



Stability and Hopf bifurcation of a ratio-dependent predator–prey model with time delay and stage structure

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Abstract. In this paper, a ratio-dependent predator–prey model described by Holling type II functional response with time delay and stage structure for the prey is investigated. By analyzing the corresponding characteristic equations, the local stability of the coexistence equilibrium of the model is discussed and the existence of Hopf bifurcations at the coexistence equilibrium is established. By using the persistence theory on infinite dimensional systems, it is proven that the system is permanent if the coexistence equilibrium exists. By introducing some new lemmas and the comparison theorem, sufficient conditions are obtained for the global stability of the coexistence equilibrium. Numerical simulations are carried out to illustrate the main results.

Keywords: ratio-dependence, time delay, stage structure, Hopf bifurcation, stability.

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1 Introduction

Predator–prey models are important in the models of multi-species population interactions. One of the important objectives in population dynamics is to comprehend the dynamical relationship between predator and prey, which had long been and will continue to be one of the dominant themes in both ecology and mathematical ecology. It is well known that the functional response is a key factor in all predator–prey interactions, which describes the number of prey consumed by per predator per unit time. Based on experiments, Holling [18] suggested three different kinds of functional responses, i.e. Holling type I, Holling type II and Holling type III, for different kinds of species to model the phenomena of predation, which made the standard Lotka–Volterra system more realistic. These functional responses are generally modeled as being a function of prey density only, i.e. the number of prey that an individual predator kills is a function of prey density only, and ignore the potential effects of predator density. So they are usually called prey-dependent functional responses. Obviously, this assumption can not explain the dynamics of the system completely when the variations

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in predator size have an influence on the system. Therefore a new theory, so-called predator-dependent functional response, has been developed to consider the influence of both prey and predator populations. There have been several famous predator-dependent functional response types: Hassel–Varley type [23]; Beddington–DeAngelis type [6, 12]; Crowley–Martin type [11]; and the well-known ratio-dependence type [2]. In the “ratio-dependence” theory, it roughly states that the per capita predator growth rate should be a function of the ratio of prey to predator abundance. Moreover, as the number of predators often changes slowly (relative to prey number), there is often competition among the predators, and the per capita rate of predation should therefore depend on the numbers of both prey and predator, most probably and simply on their ratio. These hypotheses are strongly supported by numerous field and laboratory experiment and observations (see, for example, [3–5, 17]).

Let $x(t)$ and $y(t)$ be the densities of the prey and the predator at time t , respectively, a standard predator-prey model with Holling type functional response is of the form (see [18])

$$\begin{aligned}\dot{x}(t) &= xg(x) - \Phi(x)y, \\ \dot{y}(t) &= e\Phi(x)y - dy.\end{aligned}\tag{1.1}$$

In (1.1), the function $g(x)$ represents the growth rate of the prey in the absence of predation and d is the mortality rate of the predator in the absence of prey; the function $\Phi(x)$ is called “functional response” representing the prey consumption per unit time; e is the rate of conversion of nutrients from the prey into the reproduction of the predator. But in ratio-dependent predator-prey model, model (1.1) is described as

$$\begin{aligned}\dot{x}(t) &= xg(x) - \Phi\left(\frac{x}{y}\right)y, \\ \dot{y}(t) &= e\Phi\left(\frac{x}{y}\right)y - dy.\end{aligned}\tag{1.2}$$

In (1.2), $\Phi\left(\frac{x}{y}\right)$ is the ratio-dependent predator functional response. Many authors have studied predator-prey models with functional response, especially with ratio-dependent functional response. Hsu et al. [20] investigated a predator-prey model with Hassell–Varley type functional response. It was shown that the predator free equilibrium is a global attractor only when the predator death rate is greater than its growth ability and the positive equilibrium exists if the above relation reverses. In cases of practical interest, it was shown that the local stability of the positive steady state implies its global stability with respect to positive solutions. For terrestrial predators that form a fixed number of tight groups, it was shown that the existence of an unstable positive equilibrium in the predator-prey model implies the existence of a unique nontrivial positive limit cycle. Cantrell and Cosner [9] investigated predator-prey models with Beddington–DeAngelis functional response (with or without diffusion). Criteria for permanence and for predator extinction were derived. For systems without diffusion or with no-flux boundary conditions, criteria were derived for the existence of a globally stable coexistence equilibrium or, alternatively, for the existence of periodic orbits. Kuang and Beretta [22], Berezovskaya et al. [8] investigated a ratio-dependent predator-prey model with Michaelis–Menten or Holling II type functional response, respectively. In [22], the authors proved that if the positive steady state of the system is locally asymptotically stable then the system has no nontrivial positive periodic solutions. They also gave sufficient conditions for each of the possible three steady states to be globally asymptotically stable. In [8], the authors gave a complete parametric analysis of stability properties and dynamic regimes of the model.

Beretta and Kuang [7], Xiao and Li [28] investigated a ratio-dependent predator-prey model with Michaelis–Menten functional response and time delay, respectively. In [7], the authors made use of a rather novel and non-trivial way of constructing proper Lyapunov functions to obtain some new and significant global stability or convergence results. In [28], the authors studied the effect of time delay on local stability of the interior equilibrium and investigated conditions on the delay and parameters so that the interior equilibrium of the model is conditionally stable or unstable. It was also shown that the interior equilibrium cannot be absolutely stable for all parameters. Hsu et al. [19] investigated a ratio-dependent one-prey two-predators model. It was shown that the dynamites outcome of the interactions are very sensitive to parameter values and initial dates, which reveal far richer dynamics compared to similar prey dependent models.

However, it is assumed in these works that each individual prey admits the same risk to be attacked by predator. This assumption is obviously unrealistic for many animals. In natural world, the growth of species often has its development process, immature and mature, while in each stage of its development, it always shown different characteristic. For instance, the mature species have preying capacity, while the immature species are raised by their parents and not able to prey. Hence, stage-structured models may be more realistic.

Aiello and Freedman [1] proposed and studied stage structured single-species population model with time delay. Chen et al. [10] proposed and discussed a stage structured single-species population model without time delay. Based on the ideas above, many authors have studied different kinds of biological models with stage structure. Among these models, there are many factors that affect dynamical properties of predator-prey system such as the ratio-dependent functional response, stage structure, and time delay, etc., especially the joint effect of these factors (see, for example, [13, 14, 24, 25, 27, 29, 30]).

In order to analyze the effect of stage structure for prey on the dynamics of ratio-dependent predator-prey system, in [29], the authors proposed and studied the following differential system

$$\begin{aligned}\dot{x}_1(t) &= ax_2(t) - r_1x_1(t) - bx_1(t), \\ \dot{x}_2(t) &= bx_1(t) - b_1x_2^2(t) - \frac{a_1x_2(t)y(t)}{my(t) + x_2(t)}, \\ \dot{y}(t) &= y(t) \left(-r + \frac{a_2x_2(t)}{my(t) + x_2(t)} \right).\end{aligned}$$

Sufficient conditions were derived for the uniform persistence and the global asymptotic stability of nonnegative equilibria of the model. However, time delay is an important factor in biological models, since time delay could cause a stable equilibrium to become unstable and cause the species to fluctuate.

The main purpose of this paper is to study the effect of stage structure for the prey and time delay on the dynamics of a ratio-dependent predator-prey system described by Holling type II functional response. To do so, we study the following differential system

$$\begin{aligned}\dot{x}_1(t) &= rx_2(t) - re^{-d_1\tau}x_2(t - \tau) - d_1x_1(t), \\ \dot{x}_2(t) &= re^{-d_1\tau}x_2(t - \tau) - d_2x_2^2(t) - \frac{ax_2(t)y(t)}{x_2(t) + my(t)}, \\ \dot{y}(t) &= \frac{bx_2(t)y(t)}{x_2(t) + my(t)} - d_3y(t).\end{aligned}\tag{1.3}$$

In (1.3), $x_1(t)$ and $x_2(t)$ represent the densities of the immature and the mature prey at time t , respectively; $y(t)$ represents the density of the predator at time t ; τ is the maturity of prey; r is the birth rate of the immature prey; d_1 and d_2 are the death rates of the immature and mature prey, respectively; $re^{-d_1\tau}x_2(t-\tau)$ represents the quantity which the immature born at time $t-\tau$ can survive at time t ; d_3 is the death rate of the predator; a is the capturing rate of the predator; $\frac{b}{a}$ is the conversion rate of nutrients into the reproduction of the predator; all the parameters are positive.

The initial conditions for system (1.3) take the form

$$\begin{aligned} x_1(\theta) = \varphi_1(\theta) \geq 0, \quad x_2(\theta) = \varphi_2(\theta) \geq 0, \quad y(\theta) = \varphi_3(\theta) \geq 0, \quad \theta \in [-\tau, 0], \\ \varphi_1(0) > 0, \quad \varphi_2(0) > 0, \quad \varphi_3(0) > 0, \end{aligned} \quad (1.4)$$

where $(\varphi_1(\theta), \varphi_2(\theta), \varphi_3(\theta)) \in C([-\tau, 0], R_{+0}^3), R_{+0}^3 = \{(x_1, x_2, x_3) \mid x_i \geq 0, i = 1, 2, 3\}$. In order to ensure the initial continuous, we suppose further that

$$x_1(0) = \int_{-\tau}^0 re^{d_1s} \varphi_2(s) ds.$$

The organization of this paper is as follows. In the next section, we introduce some lemmas which will be essential to our proofs and discussions. In Section 3, by analyzing the corresponding characteristic equations, the local stability of the coexistence equilibrium of system (1.3) is discussed. Furthermore, the conditions for the existence of Hopf bifurcations at the coexistence equilibrium are obtained. In Section 4, by using persistence theory on infinite dimensional systems, we prove that system (1.3) is permanent when the coexistence equilibrium exists. In Section 5, by using comparison argument, the global stability of the coexistence equilibrium of system (1.3) is discussed. In Section 6, numerical simulations are carried out to illustrate the main results. A brief conclusion is given in Section 7 to conclude this work.

2 Preliminaries

In this section, we introduce some lemmas which will be useful in next section. By the fundamental theory of functional differential equations [15], it is well known that system (1.3) has a unique solution $(x_1(t), x_2(t), y(t))$ satisfying initial conditions (1.4). Further, it is easy to show that all solutions of system (1.3) with initial conditions (1.4) are defined on $[0, +\infty)$ and remain positive for all $t \geq 0$.

Lemma 2.1. *All positive solutions of system (1.3) satisfying initial conditions (1.4) are ultimately bounded.*

Proof. We know that all solutions of system (1.3) are positive. Hence we study only in the domain

$$R_+^3 = \{(x_1, x_2, x_3) \mid x_i > 0, i = 1, 2, 3\}.$$

Let $V(t) = bx_1(t) + bx_2(t) + ay(t)$, then the derivative of $V(t)$ along solution of system (1.3) is

$$\begin{aligned} \dot{V}(t) &\leq brx_2(t) - bd_1x_1(t) - bd_2x_2^2(t) - ad_3y(t) \\ &\leq -\mu V(t) + b(r + d_2)x_2(t) - bd_2x_2^2(t) \\ &\leq -\mu V(t) + \frac{b(r + d_2)^2}{4d_2}, \end{aligned}$$

where $\mu = \min\{d_1, d_2, d_3\}$. Therefore we derive that

$$\begin{aligned} V(t) &\leq e^{-\mu t} \left(V(0) + \int_0^t \frac{b(r+d_2)^2}{4d_2} e^{\mu s} ds \right) \\ &= e^{-\mu t} V(0) + \frac{b(r+d_2)^2}{4d_2\mu} (1 - e^{-\mu t}) \\ &\rightarrow \frac{b(r+d_2)^2}{4d_2\mu} \quad (t \rightarrow +\infty). \end{aligned}$$

The proof of Lemma 2.1 is completed. \square

Lemma 2.2 ([26]). *Consider the following system*

$$\dot{u}(t) = au(t - \tau) - bu(t) - cu^2(t)$$

here $a, c, \tau > 0, b \geq 0$, and $u(t) > 0$ for $t \in [-\tau, 0]$, we have

(i) if $a < b$, then $\lim_{t \rightarrow +\infty} u(t) = 0$;

(ii) if $a > b$, then $\lim_{t \rightarrow +\infty} u(t) = \frac{a-b}{c}$.

Lemma 2.3. *Consider the following system*

$$\begin{aligned} \dot{u}_1(t) &= ru_2(t) - re^{-d_1\tau}u_2(t - \tau) - d_1u_1(t), \\ \dot{u}_2(t) &= re^{-d_1\tau}u_2(t - \tau) - d_2u_2^2(t), \end{aligned} \tag{2.1}$$

here $r, d_1, d_2, \tau > 0$ and $u_i(t) > 0$ ($i = 1, 2$) for $t \in [-\tau, 0]$, we have

$$\lim_{t \rightarrow +\infty} u_1(t) = \frac{r^2e^{-d_1\tau}(1 - e^{-d_1\tau})}{d_1d_2}, \quad \lim_{t \rightarrow +\infty} u_2(t) = \frac{re^{-d_1\tau}}{d_2}.$$

Proof. It is easy to see that system (2.1) has two equilibria $F_0(0, 0)$ and $F_1(\hat{u}_1, \hat{u}_2)$, where $\hat{u}_1 = \frac{r^2e^{-d_1\tau}(1 - e^{-d_1\tau})}{d_1d_2}$, $\hat{u}_2 = \frac{re^{-d_1\tau}}{d_2}$, and easily show that F_0 is unstable and F_1 is locally asymptotically stable. By the second equation of system (2.1) and Lemma 2.2, we derive that

$$\lim_{t \rightarrow +\infty} u_2(t) = \frac{re^{-d_1\tau}}{d_2} = \hat{u}_2.$$

Therefore the limit equation of the first equation of system (2.1) takes the form

$$\dot{u}_1(t) = \frac{r^2e^{-d_1\tau}(1 - e^{-d_1\tau})}{d_2} - d_1u_1(t),$$

which implies that

$$\lim_{t \rightarrow +\infty} u_1(t) = \frac{r^2e^{-d_1\tau}(1 - e^{-d_1\tau})}{d_1d_2} = \hat{u}_1,$$

that is, the equilibrium F_1 is globally asymptotically stable. This proves Lemma 2.3. \square

Lemma 2.4 ([8]). *Consider the following system*

$$\dot{u}(t) = \left(\frac{a}{b + mu(t)} - d \right) u(t), \quad a, b, m, d > 0.$$

We have that $\lim_{t \rightarrow +\infty} u(t) = \frac{a-bd}{md}$ if $a > bd$ and $\lim_{t \rightarrow +\infty} u(t) = 0$ if $a < bd$.

Lemma 2.5. Consider the following system

$$\dot{u}(t) = re^{-d_1\tau}u(t-\tau) - d_2u^2(t) - \frac{aPu(t)}{u(t) + mP}$$

with $r, d_1, d_2, \tau, m, a, P > 0$, $u(t) > 0$ for $t \in [-\tau, 0]$, we have $\lim_{t \rightarrow +\infty} u(t) = u^*$ if $mre^{-d_1\tau} > a$, where

$$u^* = \frac{U_0 + \sqrt{U_0^2 + 4V_0}}{2d_2}, \quad U_0 = re^{-d_1\tau} - d_2mP, \quad V_0 = d_2P(mre^{-d_1\tau} - a).$$

Proof. It is easy to know that $u(t) > 0$ for all $t > 0$. For any $t > 0$, we have

$$re^{-d_1\tau}u(t-\tau) - d_2u^2(t) - \frac{a}{m}u(t) < \dot{u}(t) < re^{-d_1\tau}u(t-\tau) - d_2u^2(t).$$

By Lemma 2.2, we know that there exists a $t_1 > 0$ such that

$$\underline{u}_1 := \frac{mre^{-d_1\tau} - a}{md_2} - \varepsilon < u(t) < \frac{re^{-d_1\tau}}{d_2} + \varepsilon =: \bar{u}_1 \quad \text{for all } t \geq t_1.$$

Then we get that

$$re^{-d_1\tau}u(t-\tau) - d_2u^2(t) - \frac{aPu(t)}{\underline{u}_1 + mP} < \dot{u}(t) < re^{-d_1\tau}u(t-\tau) - d_2u^2(t) - \frac{aPu(t)}{\bar{u}_1 + mP}.$$

By the comparison theorem and Lemma 2.2, there exists a $t_2 > t_1$ such that

$$\underline{u}_2 := \frac{re^{-d_1\tau} - \frac{aP}{\underline{u}_1 + mP}}{d_2} - \varepsilon < u(t) < \frac{re^{-d_1\tau} - \frac{aP}{\bar{u}_1 + mP}}{d_2} + \varepsilon =: \bar{u}_2 \quad \text{for all } t \geq t_2.$$

and $0 < \underline{u}_1 < \underline{u}_2 < u(t) < \bar{u}_2 < \bar{u}_1$ for all $t \geq t_2$. Continuing this process, we derive the sequence $\{\underline{u}_n\}_{n=1}^{\infty}$ and $\{\bar{u}_n\}_{n=1}^{\infty}$ with

$$0 < \underline{u}_1 < \underline{u}_2 < \cdots < \underline{u}_n < \bar{u}_n < \cdots < \bar{u}_2 < \bar{u}_1, \quad t > t_n,$$

where

$$\underline{u}_n := \frac{re^{-d_1\tau} - \frac{aP}{\underline{u}_{n-1} + mP}}{d_2} - \varepsilon, \quad \bar{u}_n = \frac{re^{-d_1\tau} - \frac{aP}{\bar{u}_{n-1} + mP}}{d_2} + \varepsilon.$$

By the bounded monotonic principle, we know that the limit of the sequence $\{\underline{u}_n\}_{n=1}^{\infty}$ and $\{\bar{u}_n\}_{n=1}^{\infty}$ exists. Denote $\underline{u} = \lim_{n \rightarrow \infty} \underline{u}_n$ and $\bar{u} = \lim_{n \rightarrow \infty} \bar{u}_n$, then we easily know that $\underline{u} = \bar{u}$ and $\lim_{t \rightarrow +\infty} u(t) = \underline{u} = \bar{u} =: u^*$, where

$$u^* = \frac{U_0 + \sqrt{U_0^2 + 4V_0}}{2d_2}, \quad U_0 = re^{-d_1\tau} - d_2mP, \quad V_0 = d_2P(mre^{-d_1\tau} - a).$$

□

3 Local stability and Hopf bifurcation

It is easy to show that system (1.3) always has a trivial equilibrium $E_0(0,0,0)$ and a predator-extinction equilibrium $E_1(\hat{x}_1, \hat{x}_2, 0)$, where

$$\hat{x}_1 = \frac{r^2 e^{-d_1 \tau} (1 - e^{-d_1 \tau})}{d_1 d_2}, \quad \hat{x}_2 = \frac{r e^{-d_1 \tau}}{d_2}.$$

Further, if $0 < b - d_3 < \frac{mbre^{-d_1 \tau}}{a}$ holds, then system (1.3) has a unique coexistence equilibrium $E_2(x_1^*, x_2^*, y^*)$, where

$$x_1^* = \frac{r(1 - e^{-d_1 \tau})}{d_1} x_2^*, \quad x_2^* = \frac{mbre^{-d_1 \tau} + ad_3 - ab}{mbd_2}, \quad y^* = \frac{b - d_3}{md_3} x_2^*.$$

In this section, we are only concerned with the local stability of the coexistence equilibrium and the existence of Hopf bifurcation for system (1.3), since the biological meaning of the coexistence equilibrium implies that immature prey and mature prey and predator all exist.

For the coexistence equilibrium $E_2(x_1^*, x_2^*, y^*)$, the characteristic equation of (1.3) has the form

$$(\lambda + d_1)[\lambda^2 + A_1 \lambda + A_2 + (B_1 \lambda + B_2)e^{-\lambda \tau}] = 0, \quad (3.1)$$

where

$$\begin{aligned} A_1 &= \frac{2b(mbre^{-d_1 \tau} + ad_3 - ab) + (b - d_3)(ab - ad_3 + mbd_3)}{mb^2}, \\ A_2 &= \frac{2d_3(b - d_3)(mbre^{-d_1 \tau} + ad_3 - ab) + ad_3(b - d_3)^2}{mb^2}, \\ B_1 &= -re^{-d_1 \tau}, \quad B_2 = -\frac{rd_3(b - d_3)e^{-d_1 \tau}}{b}. \end{aligned}$$

Clearly, $\lambda_1 = -d_1$ is a negative real root of Eq.(3.1). Other two roots of (3.1) are given by the roots of equation

$$\lambda^2 + A_1 \lambda + A_2 + (B_1 \lambda + B_2)e^{-\lambda \tau} = 0. \quad (3.2)$$

When $\tau = 0$, Eq.(3.2) becomes

$$\lambda^2 + (A_1 + B_1)\lambda + A_2 + B_2 = 0.$$

By calculation, we know that

$$\begin{aligned} A_1 + B_1 &= \frac{mbd_3(b - d_3) + ad_3^2 + b^2(mr - a)}{mb^2}, \\ A_2 + B_2 &= \frac{d_3(b - d_3)(mbr - ab + ad_3)}{mb^2} > 0. \end{aligned}$$

Hence, E_2 is locally asymptotically stable if $mbd_3(b - d_3) + ad_3^2 + b^2(mr - a) > 0$ and unstable if $mbd_3(b - d_3) + ad_3^2 + b^2(mr - a) < 0$.

If $\lambda = i\omega$ ($\omega > 0$) is a purely imaginary root of Eq.(3.2), separating real and imaginary parts, we have

$$\begin{aligned}\omega^2 - A_2 &= B_1\omega \sin(\omega\tau) + B_2 \cos(\omega\tau), \\ A_1\omega &= -B_1\omega \cos(\omega\tau) + B_2 \sin(\omega\tau).\end{aligned}$$

Eliminating $\sin(\omega\tau)$ and $\cos(\omega\tau)$, we obtain the equation with respect to ω

$$\omega^4 + (A_1^2 - B_1^2 - 2A_2)\omega^2 + A_2^2 - B_2^2 = 0. \quad (3.3)$$

Since $A_2 > 0$, $B_2 < 0$, $A_2 + B_2 > 0$, then $A_2^2 - B_2^2 > 0$. Therefore, if $B_1^2 + 2A_2 - A_1^2 < 2\sqrt{A_2^2 - B_2^2}$, Eq. (3.3) has no positive real roots. Accordingly, by [21, Theorem 3.4.1], we see that if $mbd_3(b - d_3) + ad_3^2 + b^2(mr - a) > 0$ and $B_1^2 + 2A_2 - A_1^2 < 2\sqrt{A_2^2 - B_2^2}$ hold, then E_2 is locally asymptotically stable for all $0 \leq \tau < \frac{1}{d_1} \ln \frac{mbr}{a(b-d_3)}$. If $B_1^2 + 2A_2 - A_1^2 > 2\sqrt{A_2^2 - B_2^2}$, Eq.(3.3) has two positive real roots denoted by

$$\omega_+ = \sqrt{\frac{1}{2}(B_1^2 + 2A_2 - A_1^2) + \frac{1}{2}\sqrt{\Delta}}, \quad \omega_- = \sqrt{\frac{1}{2}(B_1^2 + 2A_2 - A_1^2) - \frac{1}{2}\sqrt{\Delta}},$$

respectively, where $\Delta = (B_1^2 + 2A_2 - A_1^2)^2 - 4(A_2^2 - B_2^2)$.

Denote

$$\begin{aligned}\tau_+^{(k)} &= \frac{2k\pi + \arccos \frac{(B_2 - A_1 B_1)\omega_+^2 - A_2 B_2}{B_1^2 \omega_+^2 + B_2^2}}{\omega_+}, \\ \tau_-^{(k)} &= \frac{2k\pi + \arccos \frac{(B_2 - A_1 B_1)\omega_-^2 - A_2 B_2}{B_1^2 \omega_-^2 + B_2^2}}{\omega_-}, \\ k &= 0, 1, 2, \dots\end{aligned}$$

In the following we verify transversality condition of Eq. (3.2). Differentiating (3.2) with respect to τ , it follows that

$$[2\lambda + A_1 + B_1 e^{-\lambda\tau} - \tau(B_1\lambda + B_2)e^{-\lambda\tau}] \frac{d\lambda}{d\tau} - \lambda(B_1\lambda + B_2)e^{-\lambda\tau} = 0.$$

By direct calculation, we derive that

$$\begin{aligned}\left(\frac{d\lambda}{d\tau}\right)^{-1} &= \frac{2\lambda + A_1 + B_1 e^{-\lambda\tau} - \tau(B_1\lambda + B_2)e^{-\lambda\tau}}{\lambda(B_1\lambda + B_2)e^{-\lambda\tau}} \\ &= -\frac{2\lambda + A_1}{\lambda(\lambda^2 + A_1\lambda + A_2)} + \frac{B_1}{\lambda(B_1\lambda + B_2)} - \frac{\tau}{\lambda}, \\ \operatorname{Re} \left(\frac{d\lambda}{d\tau}\right)^{-1} \Big|_{\lambda=wi} &= \operatorname{Re} \left\{ -\frac{2\omega i + A_1}{\omega i(-\omega^2 + A_2 + A_1\omega i)} + \frac{B_1}{\omega i(B_1\omega i + B_2)} \right\} \\ &= \frac{2\omega^2 + A_1^2 - B_1^2 - 2A_2}{B_1^2 \omega^2 + B_2^2}, \\ \operatorname{sign} \left\{ \frac{d \operatorname{Re} \lambda}{d\tau} \right\} \Big|_{\lambda=wi} &= \operatorname{sign} \left\{ \operatorname{Re} \left(\frac{d\lambda}{d\tau}\right)^{-1} \right\} \Big|_{\lambda=wi} = \operatorname{sign}\{2\omega^2 + A_1^2 - B_1^2 - 2A_2\}.\end{aligned}$$

Therefore

$$\begin{aligned} \operatorname{sign} \left\{ \frac{d \operatorname{Re} \lambda}{d\tau} \right\} \Big|_{\lambda=\omega_+i} &= \operatorname{sign} \{ 2\omega_+^2 + A_1^2 - B_1^2 - 2A_2 \} = \operatorname{sign} \{ \sqrt{\Delta} \} > 0, \\ \operatorname{sign} \left\{ \frac{d \operatorname{Re} \lambda}{d\tau} \right\} \Big|_{\lambda=\omega_-i} &= \operatorname{sign} \{ 2\omega_-^2 + A_1^2 - B_1^2 - 2A_2 \} = \operatorname{sign} \{ -\sqrt{\Delta} \} < 0. \end{aligned}$$

Summarizing the above discussion, we have the following theorem on the local stability of E_2 and Hopf bifurcations of system (1.3).

Theorem 3.1. *Assume that $0 < b - d_3 < \frac{mbr e^{-d_1\tau}}{a}$. For system (1.3), we have the following.*

- (i) *If $mbd_3(b - d_3) + ad_3^2 + b^2(mr - a) > 0$ and $B_1^2 + 2A_2 - A_1^2 < 2\sqrt{A_2^2 - B_2^2}$, then the coexistence equilibrium E_2 is locally asymptotically stable for all $0 \leq \tau < \frac{1}{d_1} \ln \frac{mbr}{a(b-d_3)}$.*
- (ii) *If $mbd_3(b - d_3) + ad_3^2 + b^2(mr - a) > 0$ and $B_1^2 + 2A_2 - A_1^2 > 2\sqrt{A_2^2 - B_2^2}$, then there exists a $\tau_0 = \tau_+^{(0)}$, such that E_2 is stable for $\tau < \tau_+^{(0)}$ and unstable for $\tau > \tau_+^{(0)}$. Furthermore, system (1.3) undergoes a Hopf bifurcation at E_2 when $\tau = \tau_+^{(0)}$.*
- (iii) *If $mbd_3(b - d_3) + ad_3^2 + b^2(mr - a) < 0$ and $B_1^2 + 2A_2 - A_1^2 < 2\sqrt{A_2^2 - B_2^2}$, then the coexistence equilibrium E_2 is unstable for all $0 \leq \tau < \frac{1}{d_1} \ln \frac{mbr}{a(b-d_3)}$.*
- (iv) *If $mbd_3(b - d_3) + ad_3^2 + b^2(mr - a) < 0$ and $B_1^2 + 2A_2 - A_1^2 > 2\sqrt{A_2^2 - B_2^2}$, then there exists a $\tau_1 = \tau_-^{(0)}$, such that E_2 is unstable for $\tau < \tau_-^{(0)}$ and stable for $\tau > \tau_-^{(0)}$. Furthermore, system (1.3) undergoes a Hopf bifurcation at E_2 when $\tau = \tau_-^{(0)}$.*

4 Permanence

In this section, we are concerned with the permanence of system (1.3).

Definition 4.1. System (1.3) is said to be permanent (uniformly persistent) if there are positive constants m and M such that each positive solution of system (1.3) $(x_1(t), x_2(t), y(t))$ satisfies

$$\begin{aligned} m &\leq \liminf_{t \rightarrow +\infty} x_i(t) \leq \limsup_{t \rightarrow +\infty} x_i(t) \leq M, \quad i = 1, 2, \\ m &\leq \liminf_{t \rightarrow +\infty} y(t) \leq \limsup_{t \rightarrow +\infty} y(t) \leq M. \end{aligned}$$

In order to study the permanence of system (1.3), we present the persistence theory on infinite dimensional systems from [16].

Let X be a complete metric space with metric d . The distance $d(x, Y)$ of a point $x \in X$ from a subset Y of X is defined by

$$d(x, Y) = \inf_{y \in Y} d(x, y).$$

Assume that $X_0 \subset X$, $X^0 \subset X$ and $X_0 \cap X^0 = \emptyset$. Also, assume that $T(t)$ is a C_0 semigroup on X satisfying

$$T(t) : X_0 \rightarrow X_0, \quad T(t) : X^0 \rightarrow X^0. \quad (4.1)$$

Let $T_b(t) = T(t)|_{X_0}$ and A_b be the global attractor for $T_b(t)$.

Lemma 4.2. Suppose that $T(t)$ satisfies (4.1) and the following conditions:

- (i) there is a $t_0 \geq 0$ such that $T(t)$ is compact for $t > t_0$;
- (ii) $T(t)$ is point dissipative in X ;
- (iii) $\tilde{A}_b = \cup_{x \in A_b} \omega(x)$ is isolated and has an acyclic covering \overline{M} , where $\overline{M} = \{M_1, M_2, \dots, M_n\}$;
- (iv) $W^s(M_i) \cap X^0 = \phi$ for $i = 1, 2, \dots, n$.

Then X_0 is a uniform repeller with respect to X^0 , that is, there is an $\varepsilon > 0$ such that for any $x \in X^0$, $\lim_{t \rightarrow +\infty} \inf d(T(t)x, X_0) \geq \varepsilon$.

Theorem 4.3. If $0 < b - d_3 < \frac{mbre^{-d_1\tau}}{a}$ holds, then system (1.3) is uniformly persistent.

Proof. We need only to prove that the boundaries of R_{+0}^3 repel positive solutions of system (1.3) uniformly. Let $C^+([-\tau, 0], R_{+0}^3)$ denote the space of continuous functions mapping $[-\tau, 0]$ into R_{+0}^3 . Define

$$\begin{aligned} C_1 &= \{(\varphi_1, \varphi_2, \varphi_3) \in C^+([-\tau, 0], R_{+0}^3) \mid \varphi_1(\theta) \equiv 0, \varphi_2(\theta) \equiv 0, \theta \in [-\tau, 0]\}, \\ C_2 &= \{(\varphi_1, \varphi_2, \varphi_3) \in C^+([-\tau, 0], R_{+0}^3) \mid \varphi_1(\theta) > 0, \varphi_2(\theta) > 0, \varphi_3(\theta) \equiv 0, \theta \in [-\tau, 0]\}, \\ C_0 &= C_1 \cup C_2, \quad X = C^+([-\tau, 0], R_{+0}^3), \quad C^0 = \text{int } C^+([-\tau, 0], R_{+0}^3). \end{aligned}$$

In the following, we verify that the conditions in Lemma 4.2 are satisfied. By the definition of C^0 and C_0 , it is easy to see that C^0 and C_0 are positively invariant. Moreover, the conditions (i) and (ii) in Lemma 4.2 are clearly satisfied (see for instance [21, Theorem 2.2.8]). Thus we need only to show that the conditions (iii) and (iv) hold. Clearly, corresponding to $x_1(t) = x_2(t) = y(t) = 0$ and $x_1(t) = \hat{x}_1, x_2(t) = \hat{x}_2, y(t) = 0$, respectively, there are two constant solutions in C_0 : $\tilde{E}_0 \in C_1, \tilde{E}_1 \in C_2$ satisfying

$$\begin{aligned} \tilde{E}_0 &= \{(\varphi_1, \varphi_2, \varphi_3) \in ([-\tau, 0], R_{+0}^3) \mid \varphi_1(\theta) \equiv 0, \varphi_2(\theta) \equiv 0, \varphi_3(\theta) \equiv 0, \theta \in [-\tau, 0]\}, \\ \tilde{E}_1 &= \{(\varphi_1, \varphi_2, \varphi_3) \in ([-\tau, 0], R_{+0}^3) \mid \varphi_1(\theta) \equiv \hat{x}_1, \varphi_2(\theta) \equiv \hat{x}_2, \varphi_3(\theta) \equiv 0, \theta \in [-\tau, 0]\}. \end{aligned}$$

We now verify the condition (iii) of Lemma 4.2. If $(x_1(t), x_2(t), y(t))$ is a solution of system (1.3) initiating from C_1 , then $\dot{y}(t) = -d_3y(t)$, which yields $y(t) \rightarrow 0$ as $t \rightarrow +\infty$. If $(x_1(t), x_2(t), y(t))$ is a solution of system (1.3) initiating from C_2 with $x_1(0) > 0, x_2(0) > 0$, then it follows from the first and the second equations of system (1.3) that

$$\begin{aligned} \dot{x}_1(t) &= rx_2(t) - re^{-d_1\tau}x_2(t-\tau) - d_1x_1(t), \\ \dot{x}_2(t) &= re^{-d_1\tau}x_2(t-\tau) - d_2x_2^2(t). \end{aligned}$$

By Lemma 2.3, we get that

$$\lim_{t \rightarrow +\infty} x_1(t) = \frac{r^2e^{-d_1\tau}(1 - e^{-d_1\tau})}{d_1d_2} = \hat{x}_1, \quad \lim_{t \rightarrow +\infty} x_2(t) = \frac{re^{-d_1\tau}}{d_2} = \hat{x}_2.$$

that is, $(x_1(t), x_2(t), y(t)) \rightarrow (\hat{x}_1, \hat{x}_2, 0)$ as $t \rightarrow +\infty$.

Noting that $C_1 \cap C_2 = \phi$, it follows that the invariant sets \tilde{E}_0 and \tilde{E}_1 are isolated. Hence, $\{\tilde{E}_0, \tilde{E}_1\}$ is isolated and is an acyclic covering satisfying the condition (iii) in Lemma 4.2.

We now verify the condition (iv) of Lemma 4.2. Here we only show that $W^s(\tilde{E}_1) \cap C^0 = \phi$ holds since the proof of $W^s(\tilde{E}_0) \cap C^0 = \phi$ is simple. Assume that $W^s(\tilde{E}_1) \cap C^0 \neq \phi$.

Then there is a positive solution of system (1.3) $(x_1^0(t), x_2^0(t), y^0(t))$ initiating from C^0 with $\lim_{t \rightarrow +\infty} (x_1^0(t), x_2^0(t), y^0(t)) = E_1(\hat{x}_1, \hat{x}_2, 0)$. Therefore we have $\lim_{t \rightarrow +\infty} x_2^0(t) = \hat{x}_2$, that is, for $\varepsilon > 0$ small enough, there exists a $t_1 > 0$ such that $\hat{x}_2 - \varepsilon < x_2^0(t) < \hat{x}_2 + \varepsilon$ for all $t > t_1 + \tau$.

It follows from the third equation of system (1.3) that for $t > t_1 + \tau$

$$\dot{y}_0(t) \geq \left[\frac{b(\hat{x}_2 - \varepsilon)}{\hat{x}_2 - \varepsilon + my^0(t)} - d_3 \right] y^0(t).$$

By Lemma 2.4 and comparison theorem, we get that

$$\lim_{t \rightarrow +\infty} y^0(t) \geq \frac{(b - d_3)(\hat{x}_2 - \varepsilon)}{md_3}.$$

Since $\varepsilon > 0$ is arbitrary small, then we conclude

$$\lim_{t \rightarrow +\infty} y^0(t) \geq \frac{(b - d_3)\hat{x}_2}{md_3},$$

which contradicts $y^0(t) \rightarrow 0 (t \rightarrow +\infty)$. Hence, we have $W^s(\tilde{E}_1) \cap C^0 = \emptyset$. By Lemma 4.2, we are now able to conclude that C^0 repel positive solutions of system (1.3) uniformly. Therefore system (1.3) is permanent. The proof is complete. \square

5 Global stability

In this section, we are concerned with the global stability of the coexistence equilibrium of system (1.3).

Theorem 5.1. *The coexistence equilibrium E_2 of system (1.3) is globally asymptotically stable provided that*

$$(i) \quad 0 < b - d_3 < \frac{mrd_3e^{-d_1\tau}}{a};$$

$$(ii) \quad mre^{-d_1\tau} > 2a.$$

Proof. Let $(x_1(t), x_2(t), y(t))$ be any positive solution of system (1.3) with initial conditions (1.4). We derive from the second equation of system (1.3) that

$$\dot{x}_2(t) \leq re^{-d_1\tau}x_2(t - \tau) - d_2x_2^2(t).$$

By comparison theorem and Lemma 2.2, we have $\lim_{t \rightarrow +\infty} x_2(t) \leq \frac{re^{-d_1\tau}}{d_2}$. Therefore, for any $\varepsilon > 0$, there exists a $T_1 > 0$ such that

$$x_2(t) < \frac{re^{-d_1\tau}}{d_2} + \varepsilon =: \bar{N}_1 \quad \text{for } t > T_1.$$

We derive from the third equation of system (1.3) that

$$\dot{y}(t) \leq \left[\frac{b\bar{N}_1}{\bar{N}_1 + my(t)} - d_3 \right] y(t).$$

Since $b\bar{N}_1 - \bar{N}_1d_3 = \bar{N}_1(b - d_3) > 0$, we get from Lemma 2.4 and comparison theorem that

$$\lim_{t \rightarrow +\infty} y(t) \leq \frac{(b - d_3)\bar{N}_1}{md_3}.$$

Then there exists a $T_2 > T_1$ such that

$$y(t) < \frac{(b-d_3)\bar{N}_1}{md_3} + \varepsilon =: \bar{P}_1 \quad \text{for } t > T_2.$$

We derive from the second equation of system (1.3) that

$$\dot{x}_2(t) \geq re^{-d_1\tau}x_2(t-\tau) - d_2x_2^2(t) - \frac{a\bar{P}_1x_2(t)}{x_2(t) + m\bar{P}_1}.$$

Since $mre^{-d_1\tau} > 2a$, we get from Lemma 2.5 and comparison theorem that there exists a $T_3 > T_2$ such that

$$x_2(t) > z_1^* - \varepsilon =: \underline{N}_1 \quad \text{for } t > T_3,$$

where

$$z_1^* = \frac{U_1 + \sqrt{U_1^2 + 4V_1}}{2d_2}, \quad U_1 = re^{-d_1\tau} - d_2m\bar{P}_1, \quad V_1 = d_2\bar{P}_1(mre^{-d_1\tau} - a)$$

and z_1^* is the positive root for the equation

$$re^{-d_1\tau} - d_2x - \frac{a\bar{P}_1}{x + m\bar{P}_1} = 0.$$

We derive from the third equation of system (1.3) that

$$\dot{y}(t) > \left[\frac{b\underline{N}_1}{\underline{N}_1 + my(t)} - d_3 \right] y(t).$$

From Lemma 2.4 and comparison theorem we get that there exists a $T_4 > T_3$ such that

$$y(t) > \frac{(b-d_3)\underline{N}_1}{md_3} - \varepsilon =: \underline{P}_1 \quad \text{for } t > T_4. \quad (5.1)$$

We derive from the first equation of system (1.3) that

$$r\underline{N}_1 - re^{-d_1\tau}\bar{N}_1 - d_1x_1(t) < \dot{x}_1(t) < r\bar{N}_1 - re^{-d_1\tau}\underline{N}_1 - d_1x_1(t), \quad t \geq T_4.$$

Then there exists a $T_5 > T_4$ such that

$$\underline{M}_1 := \frac{r(\underline{N}_1 - e^{-d_1\tau}\bar{N}_1)}{d_1} - \varepsilon < x_1(t) < \frac{r(\bar{N}_1 - e^{-d_1\tau}\underline{N}_1)}{d_1} + \varepsilon =: \bar{M}_1 \quad \text{for } t > T_5.$$

Hence we have that

$$\underline{M}_1 < x_1(t) < \bar{M}_1, \quad \underline{N}_1 < x_2(t) < \bar{N}_1, \quad \underline{P}_1 < y(t) < \bar{P}_1, \quad t > T_5.$$

Replacing (5.1) into the second equation of (1.3), we have

$$\dot{x}_2(t) < re^{-d_1\tau}x_2(t-\tau) - d_2x_2^2(t) - \frac{a\underline{P}_1x_2(t)}{x_2(t) + m\underline{P}_1}.$$

By Lemma 2.5 and comparison theorem we get that there exists a $T_6 > T_5$ such that

$$x_2(t) < z_2^* + \varepsilon =: \bar{N}_2 \quad \text{for } t > T_6, \quad (5.2)$$

where

$$z_2^* = \frac{U_2 + \sqrt{U_2^2 + 4V_2}}{2d_2}, \quad U_2 = re^{-d_1\tau} - d_2m\underline{P}_1, \quad V_2 = d_2\underline{P}_1(mre^{-d_1\tau} - a).$$

Replacing (5.2) into the third equation of (1.3), we have

$$\dot{y}(t) \leq \left[\frac{b\bar{N}_2}{\bar{N}_2 + my(t)} - d_3 \right] y(t).$$

By Lemma 2.4 and comparison theorem we get that there exists a $T_7 > T_6$ such that

$$y(t) < \frac{(b - d_3)\bar{N}_2}{md_3} + \varepsilon =: \bar{P}_2 \quad \text{for } t > T_7. \quad (5.3)$$

Replacing (5.3) into the second equation of (1.3), we have

$$\dot{x}_2(t) \geq re^{-d_1\tau}x_2(t - \tau) - d_2x_2^2(t) - \frac{a\bar{P}_2x_2(t)}{x_2(t) + m\bar{P}_2}.$$

By Lemma 2.5 and comparison theorem we get that there exists a $T_8 > T_7$ such that

$$x_2(t) > z_3^* - \varepsilon =: \underline{N}_2 \quad \text{for } t > T_8, \quad (5.4)$$

where

$$z_3^* = \frac{U_3 + \sqrt{U_3^2 + 4V_3}}{2d_2}, \quad U_3 = re^{-d_1\tau} - d_2m\bar{P}_2, \quad V_3 = d_2\bar{P}_2(mre^{-d_1\tau} - a).$$

Replacing (5.4) into the third equation of (1.3), we have

$$\dot{y}(t) > \left[\frac{b\underline{N}_2}{\underline{N}_2 + my(t)} - d_3 \right] y(t).$$

By Lemma 2.4 and comparison theorem we get that there exists a $T_9 > T_8$ such that

$$y(t) > \frac{(b - d_3)\underline{N}_2}{md_3} - \varepsilon =: \underline{P}_2 \quad \text{for } t > T_9.$$

Replacing (5.2) and (5.4) into the first equation of (1.3), we have

$$r\underline{N}_2 - re^{-d_1\tau}\bar{N}_2 - d_1x_1(t) < \dot{x}_1(t) < r\bar{N}_2 - re^{-d_1\tau}\underline{N}_2 - d_1x_1(t), \quad t \geq T_9.$$

Then there exists a $T_{10} > T_9$ such that

$$\underline{M}_2 := \frac{r(\underline{N}_2 - e^{-d_1\tau}\bar{N}_2)}{d_1} - \varepsilon < x_1(t) < \frac{r(\bar{N}_2 - e^{-d_1\tau}\underline{N}_2)}{d_1} + \varepsilon =: \bar{M}_2 \quad \text{for } t > T_{10}.$$

Hence we have that

$$\begin{aligned} 0 < \underline{M}_1 < \underline{M}_2 < x_1(t) < \bar{M}_2 < \bar{M}_1, & \quad 0 < \underline{N}_1 < \underline{N}_2 < x_2(t) < \bar{N}_2 < \bar{N}_1, \\ 0 < \underline{P}_1 < \underline{P}_2 < y(t) < \bar{P}_2 < \bar{P}_1, & \quad t > T_{10}. \end{aligned}$$

Continuing this process, we derive the six sequences $\{\overline{M}_n\}_{n=1}^\infty, \{\underline{M}_n\}_{n=1}^\infty, \{\overline{N}_n\}_{n=1}^\infty, \{\underline{N}_n\}_{n=1}^\infty, \{\overline{P}_n\}_{n=1}^\infty, \{\underline{P}_n\}_{n=1}^\infty$ with

$$\begin{aligned} 0 &< \underline{M}_1 < \underline{M}_2 < \cdots < \underline{M}_n < x_1(t) < \overline{M}_n < \cdots < \overline{M}_2 < \overline{M}_1, \\ 0 &< \underline{N}_1 < \underline{N}_2 < \cdots < \underline{N}_n < x_2(t) < \overline{N}_n < \cdots < \overline{N}_2 < \overline{N}_1, \\ 0 &< \underline{P}_1 < \underline{P}_2 < \cdots < \underline{P}_n < y(t) < \overline{P}_n < \cdots < \overline{P}_2 < \overline{P}_1, \quad t > T_{4n+2}. \end{aligned}$$

Since $\underline{M}_1, \underline{N}_1, \underline{P}_1, \overline{M}_1, \overline{N}_1, \overline{P}_1 > 0$, then the sequences $\{\overline{M}_n\}_{n=1}^\infty, \{\overline{N}_n\}_{n=1}^\infty, \{\overline{P}_n\}_{n=1}^\infty$ are bounded and decrease, $\{\underline{M}_n\}_{n=1}^\infty, \{\underline{N}_n\}_{n=1}^\infty, \{\underline{P}_n\}_{n=1}^\infty$ are bounded and increase, so there exist constants $\overline{M}, \underline{M}, \overline{N}, \underline{N}, \overline{P}, \underline{P}$ such that $\lim_{t \rightarrow +\infty} \overline{M}_n = \overline{M}, \lim_{t \rightarrow +\infty} \underline{M}_n = \underline{M}, \lim_{t \rightarrow +\infty} \overline{N}_n = \overline{N}, \lim_{t \rightarrow +\infty} \underline{N}_n = \underline{N}, \lim_{t \rightarrow +\infty} \overline{P}_n = \overline{P}, \lim_{t \rightarrow +\infty} \underline{P}_n = \underline{P}$. Easily know that $\overline{M} \geq \underline{M}, \overline{N} \geq \underline{N}, \overline{P} \geq \underline{P}$. Next we prove that $\overline{M} = \underline{M}, \overline{N} = \underline{N}, \overline{P} = \underline{P}$.

From above discussion, we have

$$\overline{P}_n = \frac{(b-d_3)\overline{N}_n}{md_3} + \varepsilon, \quad \underline{P}_n = \frac{(b-d_3)\underline{N}_n}{md_3} - \varepsilon,$$

then

$$\overline{P}_n - \underline{P}_n = \frac{(b-d_3)(\overline{N}_n - \underline{N}_n)}{md_3} + 2\varepsilon.$$

But

$$\begin{aligned} \overline{N}_n - \underline{N}_n &= \frac{re^{-d_1\tau} - d_2m\underline{P}_{n-1} + \sqrt{(re^{-d_1\tau} - d_2m\underline{P}_{n-1})^2 + 4d_2\underline{P}_{n-1}(mre^{-d_1\tau} - a)}}{2d_2} \\ &\quad - \frac{re^{-d_1\tau} - d_2m\overline{P}_n + \sqrt{(re^{-d_1\tau} - d_2m\overline{P}_n)^2 + 4d_2\overline{P}_n(mre^{-d_1\tau} - a)}}{2d_2} + 2\varepsilon \\ &= \frac{re^{-d_1\tau} - d_2m\underline{P}_{n-1} + \sqrt{(re^{-d_1\tau} + d_2m\underline{P}_{n-1})^2 - 4ad_2\underline{P}_{n-1}}}{2d_2} \\ &\quad - \frac{re^{-d_1\tau} - d_2m\overline{P}_n + \sqrt{(re^{-d_1\tau} + d_2m\overline{P}_n)^2 - 4ad_2\overline{P}_n}}{2d_2} + 2\varepsilon \\ &= \frac{1}{2d_2} \left\{ d_2m(\overline{P}_n - \underline{P}_{n-1}) + \sqrt{(re^{-d_1\tau} + d_2m\underline{P}_{n-1})^2 - 4ad_2\underline{P}_{n-1}} \right. \\ &\quad \left. - \sqrt{(re^{-d_1\tau} + d_2m\overline{P}_n)^2 - 4ad_2\overline{P}_n} \right\} + 2\varepsilon \\ &= \frac{1}{2d_2} \left\{ d_2m(\overline{P}_n - \underline{P}_{n-1}) + \frac{d_2m(\underline{P}_{n-1} - \overline{P}_n)[2re^{-d_1\tau} + d_2m(\overline{P}_n - \underline{P}_{n-1}) + 4ad_2(\overline{P}_n - \underline{P}_{n-1})]}{\sqrt{(re^{-d_1\tau} + d_2m\underline{P}_{n-1})^2 - 4ad_2\underline{P}_{n-1}} + \sqrt{(re^{-d_1\tau} + d_2m\overline{P}_n)^2 - 4ad_2\overline{P}_n}} \right\} + 2\varepsilon \\ &= \frac{\overline{P}_n - \underline{P}_{n-1}}{2} \left\{ m - \frac{2mre^{-d_1\tau} + d_2m^2(\overline{P}_n + \underline{P}_{n-1}) - 4a}{\sqrt{(re^{-d_1\tau} + d_2m\underline{P}_{n-1})^2 - 4ad_2\underline{P}_{n-1}} + \sqrt{(re^{-d_1\tau} + d_2m\overline{P}_n)^2 - 4ad_2\overline{P}_n}} \right\} + 2\varepsilon \\ &< \frac{\overline{P}_n - \underline{P}_{n-1}}{2} \left\{ m - \frac{2(mre^{-d_1\tau} - 2a) + d_2m^2(\overline{P}_n + \underline{P}_{n-1})}{re^{-d_1\tau} + d_2m\underline{P}_{n-1} + re^{-d_1\tau} + d_2m\overline{P}_n} \right\} + 2\varepsilon \\ &= \frac{2a(\overline{P}_n - \underline{P}_{n-1})}{2re^{-d_1\tau} + d_2m(\overline{P}_n + \underline{P}_{n-1})} + 2\varepsilon \\ &< \frac{a}{re^{-d_1\tau}}(\overline{P}_n - \underline{P}_{n-1}) + 2\varepsilon \\ &= \frac{a}{re^{-d_1\tau}} \frac{(b-d_3)(\overline{N}_n - \underline{N}_{n-1})}{md_3} + 2\varepsilon \left(1 + \frac{a}{re^{-d_1\tau}} \right). \end{aligned}$$

Taking $n \rightarrow \infty$, we get that

$$\bar{N} - \underline{N} \leq \frac{a(b-d_3)}{mrd_3e^{-d_1\tau}}(\bar{N} - \underline{N}) + 2\varepsilon \left(1 + \frac{a}{re^{-d_1\tau}}\right).$$

That is,

$$(\bar{N} - \underline{N}) \left(1 - \frac{a(b-d_3)}{mrd_3e^{-d_1\tau}}\right) \leq 2\varepsilon \left(1 + \frac{a}{re^{-d_1\tau}}\right).$$

Since $1 - \frac{a(b-d_3)}{mrd_3e^{-d_1\tau}} = \frac{mrd_3e^{-d_1\tau} - a(b-d_3)}{mrd_3e^{-d_1\tau}} > 0$, then $\bar{N} = \underline{N}$. Therefore $\bar{P} = \underline{P}$.

With

$$\bar{M}_n = \frac{r(\bar{N}_n - e^{-d_1\tau}\underline{N}_n)}{d_1} + \varepsilon, \quad \underline{M}_n = \frac{r(\underline{N}_n - e^{-d_1\tau}\bar{N}_n)}{d_1} - \varepsilon,$$

we have

$$\bar{M}_n - \underline{M}_n = \frac{r(1 + e^{-d_1\tau})(\bar{N}_n - \underline{N}_n)}{d_1} + 2\varepsilon.$$

Taking $n \rightarrow \infty$, we get that $\bar{M} = \underline{M}$. Hence

$$\lim_{t \rightarrow +\infty} x_1(t) = \bar{M} = \underline{M}, \quad \lim_{t \rightarrow +\infty} x_2(t) = \bar{N} = \underline{N}, \quad \lim_{t \rightarrow +\infty} y(t) = \bar{P} = \underline{P}.$$

It is easy to know that $\bar{M} = \underline{M} = x_1^*$, $\bar{N} = \underline{N} = x_2^*$, $\bar{P} = \underline{P} = y^*$. Therefore $\lim_{t \rightarrow +\infty} x_1(t) = x_1^*$, $\lim_{t \rightarrow +\infty} x_2(t) = x_2^*$, $\lim_{t \rightarrow +\infty} y(t) = y^*$, that is, $E_2(x_1^*, x_2^*, y^*)$ is globally attractive. If $mre^{-d_1\tau} > 2a$, then $mbd_3(b-d_3) + ad_3^2 + b^2(mr-a) > 0$ and E_2 is locally asymptotically stable. Therefore we conclude that E_2 is globally asymptotically stable. The proof is complete. \square

6 Numerical simulations

Now we give some numerical simulations to illustrate the main results.

Example 6.1. In (1.3), we let $r = 2.17$, $a = 6.29$, $b = 1.35$, $d_1 = 0.07$, $d_2 = 1$, $d_3 = 1$, $m = 1.17$. It is easy to verify that the conditions $0 < b - d_3 < \frac{mbre^{-d_1\tau}}{a}$, $mbd_3(b-d_3) + ad_3^2 + b^2(mr-a) > 0$ and $B_1^2 + 2A_2 - A_1^2 > 2\sqrt{A_2^2 - B_2^2}$ hold. According to Theorem 3.1 (ii), there exists a $\tau_0 \approx 2.586$ such that the coexistence equilibrium E_2 of system (1.3) is locally asymptotically stable if $\tau < \tau_0$ and unstable if $\tau > \tau_0$. Furthermore, system (1.3) undergoes a Hopf bifurcation at E_2 if $\tau = \tau_0$. Numerical simulations illustrate these results (see Figure 6.1 and Figure 6.2).

Example 6.2. In (1.3), we let $r = 2.17$, $a = 6.29$, $b = 1.35$, $d_1 = 0.07$, $d_2 = 1$, $d_3 = 1$, $m = 1.141$. It is easy to verify that the conditions $0 < b - d_3 < \frac{mbre^{-d_1\tau}}{a}$, $mbd_3(b-d_3) + ad_3^2 + b^2(mr-a) < 0$ and $B_1^2 + 2A_2 - A_1^2 > 2\sqrt{A_2^2 - B_2^2}$ hold. According to Theorem 3.1 (iv), there exists a $\tau_1 \approx 0.1373$ such that the coexistence equilibrium E_2 of system (1.3) is locally asymptotically stable if $\tau > \tau_1$ and unstable if $\tau < \tau_1$. Furthermore, system (1.3) undergoes a Hopf bifurcation at E_2 if $\tau = \tau_1$. Numerical simulations illustrate these results (see Figure 6.3 and Figure 6.4).

Example 6.3. In (1.3), we let $r = 0.8$, $a = 0.1$, $b = 0.21$, $d_1 = 0.4$, $d_2 = 0.8$, $d_3 = 0.2$, $m = 0.5$, $\tau = 1$, then $0 < b - d_3 < \frac{mbre^{-d_1\tau}}{a}$ and $mre^{-d_1\tau} > 2a$ hold. By Theorem 4.3 we see that system (1.3) is uniformly persistent. By Theorem 5.1 we see that the coexistence equilibrium $E_2 \approx (0.4341, 0.6584, 0.0658)$ of system (1.3) is globally asymptotically stable. Numerical simulations illustrate these results (see Figure 6.5).

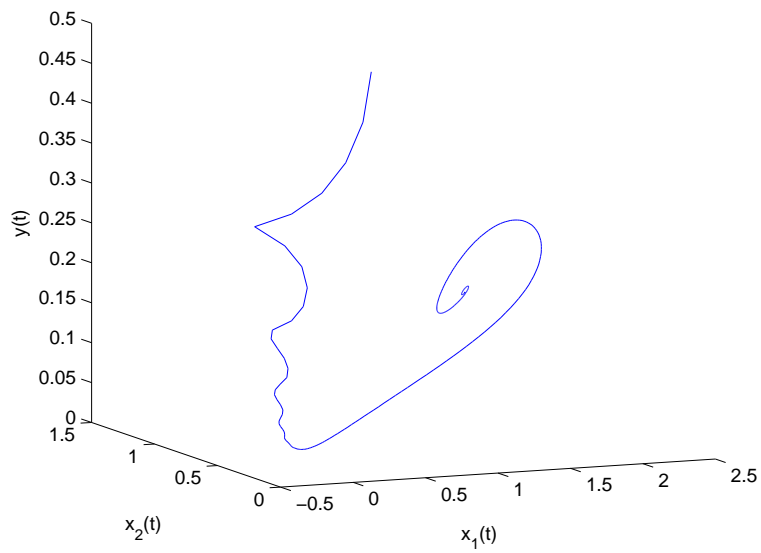
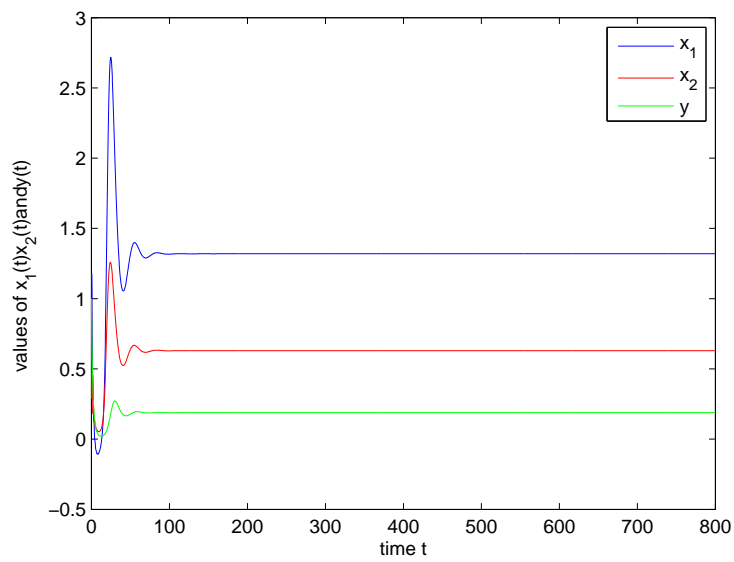


Figure 6.1: Numerical simulation shows that E_2 is locally asymptotically stable for $\tau = 1 < \tau_0$.

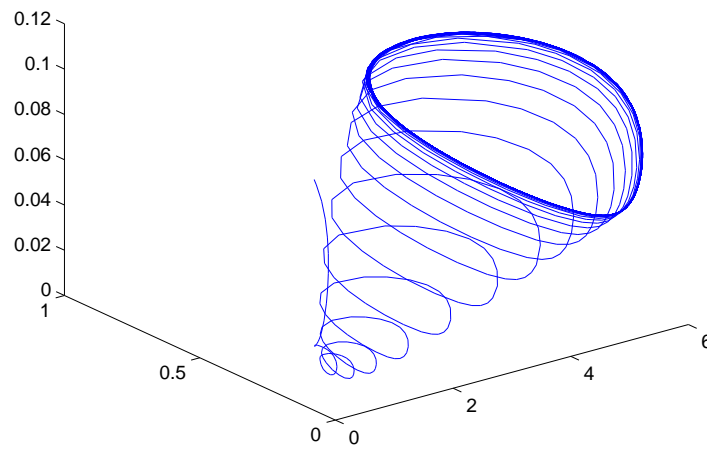
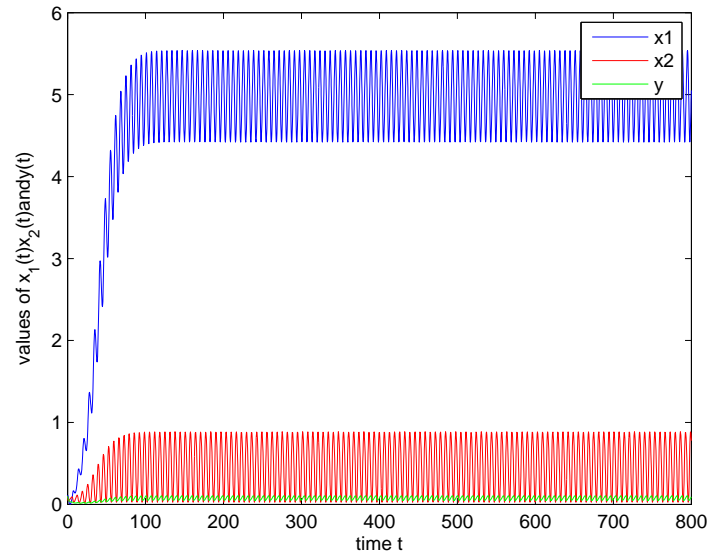


Figure 6.2: Numerical simulation shows that E_2 is unstable for $\tau = 5.98 > \tau_0$, which yields a Hopf bifurcation.

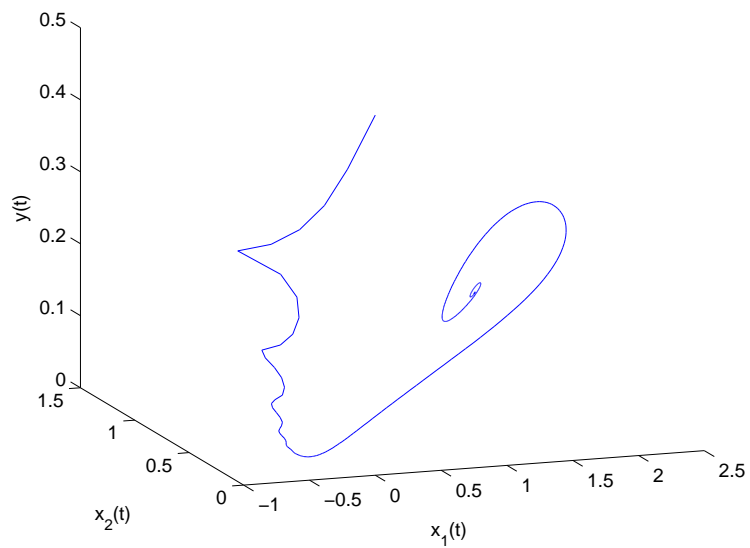
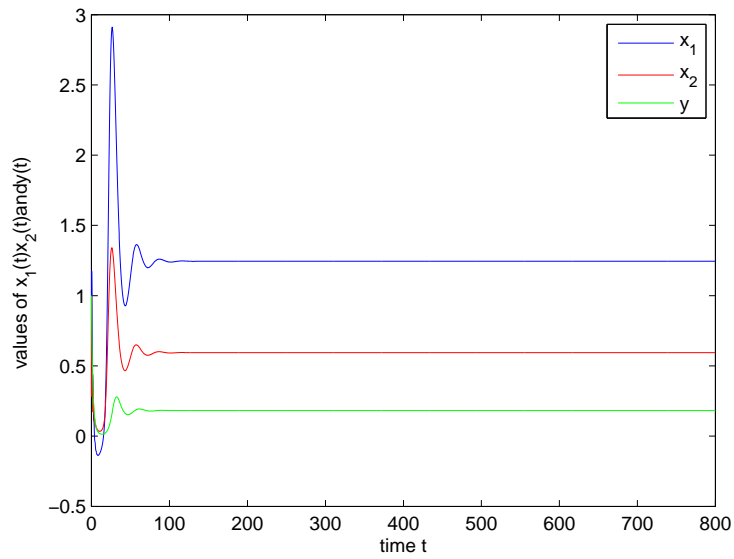


Figure 6.3: Numerical simulation shows that E_2 is locally asymptotically stable for $\tau = 1 > \tau_1$.

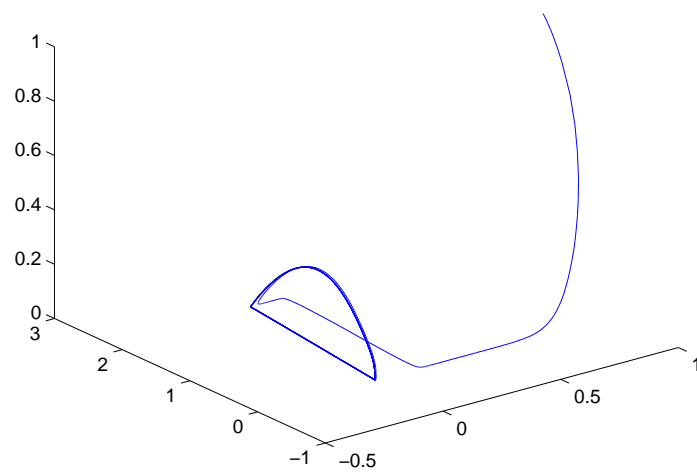
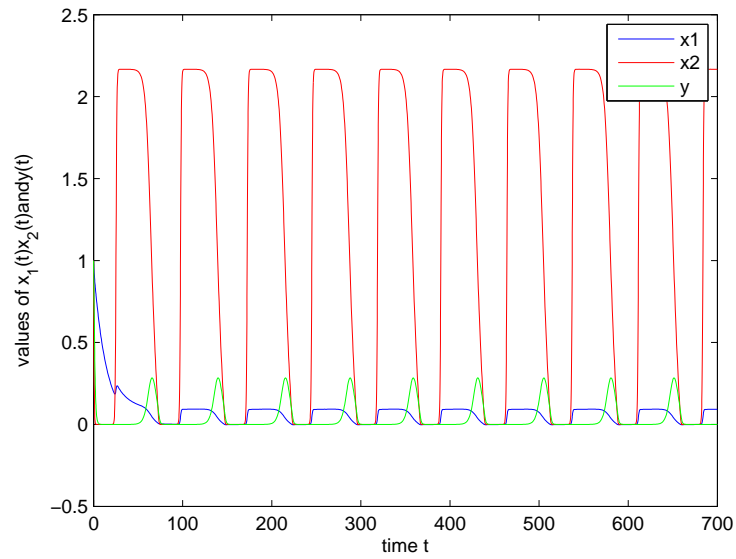


Figure 6.4: Numerical simulation shows that E_2 is unstable for $\tau = 0.02 < \tau_1$, which yields a Hopf bifurcation.

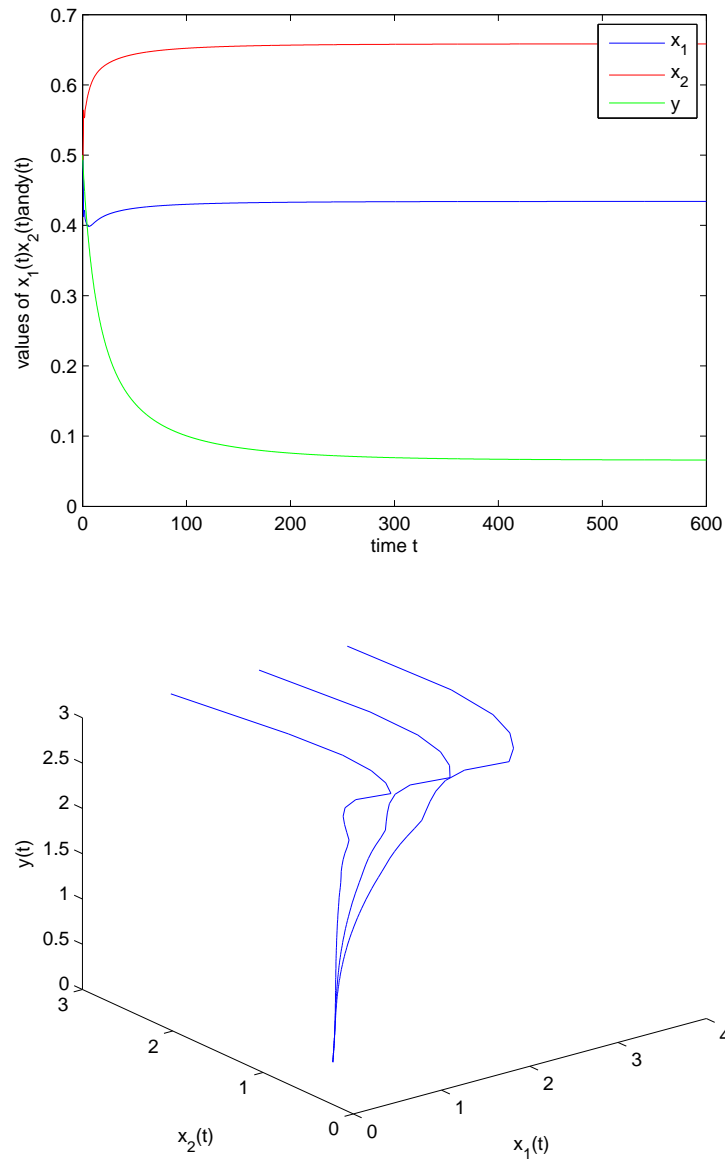


Figure 6.5: Numerical simulation shows that E_2 is globally asymptotically stable.

7 Conclusions

It is well-known that many species go through two or more life stages as they proceed from birth to death. Delay is common in population dynamics. Any biological or environmental parameters are naturally subject to fluctuation in time. Researches show that a system with time delays exhibits more complicated dynamics than that without time delay since time delay could bring a switch in the stability of equilibria and induce various oscillations and periodic solution. Gourley and Kuang [14] investigated a general predator-prey model with stage structure for the predator and constant maturation time delay. It was shown that if the juvenile death rate is nonzero, then for small and large values of maturation time delay, the population dynamics takes the simple form of a globally attractive steady state. It was also shown that if the functional response function takes the Holling I type and the resource is dynamics, as in nature, there is a window in maturation time delay parameter that generates sustainable oscillatory dynamics.

In this paper, we have investigated a ratio-dependent predator-prey model described by Holling type II functional response with time delay and stage structure for the prey. By analyzing the corresponding characteristic equations, the sufficient conditions for the local stability of the coexistence equilibrium and the existence of Hopf bifurcations are obtained. By means of the persistence theory on infinite dimensional systems, it is proven that the system is permanent if the coexistence equilibrium is feasible. By introducing some new lemmas and the comparison theorem, sufficient conditions are obtained for the global stability of the coexistence equilibrium. We have shown the effect of stage structure and time delay on the dynamics of a ratio-dependent predator-prey system.

In system (1.3), the delay τ is the time taken from birth to maturity, d_1 is the death rate of the immature prey, thus $e^{-d_1\tau}$ is the surviving rate of each immature prey before reaching maturity. By Theorem 4.3, we see that system (1.3) is uniformly persistent if the birth rate into the immature prey population, the rate of immature prey becoming mature prey, and the conversion rate and the half saturation rate of the predator are high and the capturing rate of the predator and the death rates of both the immature prey and the predator are low enough satisfying the condition $0 < b - d_3 < \frac{mbre^{-d_1\tau}}{a}$. By Theorem 5.1, we see that the coexistence equilibrium is globally asymptotically stable under somewhat stronger assumptions than those in Theorem 4.3 on the uniformly persistent of system (1.3). By the discussion of Theorem 3.1(ii) and (iv), we can see that under some conditions the equilibrium E_2 changes its stability and a periodic solution through Hopf bifurcation occurs when the delay τ passes through a critical value. This implies that the time delay is able to cause a periodic evolution of the prey and predator populations and alter the dynamics of system (1.3) significantly.

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