for $\chi > \chi^*$, $(\bar{u}, \bar{v})$ is asymptotically stable; for $\chi < \chi^*$, the spatially homogeneous steady state bifurcation occurs at $(\bar{u}, \bar{v})$. Therefore, Turing instability appears. From the condition $A_{11}d_2 - sd_1 < 0$, one can conclude that slow prey-taxis and fast self-diffusion would cause Turing patterns to occur.

(3) System (1.3) exists the spatially nonhomogeneous Hopf bifurcation at $(\bar{u}, \bar{v})$ for fast memory delay when it only has delay τ_1; model (1.3) undergoes the spatially homogeneous and nonhomogeneous Hopf bifurcation at $(\bar{u}, \bar{v})$ for fast maturation delay when it only has delay τ_2. Specially, there is no spatially homogeneous Hopf bifurcation for any delay τ_2 ($\tau_1 = 0$) when q is big enough. For the model with two delay ($\tau_1, \tau_2 \neq 0$), the structures of mode-n stability switching curves $\mathcal{T}_n$ and the crossing set Ω_n are shown as in Theorem 3.7, and the dynamical behavior are much richer than one delay.

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