

Research Article

Global Stability and Hopf Bifurcation of a Predator-Prey Model with Time Delay and Stage Structure

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A delayed predator-prey system with Holling type II functional response and stage structure for both the predator and the prey is investigated. By analyzing the corresponding characteristic equations, the local stability of each of the feasible equilibria of the system is addressed and the existence of a Hopf bifurcation at the coexistence equilibrium is established. By means of persistence theory on infinite dimensional systems, it is proved that the system is permanent. By using Lyapunov functions and the LaSalle invariant principle, the global stability of each of the feasible equilibria of the model is discussed. Numerical simulations are carried out to illustrate the main theoretical results.

1. Introduction

The predator-prey system is very important in population modelling and has been studied by many authors (see, e.g., [1–6]). A predator-prey model generally takes the form

$$\begin{aligned}\dot{x} &= xf(x) - p(x)y, \\ \dot{y} &= kp(x)y - yg(y),\end{aligned}\tag{1}$$

where $x(t)$ and $y(t)$ are the densities of prey and predator populations at time t , respectively. The function $f(x)$ represents the growth rate of the prey; $g(y)$ represents the death rate and intraspecific competition rate of the predator; $p(x)$ denotes the predator response function. In 1965, Holling [7] used the function $p(x) = mx/(a + x)$ as one of the predator response functions. It is now referred to as a Holling type II functional response. We note that in the models mentioned above, it is assumed that both the immature and the mature predators have the same ability to attack prey individuals. However, in the real world, almost all animals have stage structure of immature and mature, and only mature predators can attack prey and have reproductive ability. Stage-structured models have received great attention in recent years

(see, e.g., [2–6]). In [2], Wang proposed a predator-prey system with Holling type II functional response and stage structure under the assumptions that the predator is divided into two groups, one is immature and the other is mature, and that only mature predators can attack prey and have reproductive ability, while immature predators do not attack prey and have no reproductive ability.

It is generally recognized that some kinds of time delays are inevitable in population interactions and tend to be destabilizing in the sense that longer delays may destroy the stability of positive equilibria (see [8]). Time delay due to gestation is a common example, because generally the consumption of prey by the predator throughout its past history governs the present birth rate of the predator. Recently, great attention has been received and a large body of work has been carried out on the existence of Hopf bifurcations in delayed population models (see, e.g., [5, 6, 8, 9] and references cited therein).

Motivated by the work of [2, 6], in the present paper, we are concerned with the combined effects of stage structure for both the predator and the prey and time delay due to the gestation of the predator on the global dynamics of a predator-prey model with Holling type II functional

response. To this end, we consider the following differential system:

$$\begin{aligned} \dot{x}_1(t) &= rx_2(t) - (r_1 + d_1)x_1(t) - ax_1^2(t) - \frac{a_1x_1(t)y_2(t)}{1 + mx_1(t)}, \\ \dot{x}_2(t) &= r_1x_1(t) - d_2x_2(t), \\ \dot{y}_1(t) &= \frac{a_2x_1(t - \tau)y_2(t - \tau)}{1 + mx_1(t - \tau)} - (r_2 + d_3)y_1(t), \\ \dot{y}_2(t) &= r_2y_1(t) - d_4y_2(t), \end{aligned} \quad (2)$$

where $x_1(t)$ and $x_2(t)$ represent the densities of the immature and the mature prey at time t , respectively; $y_1(t)$ and $y_2(t)$ represent the densities of the immature and the mature predators at time t , respectively. The parameters $a, a_1, a_2, d_1, d_2, d_3, d_4, r, r_1$, and r_2 are positive constants, in which r is the birth rate of the prey; a is the intraspecific competition rate of the mature prey; d_1, d_2, d_3 , and d_4 are the death rates of the immature prey, mature prey, immature predators, and mature predators, respectively; r_1 and r_2 are the transformation rates from the immature individuals to mature individuals for the prey and the predators, respectively; a_1 is the capturing rate of the predators; a_2/a_1 is the conversion rate of nutrients into the reproduction of the predators; $\tau \geq 0$ is a constant delay due to the gestation of the predators. It is assumed in (2) that the mature individual predators feed on immature prey and have the ability to reproduce.

The initial conditions for system (2) take the form

$$\begin{aligned} x_1(\theta) &= \phi_1(\theta) \geq 0, & x_2(\theta) &= \phi_2(\theta) \geq 0, \\ y_1(\theta) &= \varphi_1(\theta) \geq 0, & y_2(\theta) &= \varphi_2(\theta) \geq 0, \\ & & \theta &\in [-\tau, 0), \\ \phi_1(0) &> 0, & \phi_2(0) &> 0, & \varphi_1(0) &> 0, & \varphi_2(0) &> 0, \\ (\phi_1(\theta), \phi_2(\theta), \varphi_1(\theta), \varphi_2(\theta)) &\in C([- \tau, 0], R_{+0}^4), \end{aligned} \quad (3)$$

where $R_{+0}^4 = \{(x_1, x_2, x_3, x_4) : x_i \geq 0, i = 1, 2, 3, 4\}$.

It is well known by the fundamental theory of functional differential equations [10] that system (2) has a unique solution $(x_1(t), x_2(t), y_1(t), y_2(t))$ satisfying initial conditions (3). It is easy to show that all solutions of system (2) corresponding to initial conditions (3) are defined on $[0, +\infty)$ and remain positive for all $t \geq 0$.

The organization of this paper is as follows. In the next section, we investigate the local stability of each of the feasible equilibria of system (2). The existence of a Hopf bifurcation at the coexistence equilibrium is studied. In Section 3, by means of persistence theory on infinite dimensional systems, we prove that system (2) is permanent when the coexistence equilibrium exists. In Section 4, by using Lyapunov functionals and the LaSalle invariant principle, we show that both the prey and the predators go to extinction, if both the predator-extinction equilibrium and the coexistence equilibrium are not feasible, and that the predator-extinction equilibrium is

globally asymptotically stable when the coexistence equilibrium does not exist, and sufficient conditions are obtained for the global asymptotic stability of the coexistence equilibrium of system (2). A brief discussion is given in Section 5 to conclude this work.

2. Local Stability

In this section, we discuss the local stability of each equilibrium of system (2) and the existence of a Hopf bifurcation. It is easy to show that system (2) always has a trivial equilibrium $E_0(0, 0, 0, 0)$ and a predator-extinction equilibrium $E_1(x_1^+, x_2^+, 0, 0)$ when $rr_1 > d_2(r_1 + d_1)$, where

$$x_1^+ = \frac{rr_1 - d_2(r_1 + d_1)}{ad_2}, \quad x_2^+ = \frac{r_1 [rr_1 - d_2(r_1 + d_1)]}{ad_2^2}. \quad (4)$$

Furthermore, if the following holds:

$$(H_1) \quad (rr_1 - d_2(r_1 + d_1))/ad_2 > d_4(r_2 + d_3)/(a_2r_2 - md_4(r_2 + d_3)) > 0,$$

then system (2) has a unique coexistence equilibrium $E^*(x_1^*, x_2^*, y_1^*, y_2^*)$, where

$$\begin{aligned} x_1^* &= \frac{d_4(r_2 + d_3)}{a_2r_2 - md_4(r_2 + d_3)}, & x_2^* &= \frac{r_1}{d_2}x_1^*, \\ y_1^* &= \frac{d_4}{r_2}y_2^*, \\ y_2^* &= \frac{(1 + mx_1^*) [rr_1 - d_2(r_1 + d_1) - ad_2x_1^*]}{a_1d_2}. \end{aligned} \quad (5)$$

The characteristic equation of system (2) at the equilibrium $E_0(0, 0, 0, 0)$ is of the form

$$\begin{aligned} &[\lambda^2 + (r_1 + d_1 + d_2)\lambda + d_2(r_1 + d_1) - rr_1] \\ &\times [\lambda^2 + (r_2 + d_3 + d_4)\lambda + d_4(r_2 + d_3)] = 0. \end{aligned} \quad (6)$$

It is readily seen from (6) that if $rr_1 < d_2(r_1 + d_2)$, then E_0 is locally asymptotically stable; if $rr_1 > d_2(r_1 + d_2)$, then E_0 is unstable.

The characteristic equation of system (2) at the equilibrium $E_1(x_1^+, x_2^+, 0, 0)$ takes the form

$$\begin{aligned} &[\lambda^2 + (r_1 + d_1 + d_2 + 2ax_1^+)\lambda + rr_1 - d_2(r_1 + d_1)] \\ &\times [\lambda^2 + p_1\lambda + p_0 + q_0e^{-\lambda\tau}] = 0, \\ p_1 &= r_2 + d_3 + d_4, & p_0 &= d_4(r_2 + d_3), \\ q_0 &= -\frac{a_2r_2x_1^+}{1 + mx_1^+}. \end{aligned} \quad (7)$$

It is easy to show that roots of $\lambda^2 + (r_1 + d_1 + d_2 + 2ax_1^+)\lambda + rr_1 - d_2(r_1 + d_1) = 0$ have only negative real parts if $rr_1 > d_2(r_1 + d_2)$. If (H_1) holds, we have $p_0 + q_0 < 0$; thus (7) has at least one

positive real root. Therefore, E_1 is unstable. If $0 < (rr_1 - d_2(r_1 + d_1))/(ad_2) < d_4(r_2 + d_3)/(a_2r_2 - md_4(r_2 + d_3))$, we have $p_0 + q_0 > 0$; then the equilibrium E_1 is locally asymptotically stable when $\tau = 0$. It is easy to show that $p_1^2 - 2p_0 > 0$, $p_0^2 - q_0^2 > 0$. Therefore, if $0 < (rr_1 - d_2(r_1 + d_1))/(ad_2) < d_4(r_2 + d_3)/(a_2r_2 - md_4(r_2 + d_3))$, by Lemma B in Kuang and So [1], we see that the equilibrium E_1 is locally asymptotically stable for all $\tau > 0$.

The characteristic equation of system (2) at the equilibrium E^* is of the form

$$\lambda^4 + p_3\lambda^3 + p_2\lambda^2 + p_1\lambda + p_0 + (q_2\lambda^2 + q_1\lambda + q_0)e^{-\lambda\tau} = 0, \tag{8}$$

where

$$\begin{aligned} p_3 &= \alpha + d_2 + r_2 + d_3 + d_4, \\ p_2 &= (\alpha + d_2)(r_2 + d_3 + d_4) + d_4(r_2 + d_3) + \alpha d_2 - rr_1, \\ p_1 &= (r_2 + d_3 + d_4)(\alpha d_2 - rr_1) + d_4(r_2 + d_3)(\alpha + d_2), \\ p_0 &= d_4(r_2 + d_3)(\alpha d_2 - rr_1), \quad q_2 = -d_4(r_2 + d_3), \\ q_1 &= d_4(r_2 + d_3) \left[\frac{a_1 y_2^*}{(1 + mx_1^*)^2} - (\alpha + d_2) \right], \\ q_0 &= d_4(r_2 + d_3) \left[\frac{a_1 d_2 y_2^*}{(1 + mx_1^*)^2} + rr_1 - \alpha d_2 \right], \\ \alpha &= r_1 + d_1 + 2ax_1^* + \frac{a_1 y_2^*}{(1 + mx_1^*)^2}. \end{aligned} \tag{9}$$

When $\tau = 0$, (8) becomes

$$\lambda^4 + p_3\lambda^3 + (p_2 + q_2)\lambda^2 + (p_1 + q_1)\lambda + p_0 + q_0 = 0. \tag{10}$$

By calculation we derive that

$$p_3 > 0, \quad p_0 + q_0 = d_4(r_2 + d_3) \frac{a_1 d_2 y_2^*}{(1 + mx_1^*)^2} > 0. \tag{11}$$

Hence, by the Routh-Hurwitz criterion, we see that if the following hold:

$$(H_2) \quad p_3(p_2 + q_2) > (p_1 + q_1), \quad p_3(p_2 + q_2)(p_1 + q_1) > (p_1 + q_1)^2 + p_3^2(p_0 + q_0),$$

then the equilibrium E^* is locally asymptotically stable when $\tau = 0$.

If $i\omega$ ($\omega > 0$) is a solution of (8), separating real and imaginary parts, we have

$$\begin{aligned} (q_2\omega^2 - q_0)\cos\omega\tau - q_1\omega\sin\omega\tau &= \omega^4 - p_2\omega^2 + p_0, \\ (q_2\omega^2 - q_0)\sin\omega\tau + q_1\omega\cos\omega\tau &= p_3\omega^3 - p_1\omega. \end{aligned} \tag{12}$$

Squaring and adding the two equations of (12), it follows that

$$\omega^8 + h_3\omega^6 + h_2\omega^4 + h_1\omega^2 + h_0 = 0. \tag{13}$$

It is easy to show that

$$\begin{aligned} h_3 &= p_3^2 - 2p_2 = \alpha^2 + d_2^2 + (r_2 + d_3)^2 + d_4^2 + 2rr_1 > 0, \\ h_2 &= p_2^2 + 2p_0 - 2p_1p_3 - q_2^2 \\ &= (\alpha d_2 - rr_1)^2 + [d_4^2 + (r_2 + d_3)^2](\alpha^2 + d_2^2 + 2rr_1) \\ &> 0, \\ h_1 &= p_1^2 - 2p_0p_2 + 2q_0q_2 - q_1^2 \\ &= (\alpha d_2 - rr_1)^2 [d_4^2 + (r_2 + d_3)^2] + d_4^2(r_2 + d_3)^2 \\ &\quad \times \frac{a_1 y_2^*}{(1 + mx_1^*)^2} \left[2(r_1 + d_1) + 4ax_1^* + \frac{a_1 y_2^*}{(1 + mx_1^*)^2} \right] \\ &> 0, \\ h_0 &= p_0^2 - q_0^2 = d_4^2(r_2 + d_3)^2 \frac{a_1 d_2 y_2^*}{(1 + mx_1^*)^2} \\ &\quad \times \left[2(\alpha d_2 - rr_1) - \frac{a_1 d_2 y_2^*}{(1 + mx_1^*)^2} \right]. \end{aligned} \tag{14}$$

If $2(\alpha d_2 - rr_1) > a_1 d_2 y_2^*/(1 + mx_1^*)^2$, that is,

$$(H_3) \quad (rr_1 - d_2(r_1 + d_1))/ad_2 < 2d_4(r_2 + d_3)/(a_2r_2 - md_4(r_2 + d_3)) + d_4(r_2 + d_3)/(a_2r_2 + md_4(r_2 + d_3)),$$

then (13) has no positive real roots. It is easy to check that (H_2) holds when (H_3) holds. Accordingly, by Theorem 3.4.1 in Kuang [8], we see that if (H_1) and (H_3) hold, then E^* is locally asymptotically stable.

If the inequality in (H_3) is reversed, then (13) has a unique positive root ω_0 ; that is, (8) has a pair of purely imaginary roots of the form $\pm i\omega_0$. Denote

$$\begin{aligned} \tau_k &= \frac{2k\pi}{\omega_0} + \frac{1}{\omega_0} \\ &\quad \times \arccos \frac{(q_2\omega_0^2 - q_0)(\omega_0^4 - p_2\omega_0^2 + p_0) + q_1\omega_0^2(p_3\omega_0^2 - p_1)}{(q_1\omega_0)^2 + (q_2\omega_0^2 - q_0)^2}, \\ &\quad k = 0, 1, 2, \dots \end{aligned} \tag{15}$$

By Theorem 3.4.1 in Kuang [8], we see that E^* remains stable for $\tau < \tau_0$.

We now claim that

$$\left. \frac{d(\operatorname{Re}(\lambda))}{d\tau} \right|_{\tau=\tau_0} > 0. \tag{16}$$

This will show that there exists at least one eigenvalue with a positive real part for $\tau > \tau_0$. Moreover, the conditions for the existence of a Hopf bifurcation [10] are then satisfied

yielding a periodic solution. To this end, differentiating (8) with respect to τ , it follows that

$$\begin{aligned} \left(\frac{d\lambda}{d\tau}\right)^{-1} &= \frac{4\lambda^3 + 3p_3\lambda^2 + 2p_2\lambda + p_1}{-\lambda(\lambda^4 + p_3\lambda^3 + p_2\lambda^2 + p_1\lambda + p_0)} \\ &+ \frac{2q_2\lambda + q_1}{\lambda(q_2\lambda^2 + q_1\lambda + q_0)} - \frac{\tau}{\lambda}. \end{aligned} \tag{17}$$

Hence, a direct calculation shows that

$$\begin{aligned} &\text{sgn} \left\{ \frac{d(\text{Re } \lambda)}{d\tau} \right\}_{\lambda=i\omega_0} \\ &= \text{sgn} \left\{ \text{Re} \left(\frac{d\lambda}{d\tau} \right)^{-1} \right\}_{\lambda=i\omega_0} \\ &= \text{sgn} \left\{ \frac{(3p_3\omega_0^2 - p_1)(p_3\omega_0^2 - p_1) + 2(2\omega_0^2 - p_2)(\omega_0^4 - p_2\omega_0^2 + p_0)}{\omega_0^2(p_1 - p_3\omega_0^2)^2 + (\omega_0^4 - p_2\omega_0^2 + p_0)^2} \right. \\ &\quad \left. + \frac{-q_1^2 + 2q_2q_0 - 2q_2^2\omega_0^2}{(q_1\omega_0)^2 + (q_2\omega_0^2 - q_0)^2} \right\}. \end{aligned} \tag{18}$$

We derive from (12) that

$$\begin{aligned} &\omega_0^2(p_1 - p_3\omega_0^2)^2 + (\omega_0^4 - p_2\omega_0^2 + p_0)^2 \\ &= (q_1\omega_0)^2 + (q_2\omega_0^2 - q_0)^2. \end{aligned} \tag{19}$$

Hence it follows that

$$\begin{aligned} &\text{sgn} \left\{ \frac{d(\text{Re } \lambda)}{d\tau} \right\}_{\lambda=i\omega_0} \\ &= \text{sgn} \left\{ \frac{4\omega_0^6 + 3h_3\omega_0^4 + 2h_2\omega_0^2 + h_1}{(q_1\omega_0)^2 + (q_2\omega_0^2 - q_0)^2} \right\} > 0. \end{aligned} \tag{20}$$

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

In conclusion, we have the following results.

Theorem 1. For system (2), one has the following.

- (i) If $rr_1 < d_2(r_1 + d_1)$, then the trivial equilibrium $E_0(0, 0, 0, 0)$ is locally asymptotically stable; if $rr_1 > d_2(r_1 + d_1)$, then E_0 is unstable.
- (ii) If $0 < (rr_1 - d_2(r_1 + d_1))/ad_2 < d_4(r_2 + d_3)/(a_2r_2 - md_4(r_2 + d_3))$, then the predator-extinction equilibrium $E_1(x_1^*, x_2^*, 0, 0)$ is locally asymptotically stable; if $(rr_1 - d_2(r_1 + d_1))/ad_2 > d_4(r_2 + d_3)/(a_2r_2 - md_4(r_2 + d_3)) > 0$, then E_1 is unstable.
- (iii) Let (H_1) hold. If (H_3) holds, then the coexistence equilibrium $E^*(x_1^*, x_2^*, y_1^*, y_2^*)$ is locally asymptotically stable for all $\tau \geq 0$; if (H_2) holds and the inequality in (H_3) is reversed, then there exists a positive number τ_0 , such that E^* is locally asymptotically stable if $0 < \tau < \tau_0$ and is unstable if $\tau > \tau_0$. Further, system (2) undergoes a Hopf bifurcation at E^* when $\tau = \tau_0$.

We now give an example to illustrate the main results in Theorem 1.

Example 2. In (2), let $a = 16, a_1 = 16, a_2 = 3, d_1 = 1/8, d_2 = 1/2, d_3 = 1/8, d_4 = 1/8, r = 5, r_1 = 1, r_2 = 1$, and $m = 1/10$. It is easy to show that $(rr_1 - d_2(r_1 + d_1))/ad_2 \approx 0.5547$ and $d_4(r_2 + d_3)/(a_2r_2 - md_4(r_2 + d_3)) \approx 0.0471$; that is, the condition (H_1) holds. Hence, system (2) has a unique coexistence equilibrium $E^*(0.0471, 0.0942, 0.0637, 0.5100)$. By calculation, we have $p_3(p_2 + q_2) - (p_1 + q_1) \approx 177.6328 > 0, p_3(p_2 + q_2)(p_1 + q_1) - (p_1 + q_1)^2 - p_3^2(p_0 + q_0) \approx 193.0344 > 0, 2(\alpha d_2 - rr_1) - a_1 d_2 y_2^*/(1 + mx_1^*)^2 \approx -3.3262 < 0$ and $\tau_0 \approx 2.3729$. By Theorem 1, E^* is locally asymptotically stable if $0 < \tau < \tau_0$ and is unstable if $\tau > \tau_0$, and system (2) undergoes a Hopf bifurcation at E^* when $\tau = \tau_0$. Numerical simulation illustrates this fact (see Figure 1).

3. Permanence

In this section, we are concerned with the permanence of system (2).

Definition 3. System (2) is said to be permanent if there are positive constants m_1, m_2, M_1 , and M_2 , such that each positive solution of system (2) satisfies

$$\begin{aligned} m_1 &\leq \liminf_{t \rightarrow +\infty} x_i(t) \leq \limsup_{t \rightarrow +\infty} x_i(t) \leq M_1, \quad i = 1, 2, \\ m_2 &\leq \liminf_{t \rightarrow +\infty} y_i(t) \leq \limsup_{t \rightarrow +\infty} y_i(t) \leq M_2, \quad i = 1, 2. \end{aligned} \tag{21}$$

Lemma 4. There are positive constants M_1 and M_2 , such that, for any positive solution $(x_1(t), x_2(t), y_1(t), y_2(t))$ of system (2),

$$\limsup_{t \rightarrow +\infty} x_i(t) \leq M_1, \quad \limsup_{t \rightarrow +\infty} y_i(t) \leq M_2, \quad i = 1, 2. \tag{22}$$

Proof. Let $(x_1(t), x_2(t), y_1(t), y_2(t))$ be any positive solution of system (2) with initial conditions (3). Define

$$V(t) = x_1(t - \tau) + \frac{r + d_2}{d_2} x_2(t - \tau) + \frac{a_1}{a_2} y_1(t) + \frac{a_1}{a_2} y_2(t). \tag{23}$$

Calculating the derivative of $V(t)$ along positive solutions of system (2), it follows that

$$\begin{aligned} \dot{V}(t) &= -d_1 x_1(t - \tau) - d_2 x_2(t - \tau) - \frac{a_1}{a_2} d_3 y_1(t) \\ &\quad - \frac{a_1}{a_2} d_4 y_2(t) + \frac{rr_1}{d_2} x_1(t - \tau) - ax_1^2(t - \tau) \\ &\leq -dV(t) - a \left(x_1(t - \tau) - \frac{rr_1}{2ad_2} \right)^2 + \frac{(rr_1)^2}{4ad_2^2} \\ &\leq -dV(t) + \frac{(rr_1)^2}{4ad_2^2}, \end{aligned} \tag{24}$$

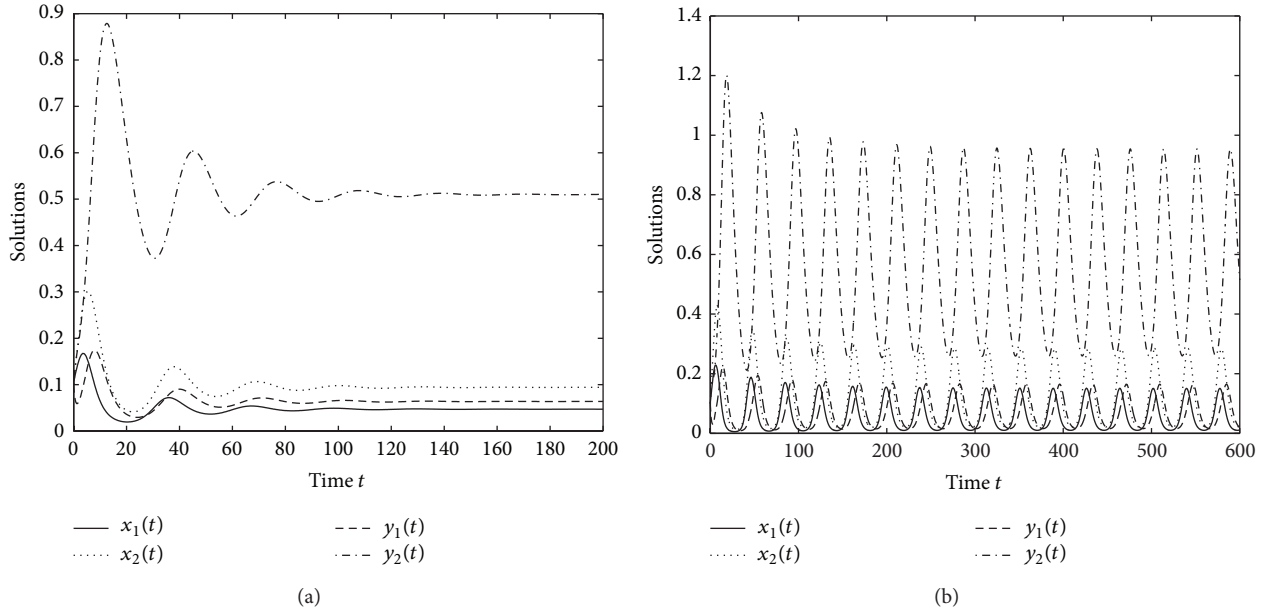


FIGURE 1: The temporal solution found by numerical integration of system (2) with $\tau = 0.1$ and $\tau = 3$, respectively; $(\phi_1, \phi_2, \varphi_1, \varphi_2) = (0.1, 0.1, 0.1, 0.1)$.

where $d = \min \{d_1, d_2^2/(r + d_2), d_3, d_4\}$. This inequality yields $\limsup_{t \rightarrow +\infty} V(t) \leq (rr_1)^2/(4add_2^2)$. If we choose $M_1 = (rr_1)^2/(4add_2(r + d_2))$ and $M_2 = a_2(rr_1)^2/(4aa_1dd_2^2)$, then (22) follows. This completes the proof. \square

In order to study the permanence of system (2), we refer to persistence theory on infinite dimensional systems developed by Hale and Waltman in [11].

Let X be a complete metric space with metric d . Suppose that $T : [0, +\infty] \times X \rightarrow X$ is a continuous map with the following properties:

$$T_t \circ T_s = T_{t+s}, \quad t, s \geq 0, \quad T_0(x) = x, \quad x \in X, \quad (25)$$

where T_t denotes the mapping from X to X given by $T_t(x) = T(t, x)$. The distance $d(x, Y)$ of a point $x \in X$ from a subset Y of X is defined by $d(x, Y) = \inf_{y \in Y} d(x, y)$. Recall that the positive orbit $\gamma^+(x) = \bigcup_{t \geq 0} \{T(t)x\}$, and its ω -limit set is $\omega(x) = \bigcap_{s \geq 0} \bigcup_{t \geq s} \{\overline{T(t)x}\}$. Define $W^s(A)$, the strong stable set of a compact invariant set A , to be $W^s(A) = \{x : x \in X, \omega(x) \neq \emptyset, \omega(x) \subset A\}$.

(A1) Assume that X^0 is open and dense in X and $X^0 \cup X_0 = X, X^0 \cap X_0 = \emptyset$. Moreover, the C^0 semigroup $T(t)$ on X satisfies

$$T(t) : X^0 \longrightarrow X^0, \quad T(t) : X_0 \longrightarrow X_0. \quad (26)$$

Let $T_b(t) = T(t)|_{X_0}$ and A_b be the global attractor for $T_b(t)$. Define $\tilde{A}_b = \bigcup_{x \in A_b} \omega(x)$.

Lemma 5 (Hale and Waltman [11]). *Suppose that $T(t)$ satisfies (A1) 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 is isolated and has an acyclic covering \widehat{M} , where $\widehat{M} = \{\widehat{M}_1, \widehat{M}_2, \dots, \widehat{M}_n\}$;*
- (iv) *$W^s(\widehat{M}_i) \cap X^0 = \emptyset$ 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 $x \in X^0, \liminf_{t \rightarrow +\infty} d(T(t)x, X_0) \geq \varepsilon$.

We are now able to state and prove the result on the permanence of system (2).

Theorem 6. *If (H₁) holds, then system (2) is permanent.*

Proof. We need only to show that the boundaries of R_{+0}^4 repel positive solutions of system (2) uniformly. Let $C^+([-\tau, 0], R_{+0}^4)$ denote the space of continuous functions mapping $[-\tau, 0]$ into R_{+0}^4 . Define

$$\begin{aligned} C_1 &= \{(\phi_1, \phi_2, \varphi_1, \varphi_2) \in C^+([-\tau, 0], R_{+0}^4) : \phi_i(\theta) \equiv 0, \\ &\quad \theta \in [-\tau, 0], i = 1, 2\}, \\ C_2 &= \{(\phi_1, \phi_2, \varphi_1, \varphi_2) \in C^+([-\tau, 0], R_{+0}^4) : \phi_i(\theta) > 0, \\ &\quad \phi_i(\theta) \equiv 0, \theta \in [-\tau, 0], i = 1, 2\}. \end{aligned} \quad (27)$$

Denote $C_0 = C_1 \cup C_2$ and $C^0 = \text{int } C^+([-\tau, 0], R_{+0}^4)$.

In the following, we show that the conditions in Lemma 5 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 and the condition (ii) in Lemma 5 is clearly satisfied. Using the smoothing property of solutions of delay differential equations introduced in

Kuang [8] (Theorem 2.2.8), it follows that condition (i) in Lemma 5 is satisfied. Thus, we need only to show that the conditions (iii) and (iv) hold. Clearly, corresponding to $x_i(t) = y_i(t) = 0$ and $x_1(t) = x_1^+$, $x_2(t) = x_2^+$, $y_i(t) = 0$, respectively, there are two constant solutions in C_0 : $\tilde{E}_0 \in C_1$ and $\tilde{E}_1 \in C_2$ satisfying

$$\begin{aligned} \tilde{E}_0 &= \{(\phi_1, \phi_2, \varphi_1, \varphi_2) \in C^+([-\tau, 0], R_{+0}^4) : \phi_i(\theta) \equiv 0, \\ &\quad \varphi_i(\theta) \equiv 0, \theta \in [-\tau, 0]\}, \\ \tilde{E}_1 &= \{(\phi_1, \phi_2, \varphi_1, \varphi_2) \in C^+([-\tau, 0], R_{+0}^4) : \phi_1(\theta) = x_1^+, \\ &\quad \phi_2(\theta) = x_2^+, \varphi_i(\theta) \equiv 0, \theta \in [-\tau, 0]\}. \end{aligned} \quad (28)$$

We now verify the condition (iii) in Lemma 5. If $(x_1(t), x_2(t), y_1(t), y_2(t))$ is a solution of system (2) initiating from C_1 , then $\dot{y}_1(t) = -(d_3 + r_2)y_1(t)$ and $\dot{y}_2(t) = r_2y_1(t) - d_4y_2(t)$, which yields $\lim_{t \rightarrow +\infty} y_i(t) = 0, i = 1, 2$. If $(x_1(t), x_2(t), y_1(t), y_2(t))$ is a solution of system (2) initiating from C_2 with $\phi_i(0) > 0$, then it follows from the first and second equations of system (2) that $\dot{x}_1(t) = rx_2(t) - (r_1 + d_1)x_1(t) - ax_1^2(t)$ and $\dot{x}_2(t) = r_1x_1(t) - d_2x_2(t)$. If $rr_1 > d_2(r_1 + d_1)$ holds, then $x_1(t) \rightarrow x_1^+$, $x_2(t) \rightarrow x_2^+$ as $t \rightarrow +\infty$. Noting that $C_1 \cap C_2 = \emptyset$, we see 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 5.

We now verify that $W^s(\tilde{E}_0) \cap C^0 = \emptyset$ and $W^s(\tilde{E}_1) \cap C^0 = \emptyset$. Here, we only prove the second equation since the proof of the first equation is simple. Assume $W^s(\tilde{E}_1) \cap C^0 \neq \emptyset$. Then there is a positive solution $(x_1(t), x_2(t), y_1(t), y_2(t))$ satisfying

$$\lim_{t \rightarrow +\infty} (x_1(t), x_2(t), y_1(t), y_2(t)) = (x_1^+, x_2^+, 0, 0). \quad (29)$$

Hence, for $\varepsilon > 0$ sufficiently small, there is a $t_0 > 0$ such that, if $t > t_0$, $x_1^+ - \varepsilon < x_2(t) < x_1^+ + \varepsilon$.

Since (H_1) holds, we can choose $\varepsilon > 0$ sufficiently small, such that

$$\frac{a_2r_2(x_1^+ - \varepsilon)}{1 + m(x_1^+ - \varepsilon)} > d_4(r_2 + d_3). \quad (30)$$

For $\varepsilon > 0$ sufficiently small satisfying (30), it follows from the third and the fourth equations of system (2) that, for $t > t_0 + \tau$,

$$\begin{aligned} \dot{y}_1(t) &\geq \frac{a_2(x_1^+ - \varepsilon)}{1 + m(x_1^+ - \varepsilon)}y_2(t - \tau) - (r_2 + d_3)y_2(t), \\ \dot{y}_2(t) &= r_2y_1(t) - d_4y_2(t). \end{aligned} \quad (31)$$

Define

$$A_\varepsilon = \begin{pmatrix} -(r_2 + d_3) & \frac{a_2(x_1^+ - \varepsilon)}{1 + m(x_1^+ - \varepsilon)} \\ r_2 & -d_4 \end{pmatrix}. \quad (32)$$

Since A_ε has positive off-diagonal elements, by the Perron-Frobenius theorem, there is a positive eigenvector η for the

maximum eigenvalue μ of A_ε . Noting that (30) holds, a direct calculation shows that $\mu > 0$. Using a similar argument as that in the proof of Theorem 2.1 in [2], one can show that $\lim_{t \rightarrow +\infty} y_i(t) = +\infty$ ($i = 1, 2$). This contradicts Lemma 4. Hence, we have $W^s(\tilde{E}_1) \cap C^0 = \emptyset$. By Lemma 5, we conclude that C_0 repels positive solutions of system (2) uniformly. Therefore, system (2) is permanent. The proof is complete. \square

4. Global Stability

In this section, we are concerned with the global stability of each of the feasible equilibria of system (2). The strategy of proofs is to use Lyapunov functionals and the LaSalle invariant principle.

Theorem 7. *If $rr_1 < d_2(r_1 + d_1)$, then the trivial equilibrium $E_0(0, 0, 0, 0)$ of system (2) is globally asymptotically stable.*

Proof. Let $(x_1(t), x_2(t), y_1(t), y_2(t))$ be any positive solution of system (2) with initial conditions (3). By Theorem 1, we see that if $rr_1 < d_2(r_1 + d_1)$, then E_0 is locally asymptotically stable. Define

$$\begin{aligned} V_1(t) &= x_1(t) + \frac{r}{d_2}x_2(t) + \frac{a_1}{a_2}y_1(t) + \frac{a_1(r_2 + d_3)}{a_2r_2}y_2(t) \\ &\quad + a_1 \int_{t-\tau}^t \frac{x_1(s)y_2(s)}{1 + mx_1(s)} ds. \end{aligned} \quad (33)$$

Calculating the derivative of $V_1(t)$ along positive solutions of system (2), it follows that

$$\begin{aligned} \dot{V}_1(t) &= \dot{x}_1(t) + \frac{r}{d_2}\dot{x}_2(t) + \frac{a_1}{a_2}\dot{y}_1(t) + \frac{a_1(r_2 + d_3)}{a_2r_2}\dot{y}_2(t) \\ &\quad + \frac{a_1x_1(t)y_2(t)}{1 + mx_1(t)} - \frac{a_1x_1(t - \tau)y_2(t - \tau)}{1 + mx_1(t - \tau)} \\ &= \frac{rr_1 - d_2(r_1 + d_1)}{d_2}x_1(t) - ax_1^2(t) \\ &\quad - \frac{a_1d_4(r_2 + d_3)}{a_2r_2}y_2(t). \end{aligned} \quad (34)$$

If $rr_1 < d_2(r_1 + d_1)$, it then follows from (34) that $\dot{V}_1(t) \leq 0$. By Theorem 5.3.1 in [10], solutions approach M , the largest invariant subset of $\{\dot{V}_1(t) = 0\}$. Clearly, we see from (34) that $\dot{V}_1(t) = 0$ if and only if $x_1(t) = 0, y_2(t) = 0$. Noting that M is invariant, for each element in M , we have $x_1(t) = 0, y_2(t) = 0$. It therefore follows from the second and fourth equations of system (2) that

$$0 = \dot{x}_1(t) = rx_2(t), \quad 0 = \dot{y}_2(t) = r_2y_1(t), \quad (35)$$

which yields $x_2(t) = 0, y_1(t) = 0$. Hence, $\dot{V}_1(t) = 0$ if and only if $(x_1(t), x_2(t), y_1(t), y_2(t)) = (0, 0, 0, 0)$. Accordingly, the global asymptotic stability of E_0 follows from LaSalle's invariant principle. This completes the proof. \square

Theorem 8. *The predator-extinction equilibrium $E_1(x_1^+, x_2^+, 0, 0)$ of system (2) is globally asymptotically stable provided that*

$$(H_4) \quad 0 < (rr_1 - d_2(r_1 + d_1))/ad_2 < d_4(r_2 + d_3)/(a_2r_2 - md_4(r_2 + d_3)).$$

Proof. Assume that $(x_1(t), x_2(t), y_1(t), y_2(t))$ is any positive solution of system (2) with initial conditions (3). By Theorem 1, we see that if (H_4) holds, then E_1 is locally asymptotically stable. System (2) can be rewritten as

$$\begin{aligned} \dot{x}_1(t) &= \frac{r}{x_1^+} [-x_2(t)(x_1(t) - x_1^+) + x_1(t)(x_2(t) - x_2^+)] \\ &\quad + x_1(t) \left[-a(x_1(t) - x_1^+) \right] - \frac{a_1 x_1(t) y_2(t)}{1 + mx_1(t)}, \\ \dot{x}_2(t) &= \frac{r_1}{x_2^+} [-x_1(t)(x_2(t) - x_2^+) + x_2(t)(x_1(t) - x_1^+)], \\ \dot{y}_1(t) &= \frac{a_2 x_1(t - \tau) y_2(t - \tau)}{1 + mx_1(t - \tau)} - (r_2 + d_3) y_1(t), \\ \dot{y}_2(t) &= r_2 y_1(t) - d_4 y_2(t). \end{aligned} \tag{36}$$

Define

$$\begin{aligned} V_{21}(t) &= x_1 - x_1^+ - x_1^+ \ln \frac{x_1}{x_1^+} + c_1 \left(x_2 - x_2^+ - x_2^+ \ln \frac{x_2}{x_2^+} \right) \\ &\quad + k_1 y_1 + k_2 y_2, \end{aligned} \tag{37}$$

where $c_1 = rx_2^+/(r_1x_1^+)$, $k_1 = a_1(1 + mx_1^+)/a_2$, and $k_2 = (r_2 + d_3)k_1/r_2$. Calculating the derivative of $V_{21}(t)$ along positive solutions of system (2), it follows that

$$\begin{aligned} \dot{V}_{21}(t) &= \frac{r(x_1(t) - x_1^+)}{x_1^+ x_1(t)} \\ &\quad \times [-x_2(t)(x_1(t) - x_1^+) + x_1(t)(x_2(t) - x_2^+)] \\ &\quad - a(x_1(t) - x_1^+)^2 - \frac{(x_1(t) - x_1^+) a_1 x_1(t) y_2(t)}{x_1(t)(1 + mx_1(t))} \\ &\quad + \frac{r(x_2(t) - x_2^+)}{x_1^+ x_2(t)} \\ &\quad \times [-x_1(t)(x_2(t) - x_2^+) + x_2(t)(x_1(t) - x_1^+)] \\ &\quad + \frac{a_2 k_1 x_1(t - \tau) y_2(t - \tau)}{1 + mx_1(t - \tau)} - k_2 d_4 y_2(t) \\ &= -\frac{r}{x_1^+} \left[\sqrt{\frac{x_2(t)}{x_1(t)}} (x_1(t) - x_1^+) - \sqrt{\frac{x_1(t)}{x_2(t)}} (x_2(t) - x_2^+) \right]^2 \\ &\quad - a(x_1(t) - x_1^+)^2 \end{aligned}$$

$$\begin{aligned} &- a_1(1 + mx_1^+) \left[\frac{x_1(t) y_2(t)}{1 + mx_1(t)} - \frac{x_1(t - \tau) y_2(t - \tau)}{1 + mx_1(t - \tau)} \right] \\ &\quad + (a_1 x_1^+ - k_2 d_4) y_2(t). \end{aligned} \tag{38}$$

Define

$$V_2(t) = V_{21}(t) + a_1(1 + mx_1^+) \int_{t-\tau}^t \frac{x_1(s) y_2(s)}{1 + mx_1(s)} ds. \tag{39}$$

We derive from (38) and (39) that

$$\begin{aligned} \dot{V}_2(t) &= -\frac{r}{x_1^+} \left[\sqrt{\frac{x_2(t)}{x_1(t)}} (x_1(t) - x_1^+) \right. \\ &\quad \left. - \sqrt{\frac{x_1(t)}{x_2(t)}} (x_2(t) - x_2^+) \right]^2 \\ &\quad - a(x_1(t) - x_1^+)^2 - (k_2 d_4 - a_1 x_1^+) y_2(t). \end{aligned} \tag{40}$$

If (H_4) holds, it then follows from (40) that $\dot{V}_2(t) \leq 0$. By Theorem 5.3.1 in [10], solutions approach M , the largest invariant subset of $\{\dot{V}_2(t) = 0\}$. Clearly, we see from (40) that $\dot{V}_2(t) = 0$ with equality if only if $x_1 = x_1^+$, $x_2 = x_2^+$, and $y_2 = 0$. It follows from the fourth equation of system (2) that $0 = \dot{y}_2(t) = r_2 y_1(t)$, which yields $y_1 = 0$. Hence, $\dot{V}_2(t) = 0$ if only if $x_1 = x_1^+$, $x_2 = x_2^+$, $y_1 = 0$, and $y_2 = 0$. Using the LaSalle invariant principle, the global asymptotic stability of E_1 follows. This completes the proof. \square

Theorem 9. *The coexistence equilibrium $E^*(x_1^*, x_2^*, y_1^*, y_2^*)$ of system (2) is globally asymptotically stable provided that*

$$(H_5) \quad \underline{x}_1 > (rr_1 - d_2(r_1 + d_1))/ad_2 - d_4(r_2 + d_3)/(a_2r_2 - md_4(r_2 + d_3)).$$

Here, \underline{x}_1 is the uniform persistency constant for x_1 satisfying $\liminf_{t \rightarrow \infty} x_1(t) \geq \underline{x}_1$.

Proof. Let $(x_1(t), x_2(t), y_1(t), y_2(t))$ be any positive solution of system (2) with initial conditions (3). Since (H_5) holds, there is a $t_1 > 0$, such that

$$x_1(t) > \frac{rr_1 - d_2(r_1 + d_1)}{ad_2} - \frac{d_4(r_2 + d_3)}{a_2r_2 - md_4(r_2 + d_3)} \tag{41}$$

for all $t \geq t_1$. Accordingly, we have

$$x_1^* > \frac{rr_1 - d_2(r_1 + d_1)}{ad_2} - \frac{d_4(r_2 + d_3)}{a_2r_2 - md_4(r_2 + d_3)}. \tag{42}$$

In this case, it is easy to show that (H_1) and (H_3) hold. By Theorem 1, E^* is locally asymptotically stable for all $\tau > 0$.

System (2) can be rewritten as

$$\begin{aligned} \dot{x}_1(t) &= \frac{r}{x_1^*} [-x_2(t)(x_1(t) - x_1^*) + x_1(t)(x_2(t) - x_2^*)] \\ &\quad + x_1(t) [-a(x_1(t) - x_1^*)] \\ &\quad + \frac{a_1 y_2^*}{1 + mx_1^*} x_1(t) - \frac{a_1 x_1(t) y_2(t)}{1 + mx_1(t)}, \\ \dot{x}_2(t) &= \frac{r_1}{x_2^*} [-x_1(t)(x_2(t) - x_2^*) + x_2(t)(x_1(t) - x_1^*)], \\ \dot{y}_1(t) &= \frac{a_2 x_1(t - \tau) y_2(t - \tau)}{1 + mx_1(t - \tau)} - (r_2 + d_3) y_1(t), \\ \dot{y}_2(t) &= r_2 y_1(t) - d_4 y_2(t). \end{aligned} \tag{43}$$

Define

$$\begin{aligned} V_{31}(t) &= x_1 - x_1^* - x_1^* \ln \frac{x_1}{x_1^*} + c_1 \left(x_2 - x_2^* - x_2^* \ln \frac{x_2}{x_2^*} \right) \\ &\quad + k_1 \left(y_1 - y_1^* - y_1^* \ln \frac{y_1}{y_1^*} \right) \\ &\quad + k_2 \left(y_2 - y_2^* - y_2^* \ln \frac{y_2}{y_2^*} \right), \end{aligned} \tag{44}$$

where $c_1 = rx_2^*/(r_1x_1^*)$, $k_1 = a_1(1 + mx_1^*)/a_2$, $k_2 = k_1(r_2 + d_3)/r_2$. Calculating the derivative of $V_{31}(t)$ along positive solutions of system (2), it follows that

$$\begin{aligned} \dot{V}_{31}(t) &= \frac{x_1(t) - x_1^*}{x_1(t)} \dot{x}_1(t) + c_1 \frac{x_2(t) - x_2^*}{x_2(t)} \dot{x}_2(t) \\ &\quad + k_1 \frac{y_1(t) - y_1^*}{y_1(t)} \dot{y}_1(t) + \frac{y_2(t) - y_2^*}{y_2(t)} \dot{y}_2(t) \\ &= \frac{r(x_1(t) - x_1^*)}{x_1^* x_1(t)} \\ &\quad \times [-x_2(t)(x_1(t) - x_1^*) + x_1(t)(x_2(t) - x_2^*)] \\ &\quad - a(x_1(t) - x_1^*)^2 + \frac{a_1 y_2^* (x_1(t) - x_1^*)}{1 + mx_1^*} \\ &\quad - \frac{a_1 y_2(t) (x_1(t) - x_1^*)}{1 + mx_1(t)} + \frac{r(x_2(t) - x_2^*)}{x_1^* x_2(t)} \\ &\quad \times [-x_1(t)(x_2(t) - x_2^*) + x_2(t)(x_1(t) - x_1^*)] \\ &\quad + \frac{a_2 k_1 (y_1(t) - y_1^*) x_1(t - \tau) y_2(t - \tau)}{y_1(t) (1 + mx_1(t - \tau))} \\ &\quad + k_2 r_2 \frac{y_1(t)}{y_2(t)} (y_2(t) - y_2^*) \\ &\quad - k_1 (r_2 + d_3) (y_1(t) - y_1^*) - k_2 d_4 (y_2(t) - y_2^*) \end{aligned}$$

$$\begin{aligned} &= -\frac{r}{x_1^*} \left[\sqrt{\frac{x_2(t)}{x_1(t)}} (x_1(t) - x_1^*) - \sqrt{\frac{x_1(t)}{x_2(t)}} (x_2(t) - x_2^*) \right]^2 \\ &\quad - a_1 (1 + mx_1^*) \frac{y_1^* x_1(t - \tau) y_2(t - \tau)}{y_1(t) (1 + mx_1(t - \tau))} \\ &\quad - a_1 (1 + mx_1^*) \frac{x_1(t) y_2(t)}{1 + mx_1(t)} \\ &\quad + a_2 k_1 \frac{x_1(t - \tau) y_2(t - \tau)}{1 + mx_1(t - \tau)} \\ &\quad + \frac{a_1 y_2^*}{1 + mx_1^*} (x_1(t) - x_1^*) - k_2 r_2 y_2^* \frac{y_1(t)}{y_2(t)} \\ &\quad - a(x_1(t) - x_1^*)^2 + k_1 (r_2 + d_3) y_1^* + k_2 d_4 y_2^*. \end{aligned} \tag{45}$$

Define

$$\begin{aligned} V_3(t) &= V_{31}(t) + a_2 k_1 \int_{t-\tau}^t \left[\frac{x_1(s) y_2(s)}{1 + mx_1(s)} - \frac{x_1^* y_2^*}{1 + mx_1^*} - \frac{x_1^* y_2^*}{1 + mx_1^*} \right. \\ &\quad \left. \times \ln \frac{(1 + mx_1^*) x_1(s) y_2(s)}{x_1^* y_2^* (1 + mx_1(s))} \right] ds. \end{aligned} \tag{46}$$

We derive from (45) and (46) that

$$\begin{aligned} \dot{V}_3(t) &= -\frac{r}{x_1^*} \left[\sqrt{\frac{x_2(t)}{x_1(t)}} (x_1(t) - x_1^*) - \sqrt{\frac{x_1(t)}{x_2(t)}} (x_2(t) - x_2^*) \right]^2 \\ &\quad - a_1 x_1^* y_2^* \left[\frac{y_2^* y_1(t)}{y_1^* y_2(t)} - 1 - \ln \frac{y_2^* y_1(t)}{y_1^* y_2(t)} \right] \\ &\quad - a_1 x_1^* y_2^* \left[\frac{y_1^* (1 + mx_1^*) x_1(t - \tau) y_2(t - \tau)}{x_1^* y_2^* y_1(t) (1 + mx_1(t - \tau))} \right. \\ &\quad \left. - 1 - \ln \frac{y_1^* (1 + mx_1^*) x_1(t - \tau) y_2(t - \tau)}{x_1^* y_2^* y_1(t) (1 + mx_1(t - \tau))} \right] \\ &\quad - a_1 x_1^* y_2^* \left[\frac{x_1^* (1 + mx_1(t))}{x_1(t) (1 + mx_1^*)} - 1 - \ln \frac{x_1^* (1 + mx_1(t))}{x_1(t) (1 + mx_1^*)} \right] \\ &\quad - (x_1(t) - x_1^*)^2 \left[a - \frac{a_1 y_2^*}{x_1(t) (1 + mx_1^*)} \right]. \end{aligned} \tag{47}$$

If (H_5) holds, for t sufficiently enough, we have $a > a_1 y_2^*/(x_1(t)(1 + mx_1^*))$. This, together with (47), implies that $\dot{V}_3(t) \leq 0$, with equality if and only if

$$\begin{aligned} x_1 &= x_1^*, \quad x_2 = x_2^*, \\ \frac{y_2^* y_1(t)}{y_1^* y_2(t)} &= \frac{y_1^* (1 + mx_1^*) x_1(t - \tau) y_2(t - \tau)}{x_1^* y_2^* y_1(t) (1 + mx_1(t - \tau))} = 1. \end{aligned} \tag{48}$$

We now look for the invariant subset M within the set

$$M = \left\{ (x_1, x_2, y_1, y_2) : x_1 = x_1^*, x_2 = x_2^*, \frac{y_2^* y_1(t)}{y_1^* y_2(t)} = \frac{y_1^* (1 + mx_1^*) x_1(t - \tau) y_2(t - \tau)}{x_1^* y_2^* y_1(t) (1 + mx_1(t - \tau))} = 1 \right\}. \quad (49)$$

Since $x_1 = x_1^*$ and $x_2 = x_2^*$ on M and consequently $0 = \dot{x}_1(t) = x_1^* [rr_1/d_2 - (r_1 + d_1) - ax_1^* - a_1 y_2(t)/(1 + mx_1^*)]$, which yields $y_2(t) = y_2^*$, it follows from the fourth equation of system (2) that $0 = \dot{y}_2(t) = r_2 y_1(t) - d_4 y_2^*$, which leads to $y_1 = y_1^*$. Hence, the only invariant set in M is $M = \{(x_1^*, x_2^*, y_1^*, y_2^*)\}$. Using the LaSalle invariant principle, the global asymptotic stability of E^* follows. This completes the proof. \square

We give an example to illustrate the result in Theorem 9.

Example 10. In (2), let $a = 160, a_1 = 5, a_2 = 3, d_1 = 1/8, d_2 = 1/4, d_3 = 1/8, d_4 = 1/8, r = 2.2, r_1 = 1, r_2 = 1,$ and $m = 1/10$. It is easy to show that $(rr_1 - d_2(r_1 + d_1))/ad_2 \approx 0.0480$ and $d_4(r_2 + d_3)/(a_2 r_2 - md_4(r_2 + d_3)) \approx 0.0471$; that is, condition (H_1) holds. Hence, system (2) has a unique coexistence equilibrium $E^*(0.0471, 0.1884, 0.0035, 0.0281)$. Hence, by Theorem 6, system (2) is permanent. From the proof of Lemma 4, we have $\limsup_{t \rightarrow \infty} y_2(t) \leq M_2 := a_2 r^2 / (4aa_1 dd_2^2) \approx 1.4520$. Hence, for $\varepsilon > 0$ sufficiently small, there is a $t_1 > 0$ such that, if $t > t_1, y_2(t) < M_2 + \varepsilon$. It follows from system (2) that, for $t > t_1,$

$$\begin{aligned} \dot{x}_1(t) &> rx_2(t) - (r_1 + d_1)x_1(t) - ax_1^2(t) \\ &\quad - a_1(M_2 + \varepsilon)x_1(t), \quad (50) \\ \dot{x}_2(t) &= r_1 x_1(t) - d_2 x_2(t), \end{aligned}$$

which yields

$$\liminf_{t \rightarrow \infty} x_1(t) \geq \frac{rr_1 - d_2(a_1 M_2 + r_1 + d_1)}{ad_2} := \underline{x}_1. \quad (51)$$

By calculation, we derive that $\underline{x}_1 \approx 0.0026$ and $(rr_1 - d_2(r_1 + d_1))/ad_2 - d_4(r_2 + d_3)/(a_2 r_2 - md_4(r_2 + d_3)) \approx 0.00087$. By Theorem 9, E^* is globally asymptotically stable. Numerical simulation illustrates this fact (see Figure 2).

5. Discussion

In this paper, we have incorporated stage structure for both the predators and the prey into a predator-prey model with time delay due to the gestation of the predator and Holling type II functional response. By using Lyapunov functionals and the LaSalle invariant principle, we have established sufficient conditions for the globally stability of each of the feasible equilibria of the system. As a result, we have shown the threshold for the permanence and extinction of the system. By Theorems 7–9, we see that (i) if $rr_1 < d_2(r_1 + d_1),$

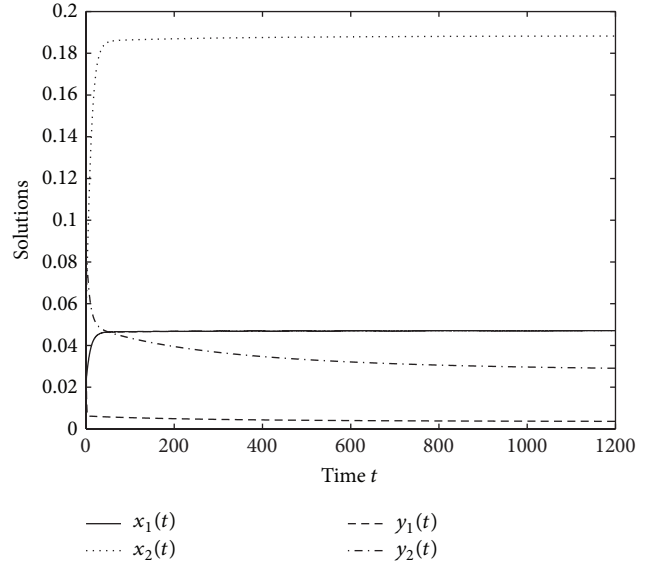


FIGURE 2: The temporal solution found by numerical integration of system (2) with $\tau = 3$.

then both the prey and the predator population go to extinction; (ii) the prey species is permanent but the predator becomes extinct if and only if $0 < (rr_1 - d_2(r_1 + d_1))/ad_2 < d_4(r_2 + d_3)/(a_2 r_2 - md_4(r_2 + d_3))$; (iii) if $x_1 > (rr_1 - d_2(r_1 + d_1))/ad_2 - d_4(r_2 + d_3)/(a_2 r_2 - md_4(r_2 + d_3))$ holds, then both the prey and predator species of system (2) are permanent.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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