Nonlinear Analysis: Modelling and Control, Vol. 24, No. 3, 387–406
https://doi.org/10.15388/NA.2019.3.5

ISSN: 1392-5113
eISSN: 2335-8963

Stability and Hopf bifurcation of a delayed reaction–diffusion predator–prey model with anti-predator behaviour*

Jia Liu[a], **Xuebing Zhang**[b, 1]

[a]Department of Basic Courses,
Huaian Vocational College of Information Technology,
Huaian 223003, China
kela3344@126.com

[b]College of Mathematics and Statistics,
Nanjing University of Information Science and Technology,
Nanjing 210044, China
zxb1030@163.com

Received: March 25, 2018 / **Revised:** November 14, 2018 / **Published online:** April 19, 2019

Abstract. In this paper, we study the dynamics of a delayed reaction–diffusion predator–prey model with anti-predator behaviour. By using the theory of partial functional differential equations, Hopf bifurcation of the proposed system with delay as the bifurcation parameter is investigated. It reveals that the discrete time delay has a destabilizing effect in the model, and a phenomenon of Hopf bifurcation occurs as the delay increases through a certain threshold. By utilizing upper-lower solution method, the global asymptotic stability of the interior equilibrium is studied. Finally, numerical simulation results are presented to validate the theoretical analysis.

Keywords: delay, stability, Hopf bifurcation, anti-predator.

1 Introduction

The predator–prey model first proposed by Lotka [11] and Volterra [25] is considered to be one of the basic models between different species in nature. Based on different settings, various types of predator–prey models described by differential systems have been proposed, and rich dynamics of these system have been investigated extensively [10, 21, 26, 27, 35]. It is noted that most of these models regard predator as winner. However, in real world, prey can sometimes inflict harm on their predators, which was called anti-predator behaviour [9]. Ives and Dobson [7] proposed a predator–prey model to describe anti-predator behaviour. Their results shows that more efficient anti-predator

---

[*] This research was supported by Natural Science Foundation of Jiangsu Province under grant BK20150420 and also supported by the Startup Foundation for Introducing Talent of NUIST.

[1] Corresponding author.

behaviour leads to increase in the density of the prey population, reduction in the ratio of predator-to-prey densities and damped oscillations. Peter and Hiroyuki [1] proposed a two-prey–one-predator system to investigate how these two consequences are changed if the prey exhibit adaptive anti-predator behaviour. The results show that the predation rate on a particular prey often decreases as the prey's density increases, and the predator then usually exhibits "negative switching" between prey. However, the presence of adaptive anti-predator behaviour does not change the short-term mutualism between prey. In this case, as a prey becomes less common, it achieves a larger growth rate by reducing its anti-predator effort.

Recently, Tang and Xiao [22] proposed a predator–prey model to describe anti-predator behaviour as follows:

$$\dot{x}(t) = rx\left(1 - \frac{x}{k}\right) - \frac{\beta xy}{a + x^2}, \qquad \dot{y}(t) = \frac{\mu\beta xy}{a + x^2} - dy - \eta xy,$$

where $x(t)$ and $y(t)$ are the densities of the prey and the predator at time t, respectively. r is the intrinsic growth rate of the prey, k is the carrying capacity of the environment, β is the capture rate of the predator, μ is the conversion rate of prey into predator, d is the natural death rate of the predator population, and η is the rate of anti-predator behaviour of prey to the predator population. The studies showed that anti-predator behaviour not only makes the coexistence of the prey and predator less likely, but also damps the predator–prey oscillations. Therefore, anti-predator behaviour helps the prey to resist predator aggression. Similar results on the predator–prey system with anti-predator behaviour were obtained by [6, 8, 13, 18, 19, 24].

However, we noted that few of these model about anti-predator consider the factor of delay and diffusion. It is well known that delays, which occur in the interaction between predator and prey, play a complicated role on a predator–prey system. It can cause the loss of stability and can induce various oscillations, periodic solutions [4, 5, 29, 30, 32]. Therefore, more realistic models of population interactions should take into account the effects of delays.

On the other hand, in real life, the species is spatially heterogeneous, and hence, individuals will tend to migrate towards regions of lower population density to add the possibility of survival [28]. For this reason, diffusion cannot be ignored in studying the predator–prey system. There have been many excellent papers with diffusion in a predator–prey system (see, for example, [2, 3, 12, 20, 23, 33, 34, 36]).

Motivated by the above discussions, let $u(x,t)$ and $v(x,t)$ represent the populations of prey and predator at time t, respectively. Assume that the predator needs a gestation period τ to give birth. Then in this case, the corresponding model with homogeneous Neumann boundary conditions is as follows:

$$\begin{aligned} \frac{\partial u}{\partial t} &= d_1\Delta u + r_1 u\left(1 - \frac{u}{K}\right) - \frac{\beta uv}{a + u}, \quad (x,t) \in \Omega \times (0, +\infty), \\ \frac{\partial v}{\partial t} &= d_2\Delta v + \frac{\alpha u(t-\tau)v}{a + u(t-\tau)} - r_2 v^2 - \eta uv, \quad (x,t) \in \Omega \times (0, +\infty), \end{aligned} \tag{1_1}$$

$$\begin{aligned} &u(x,t) = u_0(x,t) \geqslant 0, \quad v(x,t) = v_0(x,t) \geqslant 0, \quad (x,t) \in \overline{\Omega} \times [-\tau, 0], \\ &\frac{\partial u(t,x)}{\partial \phi} = \frac{\partial v(t,x)}{\partial \phi} = 0, \quad t > 0,\ x \in \partial\Omega, \end{aligned} \tag{1_2}$$

where Δ denotes the Laplacian operator, namely, $\Delta = \partial^2/\partial x^2$, $d_1, d_2 > 0$ denote the diffusion coefficients associated to u and v. Ω is a bounded domain with a smooth boundary $\partial\Omega$, and ϕ is the outside normal vector of $\partial\Omega$. The homogeneous Neumann boundary conditions indicate that there is no population flux across the boundaries. Population densities of prey and predator are respectively given by u and v. r_1 is the intrinsic growth rate of the prey, K is the carrying capacity of the environment. Here we use Holling II response function function, and β is the capture rate of the predator, a measures the extent to which environment provides protection to prey u, α is the conversion rate of prey into predator, r_2 stands for predator density dependence rate. With the same idea of [22], we use the term ηuv to model anti-predator behaviour, and η is the rate of anti-predator behaviour of prey to the predator population.

In the initial conditions, we assume that

$$u_0(x,t), v_0(x,t) \in \mathcal{C} = C\big([-\tau, 0], X\big),$$

and X is defined by

$$X = \left\{ \mathrm{u} \in W^{2,2}(\Omega)\colon \frac{\partial \mathrm{u}}{\partial \phi} = 0 \ on\ \partial\Omega \right\}$$

with the product$\langle \cdot, \cdot \rangle$.

To the best of our knowledge, few authors deal with the research of delayed diffusive predator–prey system with anti-predator behaviour. Here we aim to shed some light on the dynamics of system (1) by trying to answer the following questions: What kind of conditions can ensure the occurrence of the stability and bifurcation? How the delay affect the dynamics of system (1)?

The structure of this paper is arranged as follows. In Section 2, we consider the existence of equilibrium points of system (1), the local stability and the existence of Turing bifurcation, and the Hopf bifurcation. In Section 3, we use upper-lower solution method to derive sufficient conditions for the global asymptotic stability of the positive equilibrium of system (1). In Section 4, some numerical simulations are given to support our theoretical predictions. In Section 5, a brief discussion is given to conclude this work.

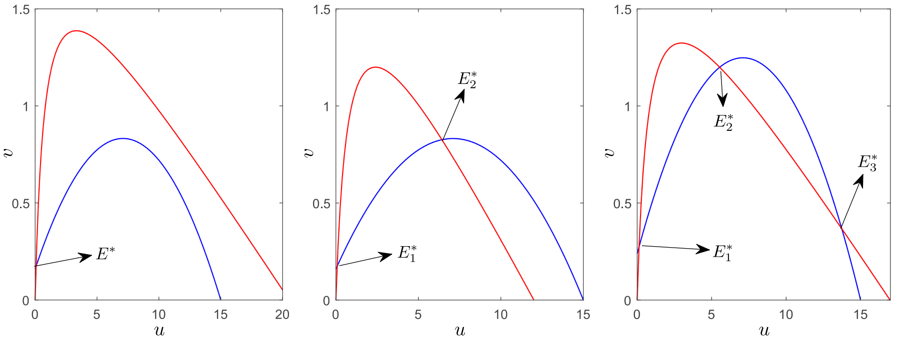
2 Local stability and bifurcation of system (1)

2.1 Existence of equilibrium points

In this section, we will find all possible non-negative equilibria.

Obviously, $E_0 = (0, 0)$ and $E_1 = (K, 0)$ are always equilibria. Other equilibria satisfy

$$r_1\left(1 - \frac{u}{K}\right) - \frac{\beta v}{a + u} = 0, \qquad \frac{\alpha u}{a + u} - r_2 v - \eta u = 0. \tag{2}$$



(a) (b) (c)

Figure 1. The blue curves are the prey-nullclines, and the red lines are the predator-isoclines. The three figures are the possible plots of predator-nullcline for three different values of r_1 and η: (a) For $r_1 = 0.1$ and $\eta = 0.015$, there is one equilibrium; (b) For $r_1 = 0.1$ and $\eta = 0.025$, both the nullclines cross two times, suggesting there are two equilibria; (c) For $r_1 = 0.15$ and $\eta = 0.018$, both the nullclines cross three times, suggesting there are three equilibria. The other parameter values are $a = 0.8$, $\beta = 0.5$, $\alpha = 0.32$, $r_2 = 0.15$, $K = 15$. (Online version in color.)

By the first equation of (2), we have

$$v = \frac{r_1}{\beta}\left(1 - \frac{u}{K}\right)(a + u). \tag{3}$$

Substitute Eq. (3) into the second equation of (2), we obtain

$$A_1 u^3 + A_2 u^2 + A_3 u + A_4 = 0, \tag{4}$$

where

$$A_1 = \frac{1}{K}, \qquad A_2 = \frac{2a}{K} - \frac{r_1 r_2}{\beta} - \eta,$$
$$A_3 = \frac{a^2}{K} + \alpha - 2a - a\eta, \qquad A_4 = -\frac{r_1 r_2 a^2}{\beta}.$$

Then, Eq. (4) has at least a positive root u^*. Therefore, the following result is obvious.

Lemma 1. *If* $u^* < K$*, then system* (1) *has at least a positive equilibrium* $E^* = (u^*, v^*)$*, where* $v^* = (r_1/\beta)(1 - u^*/K)(a + u^*)$.

The possible number of equilibria can be better analysed by studying the intersections of the nullclines, which is one of great feature of planar systems. Let $f(u, v) = 0$ and $g(u, v) = 0$, we show the existence of non-negative equilibria in Fig. 1.

Remark 1. From Fig. 1 we obtained that system (1) may have one, two or three equilibria with different parameter value. However, we can not discuss the stability of the equilibrium respectively, for that there is no actual formulas of the equilibria.

2.2 Stability of nonnegative equilibria

In this section, we discuss the local stability of nonnegative equilibria. Before developing our argument, let us set up the following notations.

Notation 1. Let $0 = \mu_0 < \mu_1 < \mu_2 < \cdots < \mu_n < \cdots \to \infty$ are the eigenvalues of $-\Delta$ on Ω under homogeneous Neumann boundary condition. We define the following space decomposition:

(i) $S(\mu_n)$ is the space of eigenfunctions corresponding to μ_n for $n = 0, 1, 2, \dots$;
(ii) $X_{ij} := \{\mathbf{c} \cdot \phi_{ij}\colon \mathbf{c} \in \mathbb{R}^2\}$, where $\{\phi_{ij}\}$ are orthonormal basis of $S(\mu_j)$ for $j = 1, 2, \dots, \dim[S(\mu_i)]$;
(iii) $\mathbf{X} := \{\mathbf{u} = (u, v) \in [C^1(\bar{\Omega})]^2\colon \partial u/\partial \mathbf{n} = \partial v/\partial \mathbf{n} = 0\}$, and so $\mathbf{X} = \bigoplus_{i=1}^{\infty} \mathbf{X}_i$, where $\mathbf{X}_i = \bigoplus_{j=1}^{\dim[S(\mu_i)]} \mathbf{X}_{ij}$.

The linearization of (1) at a constant solution $E^* = (u^*, v^*)$ can be expressed by

$$\mathbf{u}_t = (D\Delta + J_1)\mathbf{u} + J_2\mathbf{u}_\tau, \tag{5}$$

where $D = \operatorname{diag}(d_1, d_2)$, $\mathbf{u} = (u(x,t), v(x,t))^{\mathrm{T}}$, and $\mathbf{u}_\tau = (u(x, t-\tau), v(x, t-\tau))^{\mathrm{T}}$,

$$J_1 = \begin{pmatrix} r_1 - \frac{2r_1u^*}{K} - \frac{a\beta v^*}{(a+u^*)^2} & -\frac{\beta u^*}{a+u^*} \\ -\eta v^* & \frac{\alpha u^*}{a+u^*} - 2r_2v^* - \eta u^* \end{pmatrix}, \qquad J_2 = \begin{pmatrix} 0 & 0 \\ \frac{av^*\alpha \mathrm{e}^{-\lambda\tau}}{(a+u^*)^2} & 0 \end{pmatrix}.$$

In view of Notation 1, we can induce the eigenvalues of system (5) confined on the subspace $\mathbf{X}_i$. If λ is an eigenvalue of (5) on $\mathbf{X}_i$, it must be an eigenvalue of the matrix $-\mu_n D + J^*$ for each $n \geqslant 0$, where

$$J^* = \begin{pmatrix} -r_1 + \frac{2r_1u^*}{K} + \frac{a\beta v^*}{(a+u^*)^2} & \frac{\beta u^*}{a+u^*} \\ \eta v^* - \frac{av^*\alpha \mathrm{e}^{-\lambda\tau}}{(a+u^*)^2} & -\frac{\alpha u^*}{a+u^*} + 2r_2v^* + \eta u^* \end{pmatrix}.$$

For $E_0 = (0, 0)$, the corresponding characteristic equation is

$$(\lambda + d_1\mu_n - r_1)(\lambda + d_2\mu_n) = 0.$$

Clearly, we obtain

$$\lambda_1 = r_1 - d_1\mu_n, \qquad \lambda_2 = -d_2\mu_n.$$

Hence, E_0 is unstable, that is both species will never be lead to extinction simultaneously.

For $E_1 = (K, 0)$, the corresponding characteristic equation is

$$(\lambda + d_1\mu_n + r_1)\left(\lambda + d_2\mu_n + \eta K - \frac{\alpha K}{a + K}\right) = 0.$$

Obviously,

$$\lambda_1 = -r_1 - d_1\mu_n, \qquad \lambda_2 = -d_2\mu_n + \frac{\alpha K}{a + K} - \eta K.$$

Consequently, if $\alpha < \eta(a + K)$, then $E_1 = (K, 0)$ is locally asymptotically stable.

For $E^* = (u^*, v^*)$, the corresponding characteristic equation is

$$\lambda^2 + B_{1n}\lambda + B_{2n} + B_3 \mathrm{e}^{-\lambda\tau} = 0, \tag{6}$$

here

$$\begin{aligned} B_{1n} &= d_1\mu_n + a_1 + d_2\mu_n + a_2, \\ B_{2n} &= (d_1\mu_n + a_1)(d_2\mu_n + a_2) - \eta v^*\alpha_2, \\ B_3 &= \alpha a \alpha_1 \alpha_2, \quad a_1 = -\beta u^* \alpha_1 + \frac{r_1 u^*}{K}, \quad a_2 = r_2 v^* + \eta u^*, \\ \alpha_1 &= \frac{v^*}{(a+u^*)^2}, \qquad \alpha_2 = \frac{\beta u^*}{a+u^*}. \end{aligned}$$

2.3 Turing bifurcation

In this subsection, we mainly focus on the effects of diffusive on Turing instability for model (1) with $\tau = 0$. Let us consider the spatially homogeneous system corresponding to model (1)

$$\frac{\mathrm{d}u}{\mathrm{d}t} = r_1 u\left(1 - \frac{u}{K}\right) - \frac{\beta uv}{a+u}, \qquad \frac{\mathrm{d}v}{\mathrm{d}t} = \frac{\alpha uv}{a+u} - r_2 v^2 - \eta uv. \tag{7}$$

According to the work by Turing, a positive equilibrium E^* is Turing instability, meaning that it is an asymptotically positive equilibrium of model (7), but is unstable with respect to the solutions of spatial model (1). Given this, denote

$$\begin{aligned} k_1 &= \frac{d_2 a_1 + d_1 a_2 - \sqrt{(d_2 a_1 + d_1 a_2)^2 - 4 d_1 d_2 (a_1 a_2 - \eta v^* \alpha_2 + \alpha a \alpha_1 \alpha_2)}}{2 d_1 d_2}, \\ k_2 &= \frac{d_2 a_1 + d_1 a_2 + \sqrt{(d_2 a_1 + d_1 a_2)^2 - 4 d_1 d_2 (a_1 a_2 - \eta v^* \alpha_2 + \alpha a \alpha_1 \alpha_2)}}{2 d_1 d_2}, \end{aligned}$$

we can obtain the following results.

Theorem 1. *Assume that the following conditions are true*:

$$a_1 + a_2 > 0, \qquad a_1 a_2 - \eta v^* \alpha_2 + \alpha a \alpha_1 \alpha_2 > 0. \tag{8}$$

then model (1) *is Turing instability if* $0 < k_1 < \mu_i < k_2$ *for some* μ_i.

Proof. According to the above discussions, the characteristic equation of model (7) at positive equilibrium is as follows:

$$\lambda^2 + (a_1 + a_2)\lambda + a_1 a_2 - \eta v^* \alpha_2 + \alpha a \alpha_1 \alpha_2 = 0.$$

Obviously, as conditions (8) hold, the positive equilibrium of model (7) is locally asymptotically stable.

For spatial model (1), we have

$$B_{2n}+B_3=d_1d_2\mu_n^2+(d_2a_1+d_1a_2)\mu_n+a_1a_2-\eta v^*\alpha_2+\alpha a\alpha_1\alpha_2.$$

If there exists a μ_i such that $0<k_1<\mu_i<k_2$, then $B_{2i}+B_3<0$, which means that Eq. (6) has a positive real part eigenvalue, then the positive equilibrium is unstable when diffusion is present. Thus, Turing instability occurs. ☐

2.4 Hopf bifurcation

In the following part, we analyze the stability and Hopf bifurcation about the positive equilibrium $E^*(u^*,v^*)$. We make the following assumptions:

(H1) $r_1/K-\beta\alpha_1>0$;
(H2) $\alpha a\alpha_1-\eta v^*>0$;
(H3) $a_1a_2-\alpha a\alpha_1\alpha_2-\alpha_2\eta v^*>0$;
(H4) $a_1a_2-\alpha a\alpha_1\alpha_2-\alpha_2\eta v^*<0$.

Lemma 2. *If* (H1) *and* (H2) *hold, then the positive equilibrium* $E^*=(u^*,v^*)$ *is locally asymptotically stable with* $\tau=0$.

Proof. As $\tau=0$, Eq. (6) is equivalent to the following equation:

$$\lambda^2+B_{1n}\lambda+B_{2n}+B_3=0.$$

Obviously, if (H1) and (H2) hold, then

$$\begin{aligned}B_{1n}&=d_1\mu_n-\beta u^*\alpha_1+\frac{r_1u^*}{K}+d_2\mu_n+r_2v^*+\eta u^*>0,\\ B_{2n}+B_3&=\left(d_1\mu_n-\beta u^*\alpha_1+\frac{r_1u^*}{K}\right)(d_2\mu_n+r_2v^*+\eta u^*)\\ &\quad+\alpha a\alpha_1\alpha_2-\alpha_2\eta v^*>0.\end{aligned}$$

According to the Routh–Hurwitz conditions, E^* is locally asymptotically stable with $\tau=0$. ☐

Now we discuss the effect of the delay τ on the stability of the positive equilibrium of system (1). Assume that $\mathrm{i}\omega$ is a root of Eq. (6). Then ω should satisfy the following equation for some $n\geqslant 0$:

$$-\omega^2+\mathrm{i}B_{1n}\omega+B_{2n}+B_3\big(\cos(\omega\tau)-\mathrm{i}\sin(\omega\tau)\big)=0,$$

which implies that

$$\omega^2-B_{2n}=B_3\cos(\omega\tau),\qquad B_{1n}\omega=B_3\sin(\omega\tau). \tag{9}$$

From (9), adding the squared terms for both equations yields

$$\omega^4+\big(B_{1n}^2-2B_{2n}\big)\omega^2+B_{2n}^2-B_3^2=0. \tag{10}$$

Let $z = \omega^2$, Eq. (10) becomes

$$z^2 + \left(B_{1n}^2 - 2B_{2n}\right)z + B_{2n}^2 - B_3^2 = 0, \tag{11}$$

where

$$\begin{aligned} B_{1n}^2 - 2B_{2n} &= \left(d_1\mu_n + \frac{r_1u^*}{K} - \beta u^*\alpha_1\right)^2 + \left(d_2\mu_n + r_2v^* + \eta u^*\right)^2, \\ B_{2n}^2 - B_3^2 & \\ &= (B_{2n} + B_3)(B_{2n} - B_3) \\ &= \left(\left(d_1\mu_n - \beta u^*\alpha_1 + \frac{r_1u^*}{K}\right)(d_2\mu_n + r_2v^* + \eta u^*) + \alpha a\alpha_1\alpha_2 - \alpha_2\eta v^*\right) \\ &\quad \times \left(\left(d_1\mu_n - \beta u^*\alpha_1 + \frac{r_1u^*}{K}\right)(d_2\mu_n + r_2v^* + \eta u^*) - \alpha a\alpha_1\alpha_2 - \alpha_2\eta v^*\right). \end{aligned} \tag{12}$$

Theorem 2. *If* (H1), (H2) *and* (H3) *hold, then all roots of Eq.* (6) *have negative real parts for all $\tau \geqslant 0$, i.e., the positive equilibrium E^* of system* (1) *is asymptotically stable for all $\tau \geqslant 0$.*

Proof. From Eq. (12) we know that

$$B_{1n}^2 - 2B_{2n} > 0.$$

From Lemma 2 we get $B_{2n} + B_3 > 0$. Obviously, if (H1) and (H3) hold, then

$$\begin{aligned} B_{2n} - B_3 &= \left(d_1\mu_n - \beta u^*\alpha_1 + \frac{r_1u^*}{K}\right)(d_2\mu_n + r_2v^* + \eta u^*) \\ &\quad - \alpha a\alpha_1\alpha_2 - \alpha_2\eta v^* \\ &> 0 \end{aligned}$$

for any $n \geqslant 0$.

These imply that Eq. (10) has no positive roots, and hence, the characteristic Eq. (6) has no purely imaginary roots. Combined with Lemma 2, last observation implies that all roots of Eq. (6) have negative real parts as $\tau \geqslant 0$. ☐

Remark 2. In Section 3, we will prove that if system (1) has only a unique positive equilibrium, then this positive equilibrium is indeed globally asymptotically stable for any $\tau \geqslant 0$.

Denote

$$\mu^* = \frac{a_{11}d_2 + a_{22}d_1 + \sqrt{(a_{11}d_2 + a_{22}d_1)^2 - 4d_1d_2(a_{11}a_{22} - \alpha_2\eta v^* - B_3)}}{2d_1d_2},$$

where

$$a_{11} = -\left(\beta u^*\alpha_1 - \frac{r_1u^*}{K}\right), \qquad a_{12} = -(r_2v^* + \eta u^*).$$

Thus, there must exist some $N^* \in \mathbb{N}_0$ such that $\mu^* = \mu_{N^*}$ or $\mu_{N^*} < \mu^* < \mu_{N^*+1}$. Hence, we have following lemma.

Lemma 3. *If* (H1), (H2) *and* (H4) *hold, then Eq.* (6) *has a pair of purely imaginary roots* $\pm\mathrm{i}\omega_n (0 \leqslant n \leqslant N^*)$ *at*

$$\tau = \tau_n^j = \tau_n^0 + \frac{2j\pi}{\omega_n}, \quad j \in \mathbb{N}_0 := \{0, 1, 2, 3, \dots\}$$

where

$$\tau_n^0 = \frac{1}{\omega_n} \arccos \frac{\omega_n^2 - B_{2n}}{B_3},$$
$$\omega_n = \sqrt{\frac{2B_{2n} - B_{1n}^2 + \sqrt{(B_{1n}^2 - 2B_{2n})^2 - 4(B_{2n}^2 - B_3^2)}}{2}}.$$

Proof. From hypothesis (H3), we know that $B_n + C > 0$.

$$B_{2n} - B_3 = d_1 d_2 \mu_n^2 - \left(\left(\beta u^* \alpha_1 - \frac{r_1 u^*}{K}\right) d_2 + (r_2 v^* + \eta u^*) d_1\right)\mu_n + \left(\beta u^* \alpha_1 - \frac{r_1 u^*}{K}\right)(r_2 v^* + \eta u^*) - \alpha_2 \eta v^* - B_3.$$

Hence, Eq. (11) has no positive roots for $n > N^*$, and $0 \leqslant n \leqslant N^*$ is the necessary condition of Eq. (11) having positive roots. For $0 \leqslant n \leqslant N^*$, a unique positive root z_n of Eq. (11) is

$$z_n = \frac{2B_{2n} - B_{1n}^2 + \sqrt{(B_{1n}^2 - 2B_{2n})^2 - 4(B_{2n}^2 - B_3^2)}}{2},$$

and

$$\omega_n = \sqrt{\frac{2B_{2n} - B_{1n}^2 + \sqrt{(B_{1n}^2 - 2B_{2n})^2 - 4(B_{2n}^2 - B_3^2)}}{2}}$$

is the imaginary part of the purely imaginary root, at

$$\tau = \tau_n^j = \tau_n^0 + \frac{2j\pi}{\omega_n} = \frac{1}{\omega_n} \arccos \frac{\omega_n^2 - B_{2n}}{B_3} + \frac{2j\pi}{\omega_n}, \quad j \in \mathbb{N}_0. \tag{13}$$

Equation (6) has a pair of purely imaginary roots $\pm i\omega_n (0 \leqslant n \leqslant N^*)$.

It is clear from Eq. (13) that $\tau_n^{j+1} > \tau_n^j$. The following lemma shows that

$$\tau_{N^*}^j \geqslant \tau_{N^*-1}^j \geqslant \dots \geqslant \tau_1^j > \tau_0^j,$$

and hence, we have a complete ordering of the bifurcation values τ_n^j. □

Lemma 4. *If* (H1), (H2) *and* (H4) *hold, then*

$$\tau_{N^*}^j \geqslant \tau_{N^*-1}^j \geqslant \dots \geqslant \tau_1^j > \tau_0^j$$

for $j \in \mathbb{N}_0$.

Proof. From the above analysis we know

$$\omega_n^2 = \frac{2B_{2n} - B_{1n}^2 + \sqrt{(B_{1n}^2 - 2B_{2n})^2 - 4(B_{2n}^2 - B_3^2)}}{2} = \frac{2}{\sqrt{\frac{(B_{1n}^2 - 2B_{2n})^2}{(B_3^2 - B_{2n}^2)^2} + \frac{4}{B_3^2 - B_{2n}^2}} + \frac{B_{1n}^2 - 2B_{2n}}{B_3^2 - B_{2n}^2}}.$$

Obviously, $B_3^2 - B_{2n}^2$ is decreasing in n, and $B_{1n}^2 - 2B_{2n}$ is increasing in n. We obtain that

$$\omega_{N^*} \leqslant \omega_{N^*-1} \leqslant \cdots \leqslant \omega_1 < \omega_0.$$

Notice that B_n is strictly increasing in n for $0 \leqslant n \leqslant N^*$. Then we obtain $\omega_n^2 - B_n/C$ is strictly decreasing in n for $0 \leqslant N \leqslant N^*$. Thus $\tau_n^j = (1/\omega_n)\arccos((\omega_n^2 - B_n)/C) + 2j\pi/\omega_n$ is strictly increasing in n. Namely,

$$\tau_{N^*}^j \geqslant \tau_{N^*-1}^j \geqslant \cdots \geqslant \tau_1^j > \tau_0^j, \quad j \in \mathbb{N}_0.$$

From Lemma 4 we know that $\tau_0^0 = \min\{\tau_n^j\colon 0 \leqslant n \leqslant N^*, j \in \mathbb{N}_0\}$. □

Lemma 5. *Let* $\lambda_n(\tau) = \alpha_n(\tau) \pm \mathrm{i}\omega_n(\tau)$ *be the root of* (6) *near* $\tau = \tau_n^j$ *satisfying* $\alpha_n(\tau_n^j) = 0$ *for* $\omega_n(\tau_n^j) = \omega_n$. *Then the following transversality condition holds*:

$$(\alpha_n'(\tau))^{-1} > 0$$

for $j = 0, 1, 2 \ldots$ *and* $0 \leqslant n \leqslant N^*$.

Proof. Differentiating the two sides of Eq. (6) with respect to τ yields

$$\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\left(2\lambda + B_{1n} - B_3\tau\mathrm{e}^{-\lambda\tau}\right) = B_3\lambda\mathrm{e}^{-\lambda\tau}.$$

Hence,

$$\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)^{-1} = \frac{2\lambda + B_{1n} - B_3\tau\mathrm{e}^{-\lambda\tau}}{B_3\lambda\mathrm{e}^{-\lambda\tau}} = \frac{2}{B_3}\mathrm{e}^{\lambda\tau} + \frac{B_{1n}}{B_3\lambda}\mathrm{e}^{\lambda\tau} - \frac{\tau}{\lambda}.$$

Substituting τ_n^j into the above equation, we obtain

$$(\alpha_n'(\tau))^{-1} = \mathrm{Re}\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)^{-1}_{\tau=\tau_n^j} = \frac{2\cos(\omega_n\tau_n^j)}{B_3} + \frac{B_{1n}\sin(\omega_n\tau_n^j)}{B_3\omega_n}.$$

Since $B_3\cos(\omega_n\tau_n^j) = \omega_n^2 - B_{2n}$ and $B_3\sin(\omega_n\tau_n^j) = B_{1n}\omega_n$. Then we have

$$\left(\alpha_n'(\tau)\right)^{-1} = \mathrm{Re}\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)^{-1}_{\tau=\tau_n^j} = \frac{\sqrt{(B_{1n}^2 - 2B_{2n})^2 - 4(B_{2n}^2 - B_3^2)}}{B_3^2} > 0. \qquad \square$$

From the above analysis, we have the following conclusion.

Theorem 3. *If* (H1), (H2) *and* (H4) *hold, then the following statements are true*:

(i) *The positive steady state is asymptotically stable when* $\tau \in [0, \tau_0)$*, and unstable when* $\tau > \tau_0$;

(ii) *Hopf bifurcation occurs at* $\tau = \tau_0^0$*. That is, system* (1) *has a branch of periodic solutions bifurcating from the positive steady state near* $\tau = \tau_0^0$*.*

Remark 3. According to the above discussions, we can conclude that with different conditions, the system may appear different dynamic behaviours. Under certain conditions, the system may be stable or unstable (Hopf bifurcation occurs) with different delay τ, which means that the delay τ has great effect on the dynamics of the system, and it may affect the survival of the populations.

3 Global stability

In this section, we prove that when (H1)–(H3) hold, the positive equilibrium is indeed globally asymptotically stable. To achieve this, we utilize upper-lower solution method in [16, 17].

Lemma 6. (*See* [31].) *Assume that* $u(x,t)$ *is defined by*

$$\begin{aligned}
&\frac{\partial u}{\partial t} = d_1 \Delta u + ru\left(1 - \frac{u}{K}\right), \quad x \in \Omega,\ t > 0,\\
&\frac{\partial u}{\partial \nu} = 0, \quad x \in \Omega,\ t > 0,\\
&u(x,0) = u_0(x) > 0, \quad x \in \Omega,
\end{aligned}$$

then $\lim_{t \to +\infty} u(x,t) = K$*.*

Theorem 4. *Assume that* (H1)–(H3) *hold, then for any initial value* $(u_0(x,t), v_0(x,t)) > (0,0)$*, the corresponding nonnegative solution* $(u(x,t), v(x,t))$ *of system* (1) *uniformly converges to* $E^* = (u^*, v^*)$ *as* $t \to +\infty$*. That is, the unique positive equilibrium* $E^*(u^*, v^*)$ *is globally asymptotically stable.*

Proof. From the first equation of system (1), we have

$$\frac{\partial u}{\partial t} = d_1 \Delta u + r_1\left(1 - \frac{u}{K}\right) - \frac{\beta uv}{a+u} \leqslant d_1 \Delta u + r_1\left(1 - \frac{u}{K}\right),$$

then from the comparison principle of parabolic equations and Lemma 6, for an arbitrary $\varepsilon > 0$, there exists t_1 (> 0) such that for any $t > t_1$,

$$u(x,t) \leqslant \bar{c}_1, \tag{14}$$

where $\bar{c}_1 = K + \varepsilon$. This implies

$$\limsup_{t\to+\infty} \max_{x\in\bar{\Omega}} u(.,t) \leqslant K.$$

Therefore, from the second equation of system (1) and Eq. (14) we have

$$\begin{aligned}\frac{\partial v}{\partial t} &= d_2\Delta v + \frac{\alpha u(t-\tau)v}{a+u(t-\tau)} - r_2v^2 - \eta uv\\ &\leqslant d_2\Delta v + \alpha v\left(1 - \frac{a}{a+u} - \frac{r_2 v}{\alpha_2}\right)\end{aligned}$$

for $t > t_1 + \tau$. Hence, there exists $t_2 > t_1$ such that for any $t > t_2$,

$$v(x,t) \leqslant \bar{c}_2, \tag{15}$$

where $\bar{c}_2 = \bar{c}_1\alpha/(r_2(a+\bar{c}_1)) + \varepsilon$. Again, this implies

$$\limsup_{t\to+\infty} \max_{x\in\bar{\Omega}} v(.,t) \leqslant \frac{\alpha K}{r_2(a+K)}.$$

On the other hand, from the first equation of system (1) and (15) we have

$$\begin{aligned}\frac{\partial u}{\partial t} &= d_1\Delta u + u\left(r_1 + \frac{r_1 u}{K} - \frac{\beta v}{\alpha + u}\right)\\ &\geqslant d_1\Delta u + u\left(r_1 - \frac{r_1 u}{K} - \frac{\beta\bar{c}_2}{\alpha}\right)\end{aligned}$$

for $t > t_2$. Since (H1)–(H3) hold, then for small enough $\varepsilon_2 > 0$,

$$K - \frac{\beta\bar{c}_2}{\alpha r_1} - \varepsilon_2 > 0.$$

Hence, there exists $t_4 > t_3$ such that for any $t > t_4$,

$$u(x,t) \geqslant \underline{c}_1, \tag{16}$$

where

$$\underline{c}_1 = K - \frac{\beta\bar{c}_2}{\alpha r_1} - \varepsilon_2.$$

Then we apply the lower bound of u to the second equation of system (1), and we have

$$\begin{aligned}\frac{\partial v}{\partial t} &= d_2\Delta v + \frac{\alpha u(t-\tau)v}{a+u(t-\tau)} - r_2v^2 - \eta uv,\\ &\geqslant d_2\Delta v + \alpha v\left(1 - \frac{a}{a+u} - \frac{r_2 v}{\alpha} - \frac{\eta u}{\alpha}\right),\\ &\geqslant d_2\Delta v + \alpha v\left(1 - \frac{a}{a+\underline{c}_1} - \frac{r_2 v}{\alpha} - \frac{\eta\bar{c}_1}{\alpha}\right)\end{aligned}$$

for $t > t_4$. Then there exists $t_5 > t_4$ such that for any $t > t_5$,

$$v(x,t) \geqslant \underline{c}_2, \tag{17}$$

where

$$\underline{c}_2 = \frac{1}{r_2}\left(\frac{\underline{c}_1\alpha}{a+\underline{c}_1} - \eta\bar{c}_1\right) - \varepsilon.$$

From (16) and (17) we can easily obtain that

$$\liminf_{t\to+\infty}\max_{x\in\bar{\Omega}} u(.,t) \geqslant \underline{c}_1, \qquad \liminf_{t\to+\infty}\max_{x\in\bar{\Omega}} v(.,t) \geqslant \underline{c}_2.$$

It is easily obtained that

$$\underline{c}_1 \leqslant u(x,t) \leqslant \bar{c}_1, \underline{c}_2 \leqslant v(x,t) \leqslant \bar{c}_2,$$

and $\underline{c}_1$, $\bar{c}_1$, $\underline{c}_2$, $\bar{c}_2$ satisfy

$$\begin{gathered} r_1\bar{c}_1(1-\frac{\bar{c}_1}{K}) - \frac{\beta\bar{c}_1\underline{c}_2}{a+\bar{c}_1} \leqslant 0 \leqslant r_1\underline{c}_1\left(1-\frac{\underline{c}_1}{K}\right) - \frac{\beta\underline{c}_1\bar{c}_2}{a+\underline{c}_1}, \\ \frac{\alpha\underline{c}_1\bar{c}_2}{a+\underline{c}_1} - r_2\bar{c}_2^2 - \eta\underline{c}_1\bar{c}_2 \leqslant 0 \leqslant \frac{\alpha\bar{c}_1\underline{c}_2}{a+\bar{c}_1} - r_2\underline{c}_2^2 - \eta\bar{c}_1\underline{c}_2. \end{gathered} \tag{18}$$

Inequalities (18) show that $(\bar{c}_1, \bar{c}_2)$ and $(\underline{c}_1, \underline{c}_2)$ are a pair of coupled upper and lower solutions of system (1) as in the definition in [14, 15].

In addition, we have the following inequality:

$$\begin{aligned} &\left| r_1u_1\left(1-\frac{u_1}{K}\right) - \frac{\beta v_1}{a+u_1} - \left(r_1u_2\left(1-\frac{u_2}{K}\right) - \frac{\beta v_2}{a+u_2}\right)\right| \\ &\quad\leqslant \left|\left(r - \frac{r}{K}(u_1+u_2)(u_1-u_2) - \left(\frac{\beta v_1}{a+u_1} - \frac{\beta v_2}{a+u_2}\right)\right|\right. \\ &\quad\leqslant \left|\left(r - \frac{2r}{K}\underline{c}_1\right)(u_1-u_2) - \frac{\beta v_1}{a+\underline{c}_1}(v_1-v_2)\right| \\ &\quad\leqslant \left|\left(r - \frac{2r}{K}\underline{c}_1\right)\right|\bigl|(u_1-u_2)\bigr| + \left|\frac{\beta v_1}{a+\underline{c}_1}\right|\bigl|(v_1-v_2)\bigr|. \end{aligned}$$

Then there exists a positive constant M such that

$$\begin{aligned} &\left| r_1u_1\left(1-\frac{u_1}{K}\right) - \frac{\beta v_1}{a+u_1} - \left(r_1u_2\left(1-\frac{u_2}{K}\right) - \frac{\beta v_2}{a+u_2}\right)\right| \\ &\quad\leqslant M\bigl(|u_1-u_2| + |v_1-v_2|\bigr). \end{aligned}$$

Similarly, we have

$$\begin{aligned} &\left| v_1\left(\frac{\alpha u_1}{a+u_1} - r_2v_1 - \eta u_1\right) - v_2\left(\frac{\alpha u_2}{a+u_2} - r_2v_2 - \eta u_2\right)\right| \\ &\quad\leqslant M\bigl(|u_1-u_2| + |v_1-v_2|\bigr). \end{aligned}$$

We now construct two sequences $(\bar{c}_1^{(n)}, \bar{c}_2^{(n)})$ and $(\underline{c}_1^{(n)}, \underline{c}_2^{(n)})$ from the following iteration process:

$$\begin{aligned}
\bar{c}_1^{(n)} &= \bar{c}_1^{(n-1)} + \frac{1}{M}\left(r_1 \bar{c}_1^{(n-1)}\left(1 - \frac{\bar{c}_1^{(n-1)}}{K}\right) - \frac{\beta \bar{c}_1^{(n-1)} \underline{c}_2^{(n-1)}}{a + \bar{c}_1^{(n-1)}}\right),\\
\bar{c}_2^{(n)} &= \bar{c}_2^{(n-1)} + \frac{1}{M}\left(\frac{\alpha \underline{c}_1^{(n-1)} \bar{c}_2^{(n-1)}}{a + \underline{c}_1^{(n-1)}} - r_2\bigl(\bar{c}_2^{(n-1)}\bigr)^2 - \eta \bar{c}_2^{(n-1)} \underline{c}_1^{(n-1)}\right),\\
\underline{c}_1^{(n)} &= \underline{c}_1^{(n-1)} + \frac{1}{M}\left(r_1 \underline{c}_1^{(n-1)}\left(1 - \frac{\underline{c}_1^{(n-1)}}{K}\right) - \frac{\beta \underline{c}_1^{(n-1)} \bar{c}_2^{(n-1)}}{a + \underline{c}_1^{(n-1)}}\right),\\
\underline{c}_2^{(n)} &= \underline{c}_2^{(n-1)} + \frac{1}{M}\left(\frac{\alpha \bar{c}_1^{(n-1)} \underline{c}_2^{(n-1)}}{a + \bar{c}_1^{(n-1)}} - \gamma\bigl(\underline{c}_2^{(n-1)}\bigr)^2 - \eta \bar{c}_1^{(n-1)} \underline{c}_2^{(n-1)}\right)
\end{aligned} \tag{19}$$

with initial data $(\bar{c}_1^0, \bar{c}_2^0) = (\bar{c}_1, \bar{c}_2))$ and $(\underline{c}_1^0, \underline{c}_2^0) = (\underline{c}_1, \underline{c}_2)$. It is readily seen that sequences $(\bar{c}_1^{(n)}, \bar{c}_2^{(n)})$ and $(\underline{c}_1^{(n)}, \underline{c}_2^{(n)})$ possess the following property:

$$\begin{aligned}
(\underline{c}_1, \underline{c}_2) &\leqslant \bigl(\underline{c}_1^{(n)}, \underline{c}_2^{(n)}\bigr) \leqslant \bigl(\underline{c}_1^{(n+1)}, \underline{c}_2^{(n+1)}\bigr) \leqslant \bigl(\bar{c}_1^{(n+1)}, \bar{c}_2^{(n+1)}\bigr)\\
&\leqslant \bigl(\bar{c}_1^{(n)}, \bar{c}_2^{(n)}\bigr) \leqslant (\bar{c}_1, \bar{c}_2), \quad n = 1, 2, \dots .
\end{aligned}$$

Then there exists $(\tilde{c}_1, \tilde{c}_2))$ and $(\breve{c}_1, \breve{c}_2)$ such that

$$(\underline{c}_1, \underline{c}_2) \leqslant (\breve{c}_1, \breve{c}_2) \leqslant (\tilde{c}_1, \tilde{c}_2) \leqslant (\bar{c}_1, \bar{c}_2), \quad n = 1, 2, \dots .$$

Therefore,

$$\begin{aligned}
&\lim_{n\to+\infty} \bar{c}_1^{(n)} = \tilde{c}_1, \qquad \lim_{n\to+\infty} \bar{c}_2^{(n)} = \tilde{c}_2,\\
&\lim_{n\to+\infty} \underline{c}_1^{(n)} = \breve{c}_1, \qquad \lim_{n\to+\infty} \underline{c}_2^{(n)} = \breve{c}_2.
\end{aligned} \tag{20}$$

Hence, from (19) and (20) we have

$$\begin{aligned}
&\left(1 - \frac{\tilde{c}_1}{K}\right) - \frac{\beta \breve{c}_2}{a + \tilde{c}_1} = 0, \qquad \left(1 - \frac{\breve{c}_1}{K}\right) - \frac{\beta \tilde{c}_2}{a + \breve{c}_1} = 0,\\
&\frac{\beta \breve{c}_1}{a + \breve{c}_1} - r_2 \tilde{c}_2 - \eta \breve{c}_1 = 0, \qquad \frac{\beta \tilde{c}_1}{a + \tilde{c}_1} - r_2 \breve{c}_2 - \eta \tilde{c}_1 = 0.
\end{aligned} \tag{21}$$

From (21) we can easily obtain that $\tilde{c}_1 = \breve{c}_1$ and $\tilde{c}_2 = \breve{c}_2$. Then from the results in [14,15] the solution $(u(x,t), v(x,t))$ of system (1) satisfies

$$\lim_{t\to+\infty} u(x,t) = u^*, \qquad \lim_{t\to+\infty} v(x,t) = v^*$$

uniformly for $x \in \bar{\Omega}$. So the positive equilibrium (u^*, v^*) is globally asymptotically stable for system (1). □

4 Numerical simulation

In this section, we present numerical simulations of some examples to illustrate our theoretical results.

4.1 Global stability of the positive equilibrium for all $\tau \geqslant 0$

Consider system (1) with the parameters $d_1 = 0.2$, $d_2 = 0.3$, $r_1 = 0.1$, $a = 0.8$, $\beta = 0.1$, $\alpha = 0.32$, $r_2 = 0.15$, $K = 15$ and $\eta = 0.01$. Calculation reveals that system (1) has a positive equilibrium $E^* = (13.8852, 1.0914)$. According to Theorem 4, system (1) has global asymptotically stability at the unique positive equilibrium E^* for all $\tau \geqslant 0$ as shown in Fig. 2. This means that the prey and predator coexist at the steady state with the parameters above for all $\tau \geqslant 0$.

4.2 Stability and Hopf bifurcation of system (1)

Consider system (1) with the following parameters: $r_1 = 0.1$, $a = 0.8$, $\beta = 0.4$, $\alpha = 0.32$, $r_2 = 0.15$, $K = 15$ and $\eta = 0.01$. Choosing $\Omega = (0, \pi)$ and the diffusion coefficients $d_1 = 0.2$, $d_2 = 0.3$, by a direct calculation, we obtain that system (1) has a positive $E^* = (0.0962, 0.2226)$ and the critical value is $\tau_0 = 7.8613$. Obviously, the parameters satisfy the conditions of Theorem 3. According to Theorem 3, system (1) is locally asymptotically stable at E^* for $\tau = 7 \in [0, \tau_0)$ and unstable for $\tau = 8 > \tau_0$ as shown in Fig. 3. Figure 3(b) shows that the spatially homogeneous periodic solutions emerge from the positive equilibrium E^*, which implies that the prey and the predator coexist In the form of periodic oscillations.

If we let $r_1 = 0.15$ and other parameters be same as above, then system (1) has three equilibria: $E_1^* = (0.1679, 0.3589)$, $E_2^* = (5.4953, 1.4959)$ and $E_3^* = (10.4034, 1.2874)$. Simple calculation reveals that E_1^* is locally asymptotically stable for all $\tau \geqslant 0$, E_2^* is unstable and E_3^* is locally asymptotically stable for $\tau \in [0, 4.4484)$ and unstable for $\tau > 4.4484$ as shown in Figs. 4 and 5. However, as τ increases further,with the same initial values, the limit cycle disappears, and the solution converges to E_3^* as shown in

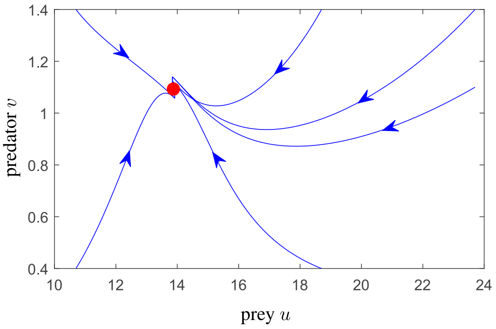
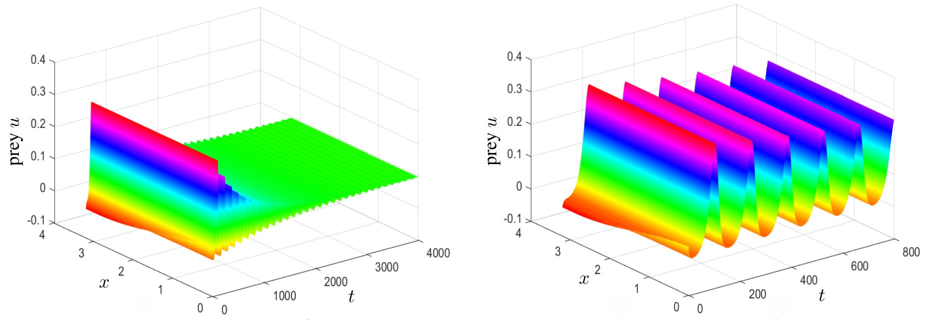


Figure 2. System (1) is globally asymptotically stable for all $\tau \geqslant 0$.



(a) (b)

Figure 3. (a) As $\tau = 7$, the positive equilibrium E^* is stable; (b) the periodic solutions emerge form the positive equilibrium E^* with $\tau = 8$.

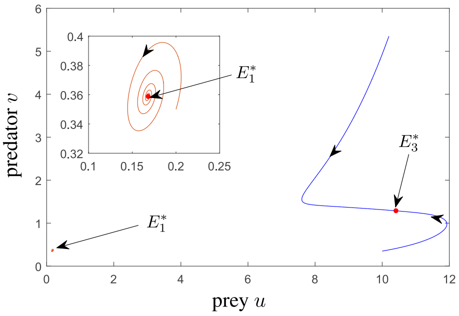


Figure 4. E_1^* and E_3^* are locally asymptotically stable with $\tau = 2$.

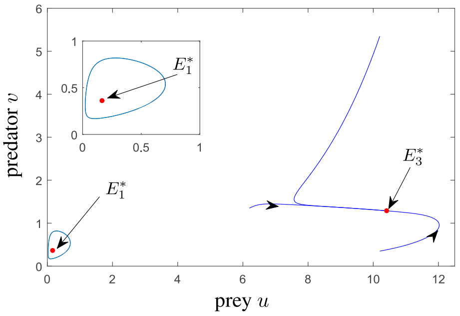
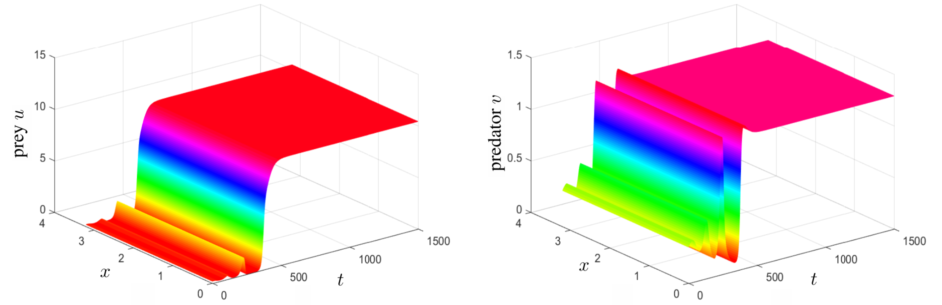


Figure 5. Hopf bifurcation occurs at E_1^* with $\tau = 5$ and E_3^* is yet stable.



(a) (b)

Figure 6. System (1) is stable at E_3^* with $\tau = 10$.

Fig. 6. It is shown that the delay τ can affect the stability of the system and with different τ the population can exist at different amounts.

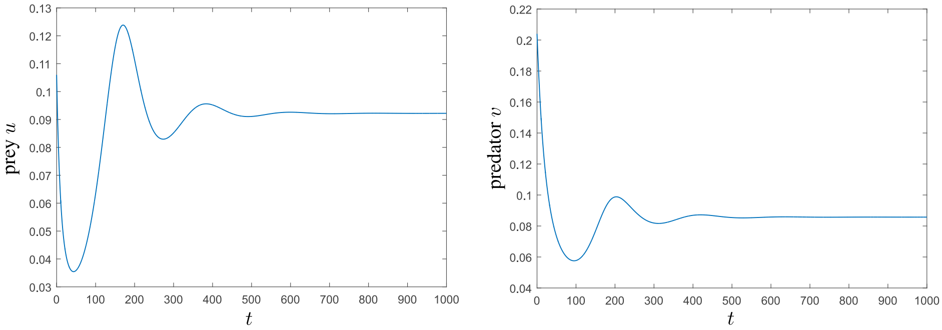


Figure 7. The positive equilibrium E^* of the ordinary differential equation is stable with $\tau = 0$.

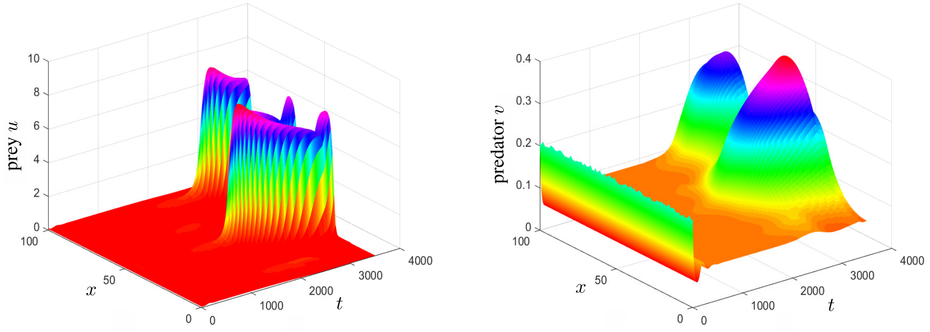


Figure 8. Turing bifurcation of system (1).

4.3 Turing bifurcation

We choose parameters as $d_1 = 0.02$, $d_2 = 6$, $r_1 = 0.05$, $a = 0.6$, $\beta = 0.4$, $\alpha = 0.2$, $r_2 = 0.3$, $K = 10$, $\eta = 0.01$ and $\tau = 0$. By calculation, we obtain that system (1) has a positive equilibrium $E^* = (0.0922, 0.0857)$. By theoretical analysis, the corresponding ordinary differential equation is stable at the positive equilibrium E^* as shown in Fig. 7. However, the positive equilibrium E^* of system (1) is unstable. Thus, Turing instability occurs, as shown in Figure 8. It shows that the prey and predator are unevenly distributed in time and space, which is caused by the Turing instability.

4.4 The effect of anti-predator behaviour

In order to investigate the effect of anti-predator behaviour, we choose parameter as $d_1 = 0.1$, $d_2 = 0.2$, $r_1 = 0.1$, $a = 0.8$, $\beta = 0.8$, $\alpha = 0.32$, $r_2 = 0.15$, $K = 15$ and η varies in $[0, 0.02]$. The positive equilibrium varies with increasing η are shown in Fig. 9. It is shown that system (1) has only a positive equilibrium. As η increases and passes through a critical value, system (1) undergoes a static bifurcation giving rise to two positive equilibria.

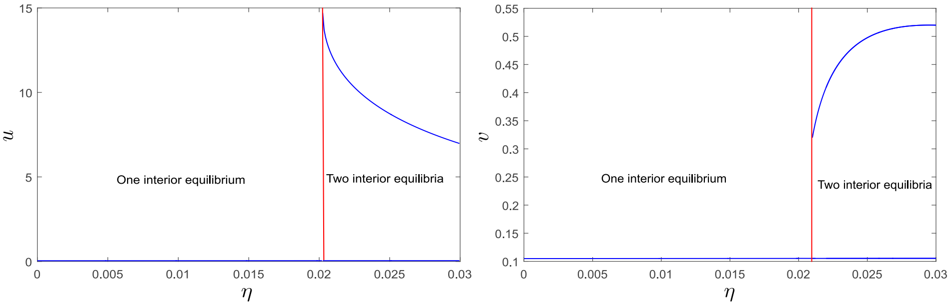


Figure 9. The positive equilibrium of system (1) varies with η increasing.

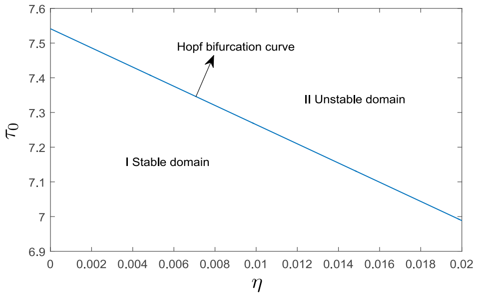


Figure 10. The stable and unstable domains vary with η increasing: I is stable domains, II is unstable domain.

Figure 10 shows that with increasing η the stability range is decreasing. It means that the rate of anti-predator behaviour of prey to the predator population has an effect on stabilizing positive equilibrium of system (1).

5 Conclusions

In this paper, by considering delay and diffusion, a delayed diffusive predator–prey model system with anti-predator behaviour is established to investigate the effects of gestation delay and the rate of anti-predator behaviour on the dynamic behavior of the system. The theoretical analysis and numerical simulation reveal that the discrete delays are responsible for the stability switch of the system, and a Hopf bifurcation occurs as the delays increase through a certain threshold.

The diffusion can induce Turing bifurcation, and the corresponding facts are obtained from Sections 2.3 and 4.3. All these means that the diffusion has important influence on survival of the species.

In addition, numerical simulations obtained in this paper suggest that the rate of anti-predator behaviour cannot only cause the static bifurcation occurs, but also change the stability of the system (see Section 4.4), which will contribute to the persistence and sustainable development of the system.

Acknowledgment. We would like to express our gratitude to the referees for their valuable comments and suggestions that led to a truly significant improvement of the manuscript.

References

1. P. Abrams, H. Matsuda, Effects of adaptive predatory and anti-predator behaviour in a two-prey–one-predator system, *Evol. Ecol.*, **7**(3):312–326, 1993.
2. Y. Cai, Y. Kang, M. Banerjee, W. Wang, Complex dynamics of a host–parasite model with both horizontal and vertical transmissions in a spatial heterogeneous environment, *Nonlinear Anal., Real World Appl.*, **40**:444–465, 2018.
3. X. Chang, J. Wei, Hopf bifurcation and optimal control in a diffusive predator–prey system with time delay and prey harvesting, *Nonlinear Anal. Model. Control*, **17**(4):379–409, 2012.
4. L. Chen, Z. Lu, W Wang, The effect of delays on the permanence for Lotka–Volterra systems, *Appl. Math. Lett.*, **8**:71–73, 1995.
5. S. Chen, J. Shi, J. Wei, A note on Hopf bifurcations in a delayed diffusive Lotka–Volterra predator–prey system, *Comput. Math. Appl.*, **62**(5):2240–2245, 2011.
6. Y. Choh, M. Ignacio, M.W. Sabelis, A. Janssen, Predator–prey role reversals, juvenile experience and adult antipredator behaviour, *Sci. Rep.*, **2**:728, 2012.
7. A.R. Ives, A.P. Dobson, Antipredator behavior and the population dynamics of simple predator–prey systems, *Am. Nat.*, **130**(3):431–447, 1987.
8. S.L. Lima, Stress and decision making under the risk of predation: Recent developments from behavioral, reproductive, and ecological perspectives, *Adv. Study Behav.*, **27**:215–290, 1998.
9. S.L. Lima, L.M. Dill, Behavioral decisions made under the risk of predation: A review and prospectus, *Can. J. Zool.*, **68**(4):619–640, 1990.
10. Z. Lin, M. Pedersen, Stability in a diffusive food-chain model with Michaelis–Menten functional response, *Nonlinear Anal., Theory Methods Appl.*, **57**(3):421–433, 2004.
11. A.J. Lotka, *Elements of Physical Biology*, Appl. Math. Sci., Williams & Wilkins, Baltimore, MD, September 1925.
12. Z.B. Ma, W.T. Li, X.P. Yan, Stability and Hopf bifurcation for a three-species food chain model with time delay and spatial diffusion, *Appl. Math. Comput.*, **219**(5):2713–2731, 2012.
13. A. Pallini, A. Janssen, M.W. Sabelis, Predators induce interspecific herbivore competition for food in refuge space, *Ecol. Lett.*, **1**:171–176, 1998.
14. C.V. Pao, On nonlinear reaction–diffusion systems, *J. Math. Anal. Appl.*, **87**(1):165–198, 1982.
15. C.V. Pao, *Nonlinear Parabolic and Elliptic Equations*, Springer, New York, 1992.
16. C.V. Pao, Dynamics of nonlinear parabolic systems with time delays, *J. Math. Anal. Appl.*, **198**(3):751–779, 1996.
17. C.V. Pao, Convergence of solutions of reaction–diffusion systems with time delays, *Nonlinear Anal., Theory Methods Appl.*, **48**(3):349–362, 2002.
18. G.A. Polis, C.A. Myers, R.D. Holt, The ecology and evolution of intraguild predation: Potential competitors that eat each other, *Annu. Rev. Ecol. Syst.*, **20**(1):297–330, 1989.

19. Y. Saitō, Prey kills predator: Counter-attack success of a spider mite against its specific phytoseiid predator, *Exp. Appl. Acarol.*, **2**(1):47–62, 1986.
20. M. Sambath, S. Gnanavel, K. Balachandran, Stability and Hopf bifurcation of a diffusive predator–prey model with predator saturation and competition, *Appl. Anal.*, **92**(12):2451–2468, 2013.
21. Y. Song, J. Wei, Local Hopf bifurcation and global periodic solutions in a delayed predator–prey system, *J. Math. Anal. Appl.*, **301**(1):1–21, 2005.
22. B. Tang, Y. Xiao, Bifurcation analysis of a predator–prey model with anti-predator behaviour, *Chaos Solitons Fractals*, **70**:58–68, 2015.
23. C. Tian, L. Zhang, Hopf bifurcation analysis in a diffusive food-chain model with time delay, *Comput. Math. Appl.*, **66**(10):2139–2153, 2013.
24. R. Tollrian, Predator-induced morphological defenses: Costs, life history shifts, and maternal effects in Daphnia pulex, *Ecology*, **76**(6):1691–1705, 1995.
25. V. Volterra, Fluctuations in the abundance of a species considered mathematically, *Nature*, **118**(1):558–560, 1926.
26. W. Wang, Y. Lin, L. Zhang, F. Rao, Y. Tan, Complex patterns in a predator–prey model with self and cross-diffusion, *Commun. Nonlinear Sci. Numer. Simul.*, **16**(4):2006–2015, 2011.
27. W. Wang, Q. Liu, Z. Jin, Spatiotemporal complexity of a ratio-dependent predator–prey system, *Phys. Rev. E*, **75**(5):051913, 2007.
28. Jianhong Wu, *Theory and Applications of Partial Functional Differential Equations*, Applied Mathematical Sciences, Springer, New York, September 1996.
29. R. Xu, Z. Ma, Global stability of a reaction-diffusion predator–prey model with a nonlocal delay, *Math. Comput. Modelling*, **50**(1–2):194–206, 2009.
30. X. Yan, Y. Chu, Stability and bifurcation analysis for a delayed Lotka–Volterra predator–prey system, *J. Comput. Appl. Math.*, **196**(1):198–210, 2006.
31. Q. Ye, Z. Li, *Introduction of Reaction–Diffusion Equations*, Regional Conferences Series in Applied Mathematics, Science Publ. House, Beijing, 1990.
32. J. Zhang, Z. Jin, J. Yan, G. Sun, Stability and Hopf bifurcation in a delayed competition system, *Nonlinear Anal., Theory, Methods Appl.*, **70**:658–670, 2009.
33. X. Zhang, H. Zhao, Bifurcation and optimal harvesting of a diffusive predator–prey system with delays and interval biological parameters, *J. Theor. Biol.*, **363**:390–403, 2014.
34. X. Zhang, H. Zhao, Stability and bifurcation of a reaction-diffusion predator–prey model with non-local delay and Michaelis–Menten-type prey-harvesting, *Int. J. Comput. Math.*, **93**(9):1447–1469, 2016.
35. W. Zuo, J. Wei, Stability and hopf bifurcation in a diffusive predator–prey system with delay effect, *Nonlinear Anal., Real World Appl.*, **12**(4):1998–2011, 2011.
36. W. Zuo, J. Wei, Stability and bifurcation in a ratio-dependent Holling-III system with diffusion and delay, *Nonlinear Anal. Model. Control*, **19**(1):132–153, 2014.