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DYNAMICS OF A BEDDINGTON-DEANGELIS PREDATOR-PREY MODEL WITH STAGE STRUCTURE

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ABSTRACT. A stage-structured predator-prey model with Beddington-DeAngelis functional response is introduced. By analyzing the characteristic equation, criteria are established for the local stability of equilibria. Further, it is proved that system undergoes Hopf bifurcation at the positive equilibrium when $\tau = \tau_0$. By using an iteration technique and comparison argument, sufficient conditions are derived for the global stability of equilibria. Numerical simulations are also presented to illustrate our main results.

Kewords: Stage structure; Time delay; Local and global stability; Hopf bifurcation; Beddington-DeAngelis

1. **Introduction**

The predator-prey system is a very important model that has been discussed by many mathematicians. There are two components that play important role in it, one is stage structure, another is the predator's functional response. In the natural world, there are many species (especially insects) whose individual members have a life history that takes them through two stages, immature and mature. Let $N_i(t)$ denotes the immature density at time t and $N_m(t)$ for the mature. Then the following stage-structured single-species model is discussed in [1]:

$$\begin{cases} \dot{N}_i(t) = B(t) - D_i(t) - W(t), \\ \dot{N}_m(t) = \alpha W(t) - D_m(t). \end{cases} \tag{1.1}$$

where $B(t)$ is the birth rate of the immature population at time t; $D_i(t)$ and $D_m(t)$ are the death rates of the immature and the mature population at time t, respectively; $W(t)$ represents the transformation rate of the immature into the mature; α is the probability of the successful transformation of the immature into the mature.

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In [2], a model of single-species population growth incorporating stage structure as a reasonable generalization of the classical logistic model is formulated and discussed. This model assumes an average age to maturity which appears as a constant time delay reflecting a delayed birth of immature and a reduced survival of immature to their maturity. The model takes the form:

$$\begin{cases} \dot{x}_1(t) = \alpha x_2(t) - \gamma x_1(t) - \alpha e^{-\gamma\tau} x_2(t-\tau), \\ \dot{x}_2(t) = \alpha e^{-\gamma\tau} x_2(t-\tau) - \beta x_2^2(t), \qquad t > \tau, \end{cases} \tag{1.2}$$

where $x_1(t)$, $x_2(t)$ denote the immature and mature population densities, respectively. Here, $\alpha > 0$ represents the per-capita birth rate; $\gamma > 0$ is the per-capita immature death rate; $\beta > 0$ is death rate due to overcrowding and τ is the "fixed" time to maturity; and the term $\alpha e^{-\gamma\tau} x_2(t-\tau)$ denotes the immature individuals who were born at time $t-\tau$ (i.e., $\alpha x_2(t-\tau)$) and survive at time t. On the basis of above two models, many kinds of predator-prey models with stage structure have been investigated (see [3, 4] and the references therein).

As for predator's functional response, there have been several famous functional response type: Holling types I-III; Beddington-DeAngelis type by Beddington [5] and DeAngelis et al. [6]; the Crowley-Martin type [7]; ratio-dependent type, and so forth. Of them, the Holling types I-III are labeled "prey-dependent" and the other types that consider the interference among predators are labeled "predator-dependent" by Arditi and Ginzburg [8]. Skalski and Gilliam [9] pointed out that the predator-dependent functional response can provide better descriptions of predator feeding over a range of predator-prey abundances, and in some cases, the Beddington-DeAngelis-type functional response performed even better. Cantrell and Cosner [10] consider the following stage-structured predator-prey system with Beddington-DeAngelis functional response

$$\begin{cases} \dot{x}_1(t) = x(t)(1-x(t)) - \frac{cx(t)y(t)}{1+nx(t)+my(t)}, \\ \dot{x}_2(t) = \frac{fx(t)y(t)}{1+nx(t)+my(t)} - dy(t), \end{cases} \tag{1.3}$$

where $x(t)$ and $y(t)$ represent prey and predator densities, respectively. The Beddington-DeAngelis functional response is different from the traditional monotone or non-monotone functional response. It is similar to the Holling type II functional response but contains an extra term $my(t)$ describing mutual interference by predator. It can be derived mechanistically via considerations of time utilization [5, 11] or spatial limits on predation [12].

The ratio-dependent form also incorporates mutual interference by predators, but it has somewhat singular behavior at low densities and has been criticized on other grounds. See [13] for a mathematical analysis and the references in [12] for some aspects of the debate among biologists about ratio dependence. The Beddington-DeAngelis form of functional response has some of the same qualitative features as the ratio-dependent models form but avoids some of the same behaviors of ratio-dependent models at low densities which have been the source of controversy. In addition, Harrision [14] showed that the Beddington-DeAngelis functional response (for intraspecific interference competition) was superior to functional response without such competition in a microbial predator-prey interaction. Therefore, it is interesting and important to study the following stage-structured predator-prey system with Beddington-DeAngelis functional response

$$\begin{cases} \dot{x}(t) = x(t)\left(r - ax(t) - \frac{\alpha y_2(t)}{k+bx(t)+cy_2(t)}\right), \\ \dot{y}_1(t) = \frac{\beta x(t-\tau)y_2(t-\tau)}{k+bx(t-\tau)+cy_2(t-\tau)} - d_1 y_1(t) - \gamma y_1(t), \\ \dot{y}_2(t) = \gamma y_1(t) - d_2 y_2(t). \end{cases} \tag{1.4}$$

The initial conditions for system (1.4) take the form

$$\begin{aligned} x(\theta) &= \Phi(\theta), \quad y_1(\theta) = \Psi_1(\theta), \quad y_2(\theta) = \Psi_2(\theta), \\ \Phi(\theta) &\geq 0, \quad \Psi_1(\theta) \geq 0, \quad \Psi_2(\theta) \geq 0, \quad \theta \in [-\tau, 0], \\ \Phi(0) &> 0, \quad \Psi_1(0) > 0, \quad \Psi_2(0) > 0. \end{aligned} \tag{1.5}$$

where $(\Phi(\theta), \Psi_1(\theta), \Psi_2(\theta)) \in C([-\tau, 0], R^3_{+0})$, the Banach space of continuous functions mapping the interval $[-\tau, 0]$ into R^3_{+0}, where $R^3_{+0} = \{(x_1, x_2, x_3,) : x_i \geq 0, i = 1, 2, 3\}$.

It is well known by the fundamental theory of functional differential equations [15] that system (1.4) has a unique solution $(x(t), y_1(t), y_2(t))$ satisfying initial conditions (1.5).

This paper is organized as follows. In the next section, we will introduce some notation and state several lemmas. In Section 3, we discuss the local stability of equilibria of system (1.4). Further, we study the existence of a Hopf bifurcation for system (1.4) at the positive equilibrium. In Section 4, by using an iteration technique and comparison theorem, sufficient conditions are derived for the global stability of equilibria of system (1.4). Numerical simulations are also carried out to illustrate the main results.

2. **Preliminaries**

In this section, we introduce some notations and state several results which were introduced in [3]. Let R^n_+ be the cone of nonnegative vectors in R^n. If $x, y \in R^n$, we write $x \leq y$ $(x < y)$ if $x_i \leq y_i$ $(x_i < y_i)$ for $1 \leq i \leq n$. Let $\{e_1, e_2, \ldots, e_n\}$ denote the standard basis in R^n. Suppose $r \geq 0$ and let $C = C([-r, 0], R^n)$ be the Banach space of continuous functions mapping the interval $[-r, 0]$ into R^n with supremum norm. If $\phi, \psi \in C$, we write $\phi \leq \psi$ $(\phi < \psi)$ when the indicated inequality holds at each point of $[-r, 0]$. Let $C^+ = \{\phi \in C : \phi \geq 0\}$ and let $\hat{}$ denote the inclusion $R^n \to C([-r, 0], R^n)$

by $x \to \hat{x}$, $\hat{x}(\theta) = x$, $\theta \in [-r, 0]$. Denote the space of functions of bounded variation on $[-r, 0]$ by $BV[-r, 0]$. If $t_0 \in R$, $A \geq 0$ and $x \in C([t_0 - r, t_0 + A], R^n)$, then for any $t \in [t_0, t_0 + A]$, we let $x_t \in C$ be defined by $x_t(\theta) = x(t + \theta)$, $-r \leq \theta \leq 0$.

We now consider

$$\dot{x}(t) = f(t, x_t) \tag{2.1}$$

We assume throughout this section that $f : R \times C \to R^n$ is continuous; $f(t, \phi)$ is continuously differentiable in ϕ; $f(t + T, \phi) = f(t, \phi)$ for all $(t, \phi) \in R \times C^+$, and some $T > 0$. Then by [15], there exists a unique solution of (2.1) through (t_0, ϕ) for $t_0 \in R$, $\phi \in C^+$. This solution will be denoted by $x(t, t_0, \phi)$ if we consider the solution in R^n, or by $x_t(t_0, \phi)$ if we work in the space C. Again by [15], $x(t, t_0, \phi)$ $(x_t(t_0, \phi))$ is continuously differentiable in ϕ. In the following, the notation $x_{t_0} = \phi$ will be used as the condition of the initial data of (2.1), by which we mean that we consider the solution $x(t)$ of (2.1) which satisfies $x(t_0 + \theta) = \phi(\theta)$, $\theta \in [-r, 0]$.

To proceed further, we need the following results from [16, 17]. Let $r = (r_1, r_2, \ldots, r_n) \in R^n_+$, $|r| = \max\{r_i\}$, and define $C_r = \prod_{i=1}^{n} C([-r_i, 0], R)$, we write $\phi = (\phi_1, \phi_2, \ldots, \phi_n)$ for a generic point of C_r. Let $C_r^+ = \{\phi \in C_r : \phi \geq 0\}$. Due to the ecological applications, we choose C_r^+ as the state space of (2.1) in the following discussions.

Fix $\phi_0 \in C_r^+$ arbitrarily. Then we set $L(t, \cdot) = D_{\phi_0} f(t, \phi_0)$, $D_{\phi_0} f(t, \phi_0)$ denotes the Frechet derivation of f with respect to ϕ_0. It is convenient to have the standard representation of $L = (L_1, L_2, \ldots, L_n)$ as $L_i(t, \phi) = \sum_{j=1}^{n} \int_{-r_j}^{0} \phi_j(\theta)\, d_\theta \eta_{ij}(\theta, t)$, $(1 \leq i \leq n)$, in which $\eta_{ij} : R \times R \to R$ satisfies

$$\begin{aligned}
\eta_{ij}(\theta, t) &= \eta_{ij}(0, t), \quad \theta \geq 0, \\
\eta_{ij}(\theta, t) &= 0, \quad \theta \leq -r_j, \\
\eta_{ij}(\cdot, t) &\in BV[-r_j, 0],
\end{aligned}$$

where $\eta_{ij}(\cdot, t)$ is continuous from the left in $(-r_j, 0)$.

We make the following assumptions for (2.1):

(h0) If $\phi, \psi \in C^+$, $\phi \leq \psi$, and $\phi_i(0) = \psi_i(0)$ for some i, then $f_i(t, \phi) \leq f_i(t, \psi)$.
(h1) For all $\phi \in C^+$ with $\phi_i(0) = 0$, $L_i(t, \phi) \geq 0$ for $t \in R$.
(h2) The matrix $A(t)$ defined by $A(t) = col(L(t, \hat{e}_1), L(t, \hat{e}_2), \ldots, L(t, \hat{e}_n)) = (\eta_{ij}(0, t))$ is irreducible for each $t \in R$.
(h3) For each j, for which $r_j > 0$, there exists i such that for all $t \in R$ and for positive constant ε sufficiently small, $\eta_{ij}(-r_j + \varepsilon, t) > 0$.
(h4) If $\phi = 0$, then $x(t, t_0, \phi) \equiv 0$ for all $t \geq t_0$.

The following results was established by Wang et al. [17].

Lemma 2.1. *Let* (h1)–(h4) *hold. Then the hypothesis* (h0) *is valid and*

(i) *If ϕ and ψ are distinct elements of C_r^+ with $\phi \le \psi$ and $[t_0, t_0+\sigma)$ with $n|r| < \sigma \le \infty$ is the intersection of the maximal intervals of existence of $x(t,t_0,\phi)$ and $x(t,t_0,\psi)$, then*

$$\begin{aligned} 0 &\le x(t,t_0,\phi) \le x(t,t_0,\psi) \text{ for } t_0 \le t < t_0+\sigma, \\ 0 &\le x(t,t_0,\phi) < x(t,t_0,\psi) \text{ for } t_0+n|r| \le t < t_0+\sigma. \end{aligned}$$

(ii) *If $\phi \in C_r^+, \phi \ne 0$, $t_0 \in R$ and $x(t,t_0,\phi)$ is defined on $[t_0, t_0+\sigma)$ with $\sigma > n|r|$, then*

$$0 < x(t,t_0,\phi) \text{ for } t_0+n|r| \le t < t_0+\sigma.$$

This lemma shows that if (h1)–(h4) *hold, then the positivity of solutions of* (2.1) *follows.*

Definition 2.2 ([18])**.** Let $A = (a_{ij})_{n\times n}$ be an $n \times n$ matrix and let $p_1, p_2, \dots, p_n$ be distinct points of the complex plane. For each nonzero element a_{ij} of A, connect p_i to p_j with a directed line $\overline{p_i p_j}$. The resulting figure in the complex plane is a directed graph for A. We say that a directed graph is strongly connected if, for each pair of nodes p_i, p_j with $i \ne j$, there is a directed path

$$\overrightarrow{p_i p_{k_1}}, \overrightarrow{p_{k_1} p_{k_2}}, \dots, \overrightarrow{p_{k_{r-1}} p_j}$$

connecting p_i and p_j. Here, the path consists of r directed lines.

Lemma 2.3 ([18])**.** *A square matrix is irreducible if and only if its directed graph is strongly connected.*

Lemma 2.4 ([16])**.** *If* (2.1) *is cooperative and irreducible in D, where D is an open subset of C, and the solutions with positive initial data is bounded, then the trajectory of* (2.1) *tends to some single equilibrium.*

Setting $M > 0$ be a constant. We now consider the following delay differential system

$$\begin{aligned} \dot{y}_1(t) &= \frac{\beta M y_2(t-\tau)}{k + bM + c y_2(t-\tau)} - d_1 y_1(t) - \gamma y_1(t), \\ \dot{y}_2(t) &= \gamma y_1(t) - d_2 y_2(t). \end{aligned} \tag{2.2}$$

with initial conditions

$$y_i(s) = \phi_i(s) \ge 0, \quad s \in [-\tau, 0),\ \phi_i(0) > 0,\ \phi_i \in C([-\tau,0], R_+)\ \ (i = 1,2).$$

System (2.2) always has a trivial equilibrium $E^0(0,0)$. If $M[\gamma\beta - bd_2(d_1+\gamma)] - kd_2(d_1+\gamma) > 0$, then system (2.2) has a unique positive equilibrium $E^+(y_1^0, y_2^0)$, where

$$y_1^0 = \frac{M[\gamma\beta - bd_2(d_1+\gamma)] - kd_2(d_1+\gamma)}{c\gamma(d_1+\gamma)}, \quad y_2^0 = \frac{M[\gamma\beta - bd_2(d_1+\gamma)] - kd_2(d_1+\gamma)}{cd_2(d_1+\gamma)}.$$

The characteristic equation of E^+ takes the form

$$\lambda^2 + a_1\lambda + a_0 + b_0 e^{-\lambda\tau} = 0,$$

where

$$a_0 = d_2(d_1+\gamma), \quad a_1 = d_2 + d_1 + \gamma, \quad b_0 = -\frac{d_2^2(d_1+\gamma)(k+bM)}{M\gamma\beta}.$$

Noting that

$$a_0 + b_0 = \frac{d_2(d_1+\gamma)}{M\gamma\beta}\left[M[\gamma\beta - bd_2(d_1+\gamma)] - kd_2(d_1+\gamma)\right],$$

We can see $a_1 > 0$, if $M[\gamma\beta - bd_2(d_1+\gamma)] - kd_2(d_1+\gamma) > 0$, then $a_1(a_0+b_0) > 0$, by Routh-Hurwitz Theorem the positive equilibrium E^+ is locally stable when $\tau = 0$. If $M[\gamma\beta - bd_2(d_1+\gamma)] - kd_2(d_1+\gamma) < 0$, then E^+ is unstable when $\tau = 0$.

It is easy to show that

$$\begin{aligned} a_1^2 - 2a_0 &= (d_1+\gamma)^2 + d_2^2 > 0, \\ a_0 - b_0 &= \frac{d_2(d_1+\gamma)}{M\gamma\beta}\left[M[\gamma\beta + bd_2(d_1+\gamma)] + kd_2(d_1+\gamma)\right] > 0. \end{aligned}$$

So, if $M[\gamma\beta - bd_2(d_1+\gamma)] - kd_2(d_1+\gamma) > 0$, then by Lemma B in Kuang and so [19], the equilibrium E^+ is locally asymptotically stable for all $\tau > 0$. If $M[\gamma\beta - bd_2(d_1+\gamma)] - kd_2(d_1+\gamma) < 0$, then E^+ is unstable for all $\tau > 0$.

Using a similar arguments as above we can obtain that if $M[\gamma\beta - bd_2(d_1+\gamma)] - kd_2(d_1+\gamma) < 0$, the equilibrium $E^0(0,0)$ is locally asymptotically stable for all $\tau \geq 0$. If $M[\gamma\beta - bd_2(d_1+\gamma)] - kd_2(d_1+\gamma) > 0$, then $E^0(0,0)$ is unstable for all $\tau \geq 0$.

Lemma 2.5. *For system* (2.2)*, we have*

(i) *If $M[\gamma\beta - bd_2(d_1+\gamma)] > kd_2(d_1+\gamma)$, then the positive equilibrium $E^+(y_1^0, y_2^0)$ is globally stable.*
(ii) *If $M[\gamma\beta - bd_2(d_1+\gamma)] < kd_2(d_1+\gamma)$, then the equilibrium $E^0(0,0)$ is globally stable.*

Proof. We represent the right-hand side of (2.2) by $f(t,x_t) = (f_1(t,x_t), f_2(t,x_t))$, and set

$$L(t,\cdot) = D_\phi f(t,\phi).$$

We have

$$\begin{aligned} L_1(t,h) &= \frac{bM}{(k+bM+c\phi_2(-\tau))^2} h_2(-\tau) - (d_1+\gamma)h_1(0), \\ L_2(t,h) &= \gamma h_1(0) - d_2 h_2(0). \end{aligned}$$

We now claim that the hypotheses (h1)–(h4) hold for system (2.2). It is easy to show that (h1) and (h4) hold for system (2.2), the matrix $A(t)$ takes the form

$$\begin{pmatrix} -(d_1+\gamma) & \frac{bM}{(k+bM+c\phi_2(-\tau))^2} \\ \gamma & -d_2 \end{pmatrix}.$$

Clearly, the matrix $A(t)$ is irreducible for each $t \in R$, hence, (h2) holds. From the definition of $A(t)$ and η_{ij}, we can readily seen that $\eta_{12}(\theta,t) = \eta_{12}(0,t) = \frac{bM}{(k+bM+c\phi_2(-\tau))^2}$, $\eta_{21}(\theta,t) = \eta_{21}(0,t) = \gamma$ for $\theta \geq 0$; and $\eta_{ij}(\theta,t) = 0$, $i \neq j$ for $\theta \leq -\tau$; and $\eta_{ij}(\cdot,t) \in BV[-\tau,0]$, where η_{ij} is a positive Borel measure on $[-\tau,0]$. Therefore, $\eta_{ij}(\cdot,t) > 0$. Thus, for each j, there is $i \neq j$ such that $\eta_{ij}(-r_j+\varepsilon,t) = \eta_{ij}(-\tau+\varepsilon,t) > 0$ for all $t \in R$ and for $\varepsilon > 0$ sufficiently small, $i = 1,2$. Hence, (h3) holds.

Thus, by Lemma 2.1, the positivity of solution of system (2.1) follows. It is easy to see that system (2.2) is cooperative. By Lemma 2.3 we see that any solution starting from $D \in C_\tau^+$ converges to some single equilibrium. However, system (2.2) has only two equilibria: E^0 and E^+. Note that if $M[\gamma\beta - bd_2(d_1+\gamma)] > kd_2(d_1+\gamma)$, then the positive equilibrium E^+ is locally stable, and the equilibrium E^0 is unstable. Hence, any solution starting from D converges to $E^+(y_1^0, y_2^0)$ if $M[\gamma\beta - bd_2(d_1+\gamma)] > kd_2(d_1+\gamma)$. similarly, we can show the global stability of the equilibrium E^0 when $M[\gamma\beta - bd_2(d_1+\gamma)] < kd_2(d_1+\gamma)$. This completes the proof. □

By a similar argument we can show that all solutions of system (1.4) with initial conditions (1.5) are defined on $[0,+\infty)$ and remain positive for all $t \geq 0$.

3. **Local stability and Hopf bifurcation**

In this section, we discuss the local stability of equilibria and the existence of Hopf bifurcation.

Let $D = d_1 + \gamma$, it is obvious that system (1.4) has a boundary equilibrium $E_1(\frac{r}{a}, 0, 0)$. Further, if the following condition holds:

(H1) $\left(A_1 + \sqrt{A_1^2 + A_2}\right)(\gamma\beta - bd_2D) - 2ac\gamma\beta kd_2D > 0$, where

$$A_1 = \alpha\,(bd_2D - \gamma\beta) + rc\gamma\beta, \quad A_2 = 4ac\gamma\beta\alpha kd_2D.$$

then system (1.4) has a unique positive equilibrium $E^*(x^*, y_1^*, y_2^*)$, where

$$\begin{aligned} x^* &= \frac{A_1 + \sqrt{A_1^2 + A_2}}{2ac\gamma\beta}, \\ y_1^* &= \frac{(\gamma\beta - bd_2D)\,x^* - kd_2D}{c\gamma D}, \\ y_2^* &= \frac{(\gamma\beta - bd_2D)\,x^* - kd_2D}{cd_2D}. \end{aligned} \tag{3.1}$$

We study E^* under the condition (H1). The characteristic equation of E^* is

$$\lambda^3 + a_2\lambda^2 + a_1\lambda + a_0 + (b_1\lambda + b_0)e^{-\lambda\tau} = 0. \tag{3.2}$$

where

$$\begin{aligned}
a_0 &= d_2 D\left(ax^* - \frac{b\alpha x^* y_2^*}{(k+bx^*+cy_2^*)^2}\right),\\
a_1 &= d_2 D + (d_2 + D)\left(ax^* - \frac{b\alpha x^* y_2^*}{(k+bx^*+cy_2^*)^2}\right),\\
a_2 &= d_2 + D + ax^* - \frac{b\alpha x^* y_2^*}{(k+bx^*+cy_2^*)^2},\\
b_0 &= -\frac{\gamma\beta x^*(k+bx^*)}{(k+bx^*+cy_2^*)^2}\left(ax^* - \frac{b\alpha x^* y_2^*}{(k+bx^*+cy_2^*)^2}\right)\\
&\quad + \frac{\alpha\gamma\beta x^* y_2^*(k+bx^*)(k+cy_2^*)}{(k+bx^*+cy_2^*)^4},\\
b_1 &= -\frac{\gamma\beta x^*(k+bx^*)}{(k+bx^*+cy_2^*)^2}.
\end{aligned} \tag{3.3}$$

It is easy to show that

$$\begin{aligned}
a_0 + b_0 &= \frac{d_2 D[ac\gamma\beta(x^*)^2 + \alpha k d_2 D]}{c\gamma^2\beta^2(x^*)^2} A_3,\\
a_0 - b_0 &= \frac{d_2 D}{\gamma\beta x^*}\left[x^*\left(\gamma\beta - bd_2 D\right) + kd_2 D\right] \times\\
&\quad \left\{r - \frac{\alpha A_3\left[x^*\left(\gamma\beta + 3bd_2 D\right) + 2kd_2 D\right]}{c\gamma\beta x^*\left[x^*\left(\gamma\beta + bd_2 D\right) + kd_2 D\right]}\right\},\\
a_1 + b_1 &= \frac{d_2 D}{\gamma\beta x^*} A_3 + (d_2 + D) \times\\
&\quad \left\{r - \frac{\alpha\left[A_4 - kd_2 D x^*\left(\gamma\beta + bd_2 D\right)\right]}{c\gamma^2\beta^2(x^*)^2}\right\}.
\end{aligned}$$

where $A_3 = x^*\left(\gamma\beta - bd_2 D\right) - kd_2 D$, $A_4 = (x^*\gamma\beta)^2 - (bd_2 D x^*)^2$.

If $i\omega$ $(\omega > 0)$ is a solution of (3.2), separating real and imaginary parts yield

$$\begin{aligned}
a_2\omega^2 - a_0 &= b_0\cos\omega\tau + b_1\omega\sin\omega\tau,\\
-\omega^3 + a_1\omega &= b_0\sin\omega\tau - b_1\omega\cos\omega\tau.
\end{aligned} \tag{3.4}$$

From (3.4), we have

$$\omega^6 + (a_2^2 - 2a_1)\omega^4 + (a_1^2 - 2a_0 a_2 - b_1^2)\omega^2 + a_0^2 - b_0^2 = 0 \tag{3.5}$$

It is easy to show that

$$\begin{aligned} a_2^2 - 2a_1 &= d_2^2 + D^2 + \left(ax^* - \frac{b\alpha x^* y_2^*}{(k + bx^* + cy_2^*)^2} \right)^2 > 0, \\ a_1^2 - 2a_0 a_2 - b_1^2 &= \frac{d_2^2 D^2}{(\gamma\beta x^*)^2} \left[(\gamma\beta x^*)^2 - ((k + bx^*) d_2 D)^2 \right] \\ &\quad + \left[d_2^2 + D^2 \right] \left(ax^* - \frac{b\alpha x^* y_2^*}{(k + bx^* + cy_2^*)^2} \right)^2 . \end{aligned}$$

Then, we have the following lemma.

Lemma 3.1 ([20]). *Eq. (3.2) has a unique pair of purely imaginary roots if $a_0 < b_0$.*

From (H1) we can deduce $x^* (\gamma\beta - bd_2 D) - kd_2 D > 0$, consequently, $a_0 + b_0 > 0$. Hence if $a_2 > 0$, $a_2(a_1 + b_1) > a_0 + b_0$, then by Routh-Hurwitz Theorem the positive equilibrium E^* of system (1.4) is locally stable when $\tau = 0$.

From (H1), we have $a_1^2 - 2a_0 a_2 - b_1^2 > 0$. If $a_0 > b_0$ then equation (3.5) has no positive roots, then stability of E^* unchange. Hence, if $a_2 > 0$, $a_2(a_1 + b_1) > a_0 + b_0$, $a_0 > b_0$, then the positive equilibrium E^* of system (1.4) is locally asymptotically stable for all $\tau > 0$. If $a_0 < b_0$, then from Lemma 3.1 we know Eq. (3.5) has a unique positive root ω_0, that is, (3.2) has a unique pair of purely imaginary roots of the form $\pm\omega_0$. From (3.4) we see that τ_n corresponding to ω_0 is

$$\tau_n = \frac{1}{\omega_0} \arccos \frac{b_1 \omega_0^4 - (a_2 b_0 - a_1 b_1)\omega_0^2 - a_0 b_0}{b_0^2 + b_1^2 \omega_0^2} + \frac{2n\pi}{\omega_0}, \quad n = 0, 1, 2, \ldots$$

Note that if $a_2 > 0$, $a_2(a_1 + b_1) > a_0 + b_0$, E^* is locally stable when $\tau = 0$. Hence, by the general theory on characteristic equations of delay differential equations from [21], if $a_2 > 0$, $a_2(a_1 + b_1) > a_0 + b_0$, $a_0 < b_0$, E^* remains locally stable for $\tau < \tau_0$. Next, we turn to show

$$\frac{dRe\lambda)}{d_\tau}|_{\tau=\tau_0} > 0. \tag{3.6}$$

This will signify that there exists at least one eigenvalue with positive real part for $\tau > \tau_0$. Moreover, the conditions for the existence of a Hopf bifurcation [15] are then satisfied yielding a periodic solution. We differentiating equation (3.2) with respect τ, it follows that

$$[3\lambda^2 + 2a_2\lambda + a_1 + b_1 e^{-\lambda\tau} - \tau(b_1\lambda + b_0)e^{-\lambda\tau}] \frac{d_\lambda}{d_\tau} = \lambda(b_1\lambda + b_0)e^{-\lambda\tau}.$$

That is

$$\begin{aligned} \left(\frac{d_\lambda}{d_\tau} \right)^{-1} &= \frac{(3\lambda^2 + 2a_2\lambda + a_1) + b_1 e^{-\lambda\tau}}{\lambda(b_1\lambda + b_0)e^{-\lambda\tau}} - \frac{\tau}{\lambda} \\ &= \frac{3\lambda^2 + 2a_2\lambda + a_1}{\lambda(\lambda^3 + a_2\lambda^2 + a_1\lambda + a_0)} + \frac{b_1}{\lambda(b_1\lambda + b_0)} - \frac{\tau}{\lambda}. \end{aligned}$$

Thus

$$\Re\left(\frac{d_\lambda}{d_\tau}\right)^{-1}\Bigg|_{\lambda=i\omega_0} = \Re\left[-\frac{a_1-3\omega_0^2+2a_2i\omega_0}{i\omega_0\left[(a_0-a_2\omega_0^2)+i\omega_0(a_1-\omega_0^2)\right]}+\frac{b_1}{i\omega_0(b_1i\omega_0+b_0)}\right]$$
$$= \frac{2b_1^2\omega_0^6+\left[3b_0^2+b_1^2(a_2^2-2a_1)\right]\omega_0^4+2b_0^2(a_2^2-2a_1)\omega_0^2+b_0^2(a_1^2-2a_0a_2)-a_0^2b_1^2}{(b_0^2+b_1^2\omega_0^2)\left[\omega_0^2(a_1-\omega_0^2)^2+(a_0-a_2\omega_0^2)^2\right]}.$$

It is easy to show that $a_2^2-2a_1>0$, $a_1^2-2a_0a_2-b_1^2>0$. Hence, if $a_0<b_0$, then $b_0^2(a_1^2-2a_0a_2)-a_0^2b_1^2>b_0^2(a_1^2-2a_0a_2-b_1^2)>0$. Then we obtain

$$\frac{d(\Re\lambda)}{d_\tau}|_{\tau=\tau_0}>0.$$

We know the transversal condition holds and a Hopf bifurcation occurs at $\omega=\omega_0$, $\tau=\tau_0$.

The characteristic equation of system (1.4) at the boundary equilibrium $E_1(r/a,0,0)$ takes the form

$$\lambda^3+p_2\lambda^2+p_1\lambda+p_0+(q_1\lambda+q_0)e^{-\lambda\tau}$$

where

$$\begin{aligned} p_0 &= d_2Dr, \quad p_1=d_2D+r(d_2+D), \quad p_2=d_2+D+r>0,\\ q_0 &= -\frac{\gamma\beta r^2}{ak+br}, \quad q_1=-\frac{\gamma\beta r}{ak+br}. \end{aligned}$$

Noting that if $\frac{r}{a}[\gamma\beta-bd_2D]<kd_2D$, then $p_2>0$, $p_2(p_1+q_1)>p_0+q_0>0$, the equilibrium $E_1(r/a,0,0)$ is locally stable when $\tau=0$. Hence, using a similar argument as above we see that if $\frac{r}{a}[\gamma\beta-bd_2D]<kd_2D$, then the equilibrium $E_1(r/a,0,0)$ is locally stable for all $\tau\geq 0$; if $\frac{r}{a}[\gamma\beta-bd_2D]>kd_2D$, then E_1 is unstable.

We therefore obtain the following results.

Theorem 3.2. *Let* (H1) *hold. For system* (1.4), *we have*

(i) *If $a_2>0$, $a_2(a_1+b_1)>a_0+b_0$, $a_0>b_0$, then the positive equilibrium E^* of system* (1.4) *is locally asymptotically stable.*
(ii) *If $a_2>0$, $a_2(a_1+b_1)>a_0+b_0$, $a_0<b_0$, system* (1.4) *undergoes Hopf bifurcation at E^* when $\tau=\tau_n$, $n=0,1,2,\ldots$; furthermore E^* is locally asymptotically stable if $\tau\in[0,\tau_0)$ and unstable if $\tau>\tau_0$.*

Theorem 3.3. *If $\frac{r}{a}[\gamma\beta-bd_2D]<kd_2D$, then the boundary equilibrium E_1 is locally stable; if $\frac{r}{a}[\gamma\beta-bd_2D]>kd_2D$, then E_1 is unstable.*

4. **Global stability**

In this section, we discuss the global stability of E^* and E_1 of system (1.4), respectively.

Theorem 4.1. *The positive equilibrium $E^*(x^*, y_1^*, y_2^*)$ of system* (1.4) *is globally stable provided that* (H2) *holds and either* (H3) *or* (H4) *hold true:*

(H2) $rc - \alpha > 0$, $\frac{rc-\alpha}{ac}[\gamma\beta - bd_2D] - kd_2D > 0$
(H3) $bd_2D - \gamma\beta < 0$, $\gamma\beta - 2bd_2D \le 0$
(H4) $\left[rc - \frac{(\alpha\gamma\beta - bd_2D)(\gamma\beta + 2bd_2D)}{\gamma^2\beta^2}\right](\overline{x} + \underline{x}) + \frac{4b\alpha kd_2^2D^2}{\gamma^2\beta^2} > 0$ *where,* $\overline{x} + \underline{x}$ *is defined by* (4.14).

Proof. Let $(x(t),\ y_1(t),\ y_2(t))$ be any positive solution of system (1.4) with initial conditions (1.5). By the first equation of system (1.4), for sufficiently small $\varepsilon > 0$, there exists a $T_1 > 0$ such that $x(t) \le \frac{r}{a} + \varepsilon := \overline{x_1}$ for $t \ge T_1$. Replacing this inequality into the second equation of (1.4), it follows that for $t \ge T_1 + \tau$

$$\dot{y}_1(t) \le \frac{\beta\overline{x_1}y_2(t-\tau)}{k + b\overline{x_1} + cy_2(t-\tau)} - (d_1+\gamma)y_1(t).$$

Consider the following auxiliary system

$$\begin{aligned} \dot{u}_1(t) &= \frac{\beta\overline{x_1}u_2(t-\tau)}{k + b\overline{x_1} + cu_2(t-\tau)} - (d_1+\gamma)u_1(t), \\ \dot{u}_2(t) &= \gamma u_1(t) - d_2u_2(t), \\ u_1(t) &\equiv y_1(t),\ u_2(t) \equiv y_2(t),\ t \in [T_1, T_1+\tau]. \end{aligned} \tag{4.1}$$

Obviously, for sufficiently small $\varepsilon > 0$, $\overline{x_1} > \frac{rc-\alpha}{ac}$, by (H2) we know, $\overline{x_1}[\gamma\beta - bd_2D] - kd_2D > 0$, by Lemma 2.4 it follows from (4.1) that

$$\begin{aligned} \lim_{t\to+\infty} u_1(t) &= \frac{\overline{x_1}[\gamma\beta - bd_2D] - kd_2D}{c\gamma D}, \\ \lim_{t\to+\infty} u_2(t) &= \frac{\overline{x_1}[\gamma\beta - bd_2D] - kd_2D}{cd_2D}. \end{aligned}$$

By comparison theorem, we have $y_1(t) \le u_1(t)$, $y_2(t) \le u_2(t)$ for $t \ge T_1 + \tau$. Then for sufficiently small $\varepsilon > 0$, there is a $T_2 > T_1 + \tau$ such that if $t \ge T_2$

$$\begin{aligned} y_1(t) &\le \frac{\overline{x_1}[\gamma\beta - bd_2D] - kd_2D}{c\gamma D} + \varepsilon := \overline{y_{11}}, \\ y_2(t) &\le \frac{\overline{x_1}[\gamma\beta - bd_2D] - kd_2D}{cd_2D} + \varepsilon := \overline{y_{21}}. \end{aligned} \tag{4.2}$$

Replacing the second inequality of (4.2) into the first equation of system (1.4) that for $t \ge T_2$

$$\dot{x}(t) \ge x(t)\left(r - ax(t) - \frac{\alpha\overline{y_{21}}}{k + c\overline{y_{21}}}\right).$$

By (H2), we know $rc - \alpha > 0$. Using the comparison theorem , for $\varepsilon > 0$ sufficiently small, there is a $T_3 > T_2$ such that if $t \ge T_3$

$$x(t) \ge \frac{rk + (rc-\alpha)\overline{y_{21}}}{a(k + c\overline{y_{21}})} - \varepsilon := \underline{x_1} > 0.$$

Replacing this inequality into the second equation of (1.4), it follows that for $t \geq T_3+\tau$

$$\dot{y}_1(t) \geq \frac{\beta \underline{x_1} y_2(t-\tau)}{k+b\underline{x_1}+cy_2(t-\tau)} - (d_1+\gamma)y_1(t).$$

Consider the following auxiliary system

$$\begin{aligned} \dot{u}_1(t) &= \frac{\beta \underline{x_1} u_2(t-\tau)}{k+b\underline{x_1}+cu_2(t-\tau)} - (d_1+\gamma)u_1(t), \\ \dot{u}_2(t) &= \gamma u_1(t) - d_2u_2(t), \\ u_1(t) &\equiv y_1(t),\ u_2(t) \equiv y_2(t),\ t \in [T_3, T_3+\tau] \end{aligned} \tag{4.3}$$

It is easy to show that $\underline{x_1} = \frac{r}{a} - \frac{\alpha}{ac-\frac{ak}{\overline{y_{21}}}} - \varepsilon$. We can choose $\varepsilon > 0$ sufficiently small such that $\frac{r}{a} - \frac{\alpha}{ac-\frac{ak}{\overline{y_{21}}}} - \varepsilon > \frac{r}{a} - \frac{\alpha}{ac} = \frac{rc-\alpha}{ac}$, hence, $\underline{x_1}[\gamma\beta - bd_2D] - kd_2D > 0$, by Lemma 2.4 it follows from (4.3) that

$$\begin{aligned} \lim_{t\to+\infty} u_1(t) &= \frac{\underline{x_1}[\gamma\beta - bd_2D] - kd_2D}{c\gamma D}, \\ \lim_{t\to+\infty} u_2(t) &= \frac{\underline{x_1}[\gamma\beta - bd_2D] - kd_2D}{cd_2D}. \end{aligned}$$

By comparison theorem, we have $y_1(t) \geq u_1(t)$, $y_2(t) \geq u_2(t)$ for $t \geq T_3+\tau$. Then for sufficiently small $\varepsilon > 0$, there is a $T_4 > T_3+\tau$ such that if $t \geq T_4$

$$\begin{aligned} y_1(t) &\geq \frac{\underline{x_1}[\gamma\beta - bd_2D] - kd_2D}{c\gamma D} - \varepsilon := \underline{y_{11}}, \\ y_2(t) &\geq \frac{\underline{x_1}[\gamma\beta - bd_2D] - kd_2D}{cd_2D} - \varepsilon := \underline{y_{21}}. \end{aligned} \tag{4.4}$$

Therefore we have that for $t \geq T_4$

$$\overline{x_1} \leq x(t) \leq \underline{x_1},\ \underline{y_{i1}} \leq y_i(t) \leq \overline{y_{i1}},\ (i=1,2).$$

hold for system (1.4).

Replacing the second inequality of (4.4) into the first equation of system (1.4) that for $t \geq T_4$,

$$\dot{x}(t) \leq x(t)\left(r - ax(t) - \frac{\alpha \underline{y_{21}}}{k+b\overline{x_1}+c\underline{y_{21}}}\right). \tag{4.5}$$

Since $rc - \alpha > 0$, by comparison theorem, for $\varepsilon > 0$ sufficiently small, there is a $T_5 > T_4$ such that if $t \geq T_5$

$$x(t) \leq \frac{rk + rb\overline{x_1} + (rc-\alpha)\underline{y_{21}}}{a(k+b\overline{x_1}+c\underline{y_{21}})} + \varepsilon := \overline{x_2} > 0. \tag{4.6}$$

It is easy to show that

$$\overline{x_2} \leq \frac{r}{a} \leq \overline{x_1}.$$

Replacing (4.6) into the second equation of (1.4), it follows that for $t \geq T_5+\tau$

$$\dot{y}_1(t) \leq \frac{\beta \overline{x_2} y_2(t-\tau)}{k+b\overline{x_2}+cy_2(t-\tau)} - (d_1+\gamma)y_1(t).$$

Similarly, we can find $\varepsilon > 0$ sufficiently small such that $\overline{x_2} > \frac{rc-\alpha}{ac}$, hence, $\overline{x_2}[\gamma\beta - bd_2D] - kd_2D > 0$. By Lemma 2.4 and the similar arguments to $\overline{y_{i1}}$, $(i = 1, 2)$, for the above selected $\varepsilon > 0$, there is a $T_6 > T_5 + \tau$ such that if $t \geq T_6$

$$\begin{aligned} y_1(t) &\leq \frac{\overline{x_2}[\gamma\beta - bd_2D] - kd_2D}{c\gamma D} + \varepsilon := \overline{y_{12}}, \\ y_2(t) &\leq \frac{\overline{x_2}[\gamma\beta - bd_2D] - kd_2D}{cd_2D} + \varepsilon := \overline{y_{22}}. \end{aligned} \tag{4.7}$$

by (4.2) and (4.7) we obtain $\overline{y_{i2}} \leq \overline{y_{i1}}$, $(i = 1, 2)$. Replacing the second inequality of (4.7) into the first equation of system (1.4) that for $t \geq T_6$

$$\dot{x}(t) \geq x(t)\left(r - ax(t) - \frac{\alpha\overline{y_{22}}}{k + b\underline{x_1} + c\overline{y_{22}}}\right).$$

Since $rc - \alpha > 0$. Then by comparison theorem, for $\varepsilon > 0$ sufficiently small, there is a $T_7 > T_6$ such that if $t \geq T_7$

$$x(t) \geq \frac{r(k + b\underline{x_1}) + (rc - \alpha)\overline{y_{22}}}{a(k + b\underline{x_1} + c\overline{y_{22}})} - \varepsilon := \underline{x_2} > 0$$

Replacing this inequality into the second equation of (1.4), then by arguments similar to those for $\underline{y_{i1}}$, $(i = 1, 2)$, we obtain that there exists a $T_8 > T_7 + \tau$ such that

$$\begin{aligned} y_1(t) &\geq \frac{\underline{x_2}[\gamma\beta - bd_2D] - kd_2D}{c\gamma D} - \varepsilon := \underline{y_{12}} > 0, \\ y_2(t) &\geq \frac{\underline{x_2}[\gamma\beta - bd_2D] - kd_2D}{cd_2D} - \varepsilon := \underline{y_{22}} > 0. \end{aligned}$$

and we obtain $\underline{y_{i2}} \geq \underline{y_{i1}}$, $(i = 1, 2)$.

Therefore, it follows that

$$0 < \underline{x_1} \leq \underline{x_2} \leq x(t) \leq \overline{x_2} \leq \overline{x_1}, \quad 0 < \underline{y_{i1}} \leq \underline{y_{i2}} \leq y_i(t) \leq \overline{y_{i2}} \leq \overline{y_{i1}},\ (i = 1, 2),\ t \geq T_8.$$

Repeating the above arguments, we obtain six sequences $\{\overline{x_n}\}_{n=1}^{\infty}$, $\{\underline{x_n}\}_{n=1}^{\infty}$ $\{\overline{y_{in}}\}_{n=1}^{\infty}$ $\{\underline{y_{in}}\}_{n=1}^{\infty}$ $(i = 1, 2)$ with the form

$$\begin{aligned} &0 < \underline{x_1} \leq \underline{x_2} \leq \cdots \leq \underline{x_n} \leq x(t) \leq \overline{x_n} \leq \cdots \leq \overline{x_2} \leq \overline{x_1}, \\ &0 < \underline{y_{i1}} \leq \underline{y_{i2}} \leq \cdots \leq \underline{y_{in}} \leq y_i(t) \leq \overline{y_{in}} \leq \cdots \leq \overline{y_{i2}} \leq \overline{y_{i1}},\ (i = 1, 2),\ t \geq T_{4n}. \end{aligned} \tag{4.8}$$

From (4.8) follows that the limit of each sequences in $\{\overline{x_n}\}_{n=1}^{\infty}$, $\{\underline{x_n}\}_{n=1}^{\infty}$ $\{\overline{y_{in}}\}_{n=1}^{\infty}$ $\{\underline{y_{in}}\}_{n=1}^{\infty}$ exists. Denote

$$\begin{aligned} \overline{x} &= \lim_{n\to+\infty} \overline{x_n}, \quad \underline{x} = \lim_{n\to+\infty} \underline{x_n}, \\ \overline{y}_i &= \lim_{n\to+\infty} \overline{y_{in}}, \quad \underline{y_i} = \lim_{n\to+\infty} \underline{y_{in}} \quad (i = 1, 2). \end{aligned}$$

By the definition of $\overline{x_n}$, $\underline{x_n}$, $\overline{y_{in}}$, $\underline{y_{in}}$, we have

$$
(4.9)\qquad
\begin{aligned}
\overline{x_n} &= \frac{rk + rb\overline{x_{n-1}} + (rc-\alpha)\underline{y_{2(n-1)}}}{a(k + b\overline{x_{n-1}} + c\underline{y_{2(n-1)}})},\ \underline{x_n} = \frac{rk + rb\underline{x_{n-1}} + (rc-\alpha)\overline{y_{2n}}}{a(k + b\underline{x_{n-1}} + c\overline{y_{2n}})},\\
\overline{y_{1n}} &= \frac{\overline{x_n}m_1 - m_2}{c\gamma D},\ \underline{y_{1n}} = \frac{\underline{x_n}m_1 - m_2}{c\gamma D},\\
\overline{y_{2n}} &= \frac{\overline{x_n}m_1 - m_2}{cd_2 D},\ N_n^{y_2} = \frac{\underline{x_n}m_1 - m_2}{cd_2 D}.
\end{aligned}
$$

where

$$m_1 = \gamma\beta - bd_2D, \quad m_2 = kd_2D.$$

We therefore obtain from (4.8) and (4.9) that

$$
(4.10)\qquad
\begin{aligned}
\overline{x} &= \frac{rk + rb\overline{x} + (rc-\alpha)\underline{y_2}}{a(k + b\overline{x} + c\underline{y_2})}, \quad \underline{x} = \frac{rk + rb\underline{x} + (rc-\alpha)\overline{y_2}}{a(k + b\underline{x} + c\overline{y_2})},\\
\overline{y_1} &= \frac{\overline{x}m_1 - m_2}{c\gamma D}, \quad \underline{y_1} = \frac{\underline{x}m_1 - m_2}{c\gamma D},\\
\overline{y_2} &= \frac{\overline{x}m_1 - m_2}{cd_2 D}, \quad \underline{y_2} = \frac{\underline{x}m_1 - m_2}{cd_2 D}.
\end{aligned}
$$

We obtain $\overline{x} \geq \underline{x}$, $\overline{y}_i \geq \underline{y_i}$. To complete the proof, it suffices to prove $\overline{x} = \underline{x}$, $\overline{y}_i = \underline{y_i}$.

It follows from (4.10) that

$$(4.11)\qquad ab\overline{x}^2 + \frac{am_1}{d_2D}\overline{x}\underline{x} = rb\overline{x} + \frac{(rc-\alpha)m_1}{cd_2D}\underline{x} + \frac{\alpha k}{c}.$$

$$(4.12)\qquad ab\underline{x}^2 + \frac{am_1}{d_2D}\overline{x}\underline{x} = rb\underline{x} + \frac{(rc-\alpha)m_1}{d_2D}\overline{x} + \frac{\alpha k}{c}.$$

(4.11) minus (4.12)

$$(4.13)\qquad ab(\overline{x} + \underline{x})(\overline{x} - \underline{x}) = rb(\overline{x} - \underline{x}) + \frac{(rc-\alpha)m_1}{cd_2D}(\underline{x} - \overline{x}).$$

Assume that $\overline{x} \neq \underline{x}$. Then we derive from (4.13) that

$$(4.14)\qquad (\overline{x} + \underline{x}) = \frac{r}{a} - \frac{(rc-\alpha)m_1}{abcd_2D}.$$

(4.11) plus (4.12)

$$(4.15)\qquad ab(\overline{x} + \underline{x})^2 + \frac{2a[\gamma\beta - 2bd_2D]}{d_2D}\overline{x}\underline{x} = rb(\overline{x} + \underline{x}) + \frac{(rc-\alpha)m_1}{cd_2D}(\overline{x} + \underline{x}) + \frac{2\alpha k}{c}.$$

On substituting (4.14) into (4.15), it follows that

$$(4.16)\qquad a[\gamma\beta - 2bd_2D]\overline{x}\underline{x} = \frac{(rc-\alpha)m_1}{c}(\overline{x} + \underline{x}) + \frac{\alpha k r_2(r_1 + D)}{c}.$$

Note that $\overline{x} > 0$, $\underline{x} > 0$.

(i) Let (H2) and (H3) hold. If $rc > \alpha$, $\gamma\beta > bd_2D$, we derive from (4.16) that $\gamma\beta > 2bd_2D$. This is a contradiction. Hence, we have $\overline{x} = \underline{x}$. It therefore follows from (4.10) that $\overline{y_1} = \underline{y_1}$, $\overline{y_2} = \underline{y_2}$. Hence, the positive equilibrium E^* is globally stable.

(ii) Let (H2) and (H4) hold. It follows from (4.14) and (4.16) that

$$(\overline{x}+\underline{x})^2-4\overline{x}\underline{x} = -\frac{\gamma^2\beta^2}{abcd_2D[\gamma\beta-2bd_2D]}\times\left\{\left[rc-\frac{\alpha[\gamma\beta-bd_2D][\gamma\beta+2bd_2D]}{\gamma^2\beta^2}\right](\overline{x}+\underline{x})+\frac{4b\alpha kd_2^2D^2}{\gamma^2\beta^2}\right\}.$$

Hence, we have $(\overline{x}+\underline{x})^2 - 4\overline{x}\underline{x} < 0$. This is a contradiction. Accordingly, we have $\overline{x} = \underline{x}$. It therefore follows from (4.10) that $\overline{y_1} = \underline{y_1}$, $\overline{y_2} = \underline{y_2}$. Hence, the positive equilibrium E^* is globally stable. The proof is complete. □

Theorem 4.2. *The boundary equilibrium $E_1(r/a, 0, 0)$ is globally stable provided that*

(H5) *$rc > \alpha$, $\frac{r}{a}[\gamma\beta - bd_2D] < kd_2D$ holds true.*

Proof. Let $(x(t), y_1(t), y_2(t))$ be any positive solution of system (1.4) with initial condition (1.5). We derive from the first equation of system (1.4) that

$$\dot{x}(t) \le x(t)(r - ax(t)).$$

By comparison it follows that

$$\lim_{t\to+\infty}\sup x(t) \le \frac{r}{a}. \tag{4.17}$$

Then for $\varepsilon > 0$ sufficiently small there exists a $T_1 > 0$ such that if $t \ge T_1$, $x(t) \le \frac{r}{a}+\varepsilon$. Replacing this inequality into the second equation of system (1.4) that for $t \ge T_1 + \tau$

$$\dot{y}_1(t) \le \frac{\beta(\frac{r}{a}+\varepsilon)y_2(t-\tau)}{k+b(\frac{r}{a}+\varepsilon)+cy_2(t-\tau)} - d_1y_1(t) - \gamma y_1(t).$$

Consider the following auxiliary system

$$\begin{aligned}
\dot{u}_1(t) &= \frac{\beta(\frac{r}{a}+\varepsilon)u_2(t-\tau)}{k+b(\frac{r}{a}+\varepsilon)+cu_2(t-\tau)} - d_1u_1(t) - \gamma u_1(t),\\
\dot{u}_2(t) &= \gamma u_1(t) - d_2u_2(t),\\
u_1(t) &\equiv y_1(t),\ u_2(t) \equiv y_2(t),\ t \in [T_1, T_1+\tau].
\end{aligned} \tag{4.18}$$

If $\frac{r}{a}[\gamma\beta - bd_2D] < kd_2D$, then by Lemma 2.4 it follows from (4.18) that

$$\lim_{t\to+\infty} u_1(t) = 0, \quad \lim_{t\to+\infty} u_2(t) = 0.$$

By comparison theorem, it follows that

$$\lim_{t\to+\infty} y_1(t) = 0, \quad \lim_{t\to+\infty} y_2(t) = 0.$$

Therefore, for $\varepsilon > 0$ sufficiently small there exists a $T_2 > T_1 + \tau$ such that if $t \ge T_2$, $y_1(t) < \varepsilon$, $y_2(t) < \varepsilon$. It follows from the first equation of system (1.4) that for $t > T_2$

$$\dot{x}(t) \ge x(t)\left(r - ax(t) - \frac{\alpha\varepsilon}{k+bx(t)+c\varepsilon}\right).$$

By comparison theorem, it follows that

$$\lim_{t\to+\infty}\inf x(t) \geq \frac{br-ak-ac\varepsilon+\sqrt{(br-ak-ac\varepsilon)^2+4ab\left(rk+\varepsilon(rc-\alpha)\right)}}{2ab} > 0.$$

Setting $\varepsilon \to 0$, we have that $\lim_{t\to+\infty}\inf x(t) \geq \frac{r}{a}$. This, together with (4.17), yields

$$\lim_{t\to+\infty} x(t) = \frac{r}{a}.$$

Noting that if $\frac{r}{a}[\gamma\beta - bd_2D] < kd_2D$, by Theorem 3.2, the equilibrium $E_1(r/a, 0, 0)$ is locally stable. Hence, if (H5) holds, then the equilibrium E_1 is globally stable. This completes the proof. □

5. **Numerical simulation**

In this section, we present some numerical simulations to verify our theoretical results proved in previous sections by using MATLAB(7.0) programming.

Example 1. In system (1.4), we let $r = 5$, $a = 1$, $\alpha = 2$, $\beta = 2$, $k = 1$, $b = 1$, $c = 2$, $\gamma = 2$, $d_1 = d_2 = 1$. System (1.4) with above coefficients has a unique positive equilibrium $E^*(4.9030,\ 0.1586,\ 0.3172)$. It is easy to show that $rc - \alpha = 8$, $\frac{rc-\alpha}{ac}[\gamma\beta - bd_2D] - kd_2D = 1$, $bd_2D - \gamma\beta = -1$, $\gamma\beta - 2bd_2D = -2$, hence, (H2) and (H3) hold. By Theorem 4.1 we see that the positive equilibrium E^* is globally stable. Numerical simulation illustrates our result (see Fig. 1).

Example 2. In system (1.4), we let $r = 2.5$, $a = 1$, $\alpha = 1$, $\beta = 2$, $k = 1$, $b = 1$, $c = 1$, $\gamma = 2$, $d_1 = 1$, $d_2 = 0.5$. System (1.4) with above coefficients has a unique positive equilibrium $E^*(2.0573,\ 0.6072,\ 2.4288)$. It is easy to show that $rc - \alpha = 1.5$, $\frac{rc-\alpha}{ac}[\gamma\beta - bd_2D] - kd_2D = 2.25$, $\left[rc - \frac{\alpha[\gamma\beta-bd_2D][\gamma\beta+2bd_2D]}{\gamma^2\beta^2}\right](\overline{x}+\underline{x}) + \frac{4b\alpha kd_2^2D^2}{\gamma^2\beta^2} = 0.5625$, hence, (H2) and (H4) hold. By Theorem 4.1 we see that the positive equilibrium E^* is globally stable. Numerical simulation illustrates our result (see Fig. 2).

Example 3. In system (1.4), we let $r = 0.5$, $a = 1$, $\alpha = 2$, $\beta = 2$, $k = 0.1$, $b = 0.5$, $c = 1.5$, $\gamma = 2$, $d_1 = 1$, $d_2 = 0.2$. System (1.4) with above coefficients has a unique positive equilibrium $E^*(0.0263,\ 0.0042,\ 0.0416)$. It is easy to show that $p_0 - q_0 = -0.1786 < 0$, $\omega_0 = 0.2166$, $\tau_0 = 0.843$. By Theorem 3.1, there is a $\tau_0 = 0.843 > 0$ such that for $\tau < \tau_0$, the positive equilibrium E^* is locally stable; for $\tau > \tau_0$, the positive equilibrium E^* undergoes Hopf bifurcation. Numerical simulation illustrates our result (see Fig. 3 and Fig. 4).

Example 4. In system (1.4), we let $r = 2$, $a = 1$, $\alpha = 2$, $\beta = 3$, $k = 2$, $b = 1$, $c = 2$, $\gamma = 2$, $d_1 = 1$, $d_2 = 1.5$. It is easy to show that $rc - \alpha = 2 > 0$, $\frac{r}{a}[\gamma\beta - bd_2D] < kd_2D = -6 < 0$. By Theorem 4.2 we see that the boundary equilibrium $E_1(2, 0, 0)$ of system (1.4) is globally stable. Numerical simulation illustrates our result (see Fig. 5).

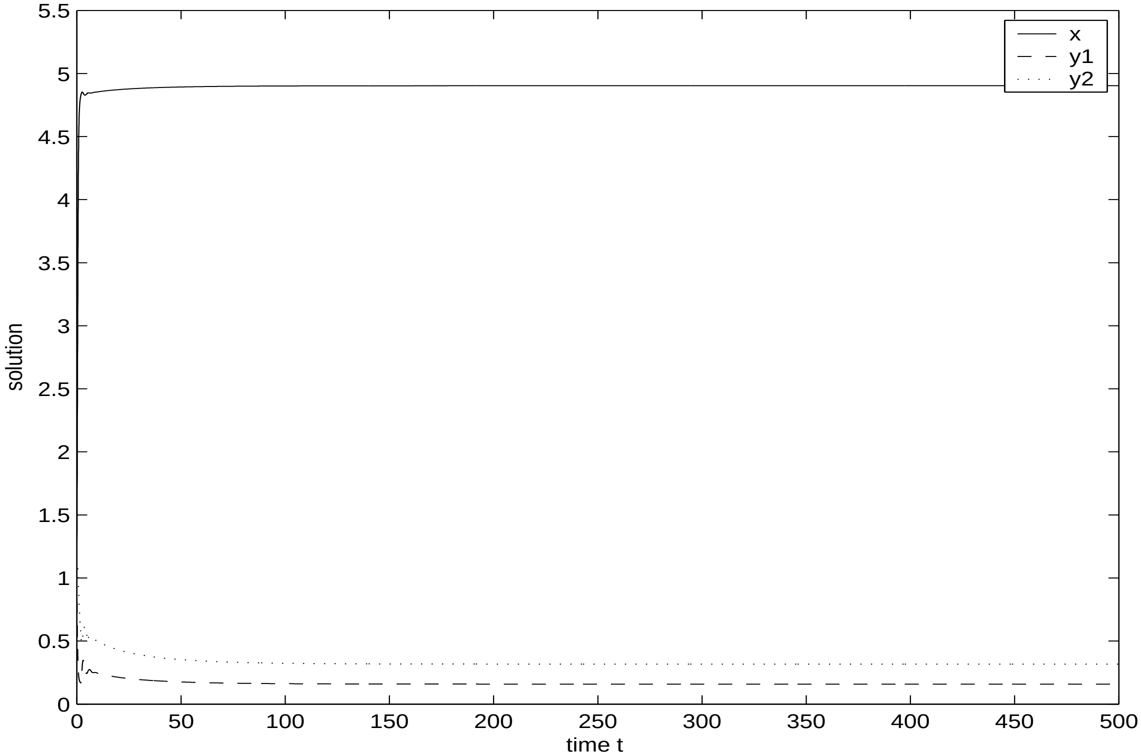

FIGURE 1. When $\tau = 2$ and the initial value $(\Phi(\theta), \Psi_1(\theta), \Psi_2(\theta)) = (1, 1, 1)$, the positive equilibrium $E^*(4.9030,\ 0.1586,\ 0.3172)$ is globally stable.

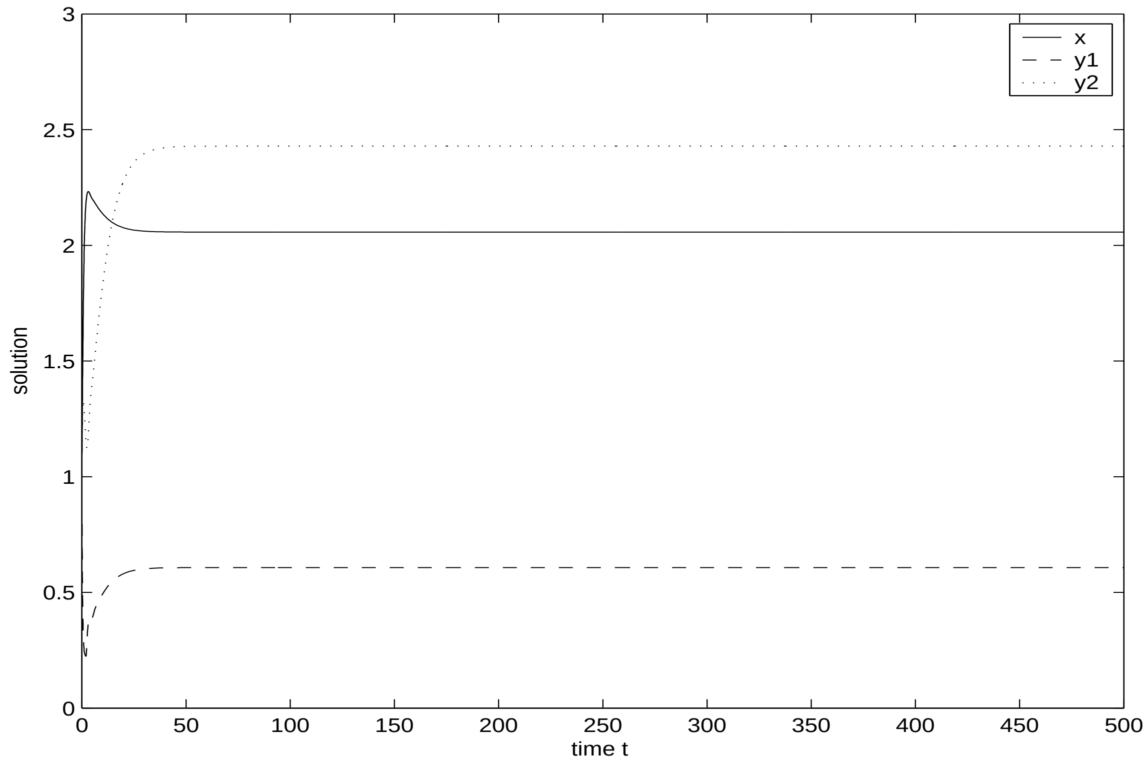

FIGURE 2. When $\tau = 2$ and the initial value $(\Phi(\theta),\ \Psi_1(\theta),\ \Psi_2(\theta)) = (1, 1, 1)$, the positive equilibrium $E^*(2.0573,\ 0.6072,\ 2.4288)$ is globally stable.

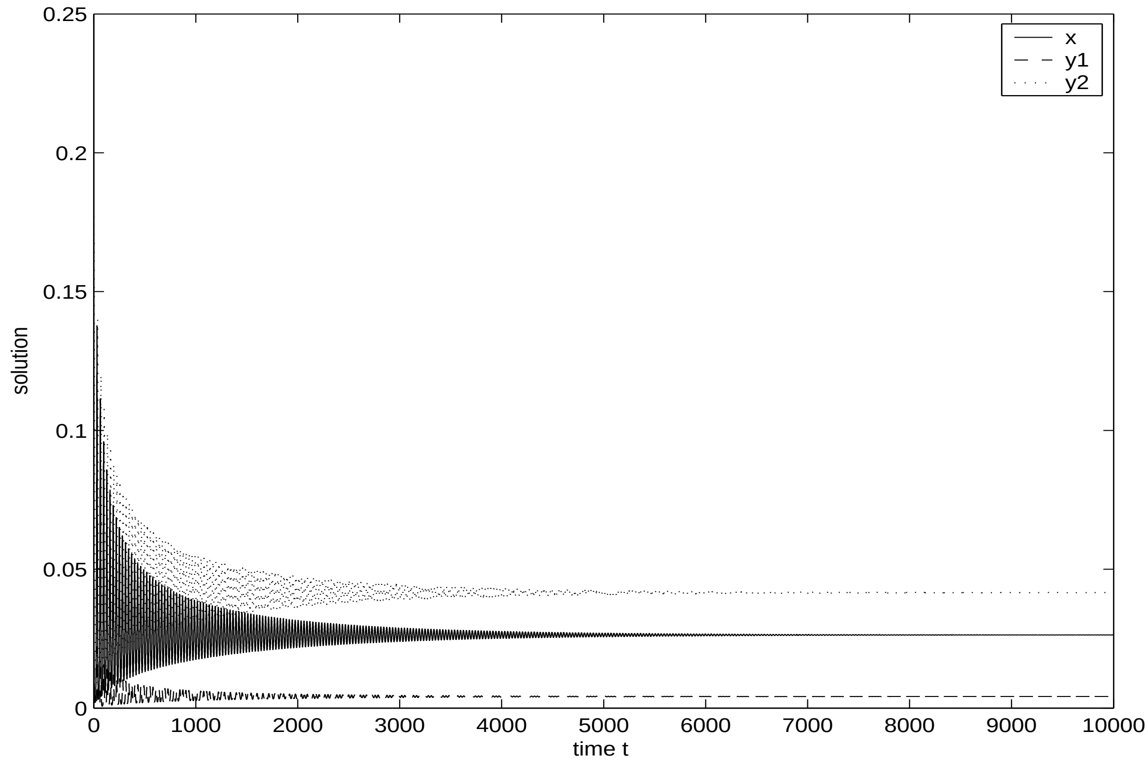

FIGURE 3. When $\tau = 0.8 < \tau_0$ and the initial value $(\Phi(\theta),\ \Psi_1(\theta),\ \Psi_2(\theta)) = (0.1, 0.1, 0.1)$, the positive equilibrium $E^*(0.0263,\ 0.0042,\ 0.0416)$ is locally stable.

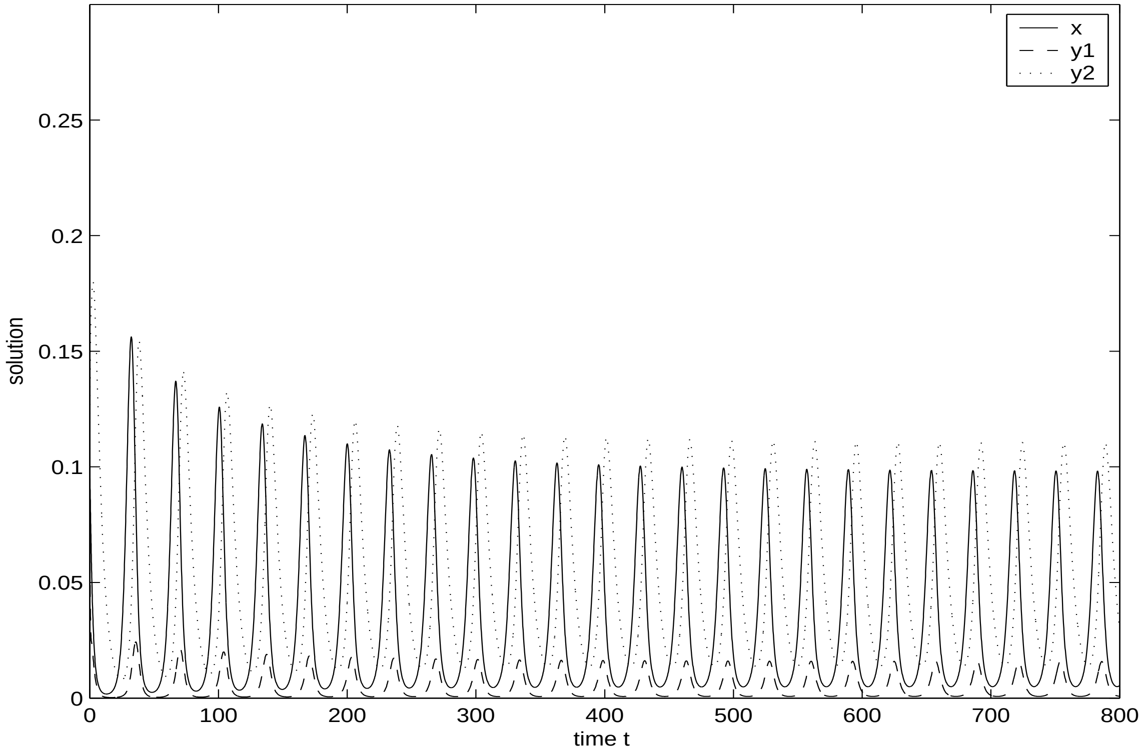

FIGURE 4. When $\tau = 1 > \tau_0$ and the initial value $(\Phi(\theta),\ \Psi_1(\theta),\ \Psi_2(\theta)) = (0.1, 0.1, 0.1)$, the positive equilibrium $E^*(0.0263,\ 0.0042,\ 0.0416)$ undergoes Hopf bifurcation.

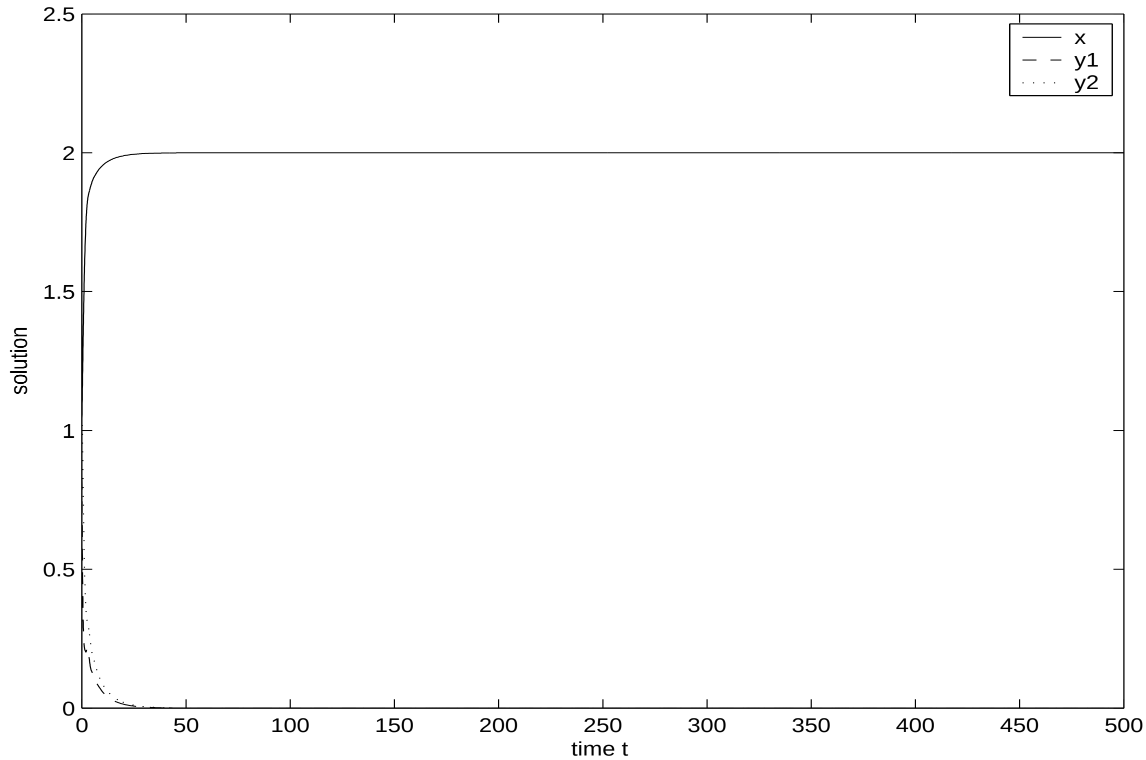

FIGURE 5. When $\tau = 2$ and initial value $(\Phi(\theta), \Psi_1(\theta), \Psi_2(\theta)) = (1, 1, 1)$. The boundary equilibrium $E_1(2, 0, 0)$ is globally stable.

REFERENCES

[1] L. Chen, X. Song, Z. Lu, Mathematical Models and Methods in Ecology, Sichuan Science and Technology Press, 2003.

[2] W. G. Aiello and H. I. Freedman, A time-delay model of single species growth with stage structure, Math. Biosci. 101:139–153 (1990).

[3] R. Xu, Z. Ma, Stability and Hopf bifurcation in a ratio-dependent predator-prey system with stage structure, Chaos, Solitons & Fractals, 38(3):669–684 (2008).

[4] R. Xu, Z. Ma, Stability and Hopf bifurcation in a predator-prey model with stage structure for the predator, Nonlinear Anal.: Real World Appl., 9(4):1444–1460 (2008).

[5] J. R. Beddington, Mutual interference between parasites or predators and its effect on searching efficiency, J. Animal Ecol. 44:331–340 (1975)

[6] D. L. DeAngelis, R. A. Goldstein, R. V. O'Neill, A model for trophic interaction, Ecology 56:881–892 (1975).

[7] P. H. Crowley, E. K. Martin, Functional responses and interference within and between year classes of a dragonfly population, J. North American Benthological Soc. 8:211–221 (1989).

[8] R. Arditi, L. R. Ginzburg, Coupling in predator-prey dynamics: Ratio-dependence, J. Theoret. Biol. 139:311–326 (1989).

[9] G. T. Skalski, J. F. Gilliam, Functional responses with predator interference: Viable alternatives to the Holling type II model, Ecology 82:3083–3092 (2001).

[10] R. S. Cantrell, C. Cosner, On the dynamics of predator-prey models with the Beddington-DeAngelis functional response, J. Math. Anal. Appl. 257:206–222 (2001).

[11] G. Ruxton, W. S. C. Gurney, A. DeRoos, Interference and generation cycles, Theoret Populat Biol. 42:235–253 (1992).

[12] C. Cosner, D. L. DeAngelis, J. S. Ault, D. B. Olson, Effects of spatial grouping on the functional response of predators, Theoret. Populat. Biol. 56:65–75 (1999).

[13] Y. Kuang, E. Baretta, Global qualitative analysis of a ratio-dependent predator-prey system, J. Math. Biol. 36:389–406 (1998).

[14] G. W. Harrision, Comparing predator-prey models to Luckinbill's experiment with didinium and paramecium, Ecology 76:357–369 (1995).

[15] J. K. Hale, Theory of functional differential equations. Springer-Verlag, Heidelberg, 1977.

[16] H. Smith, Monotone dynamical system: an introduction to the theory of competitive and cooperative system. Providence, RI: American Mathematical Society, 1995.

[17] W. Wang, P. Fergola, C. Tenneriello, Global attractivity of periodic solutions of population models, J. Math. Anal. Appl. 211:498–511 (1997).

[18] P. Lancaster, M. Tismenetsky, The theory of matrices. 2nd ed. New York, Academic Press, 1985.

[19] Y. Kunag, J. W. H. So, Analysis of a delayed two-stage population with space-limited recruitment, SIAM J. Appl. Math. 55:1675–1695 (1995).

[20] Y. Chen, C. Song, Stability and Hopf bifurcation analysis in a prey-predator system with stage-structure for prey and time delay, Chaos, Solitons & Fractals, 38: 1104–1114(2008).

[21] Y. Kuang, Delay differential equations with applications in population dynamics. New York, Academic Press, 1993.