

Global stability and Hopf bifurcation of a predator-prey model with stage structure and delayed predator response

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Abstract A Holling type predator-prey model with stage structure for the predator and a time delay due to the gestation of the mature predator is investigated. By analyzing the characteristic equations, the local stability of a predator-extinction equilibrium and a coexistence equilibrium of the model is addressed and the existence of Hopf bifurcations at the coexistence equilibrium is established. 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 using Lyapunov functionals and the LaSalle invariance principle, it is shown that the predator-extinction equilibrium is globally asymptotically stable when the coexistence equilibrium is not feasible, and sufficient conditions are derived for the global stability of the coexistence equilibrium. Numerical simulations are carried out to illustrate the main theoretical results.

Keywords Stage structure · Time delay · Hopf bifurcation · The LaSalle invariance principle · Global stability

1 Introduction

Predator-prey models are important in the modelling of multi-species populations interactions and have been studied by many authors (see, for example, [4, 7, 11]). It is assumed in the classical predator-prey model that each individual predator admits the same ability to prey. This assumption seems not to be realistic for many animals. In the natural world, there are many species whose individuals have a life history that takes them through two stages, immature and mature, where immature predators are raised by their parents, and the rate they attack at prey and the reproductive rate can be ignored. Stage-structured population models have received great attention in the last two decades (see, for example, [1, 6, 14, 16, 18, 19]). In order to analyze the effect of a stage structure for the predator on the dynamics of a predator-prey system, in [16], Wang considered the following stage-structured predator-prey model:

$$\begin{aligned}\dot{x}(t) &= x(t) \left(r - ax(t) - \frac{a_1 y_2(t)}{1 + mx(t)} \right), \\ \dot{y}_1(t) &= \frac{a_2 x(t) y_2(t)}{1 + mx(t)} - r_1 y_1(t) - D y_1(t), \\ \dot{y}_2(t) &= D y_1(t) - r_2 y_2(t).\end{aligned}\tag{1.1}$$

In (1.1), $x(t)$ represents the density of the prey at time t , $y_1(t)$ and $y_2(t)$ represent the densities of the immature and the mature predator at time t , respectively;

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the parameters $a, a_1, a_2, m, r, r_1, r_2$, and D are positive constants in which a is the intraspecific competition rate of the prey, r is the intrinsic growth rate of the prey, r_1 and r_2 are the death rates of the immature and the mature predator, respectively, $\frac{a_1 x}{1+mx}$ is the response function of the mature predator, a_1 is the capturing rate of the mature predator, a_2/a_1 is the rate of conversing prey into new immature predator, $D > 0$ denotes the rate of immature predator becoming mature predator. It is assumed that this rate is proportional to the density of the immature predator. Sufficient conditions were derived in [16] for the global stability of a coexistence equilibrium of system (1.1) by using a general Lyapunov function and Razumikhin-type theorem. In [18], Xiao and Chen further considered system (1.1) and sufficient conditions were obtained for the global asymptotic stability of the coexistence equilibrium of system (1.1) by using the theory of competitive systems, compound matrices and stability of periodic orbits, and the work of Wang [16] was therefore improved. In [6], Georgescu and Hsieh further studied the global dynamics of system (1.1). By constructing a suitable Lyapunov function and using the LaSalle invariance principle, the global asymptotic stability of the coexistence equilibrium of system (1.1) is derived under weaker hypotheses than those used in Xiao and Chen [18].

Time delays of one type or another have been incorporated into biological models by many researchers; we refer to the monographs of Cushing [5], Gopalsamy [8], Kuang [12], and MacDonald [13] for general delayed biological systems and to Bartlett [2], Beretta and Kuang [3], and Wangersky and Cunningham [17], and references cited therein for studies on delayed predator-prey systems. In general, delay differential equations exhibit much more complicated dynamics than ordinary differential equations since a time delay could cause a stable equilibrium to become unstable and cause the population to fluctuate. 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. Therefore, more realistic models of population interactions should take into account the effect of time delays.

Motivated by the work of Georgescu and Hsieh [6], Wang [16], Wangersky and Cunningham [17], and Xiao and Chen [18], in the present paper, we are concerned with the combined effect of stage structure for

the predator and time delay due to the gestation of mature predator on the global dynamics of a predator-prey model with Holling type functional response. To this end, we consider the following delay differential system:

$$\begin{aligned} \dot{x}(t) &= x(t) \left(r - ax(t) - \frac{a_1 y_2(t)}{1 + mx(t)} \right), \\ \dot{y}_1(t) &= \frac{a_2 x(t - \tau) y_2(t - \tau)}{1 + mx(t - \tau)} - r_1 y_1(t) \\ &\quad - D y_1(t), \\ \dot{y}_2(t) &= D y_1(t) - r_2 y_2(t). \end{aligned} \tag{1.2}$$

In system (1.2), $x(t)$ represents the density of the prey at time t , $y_1(t)$ and $y_2(t)$ represent the densities of the immature and the mature predator at time t , respectively; the parameters a, a_1, a_2, r, r_1, r_2 , and D are defined as in model (1.1). The constant $\tau \geq 0$ denotes the time delay due to the gestation of the mature predator, that is, mature adult predators can only contribute to the reproduction of the predator biomass. This is based on the assumption that the change rate of predators depends on the number of prey and of mature predators present at some previous time.

The initial conditions for system (1.2) take the form

$$\begin{aligned} x(\theta) &= \phi(\theta), & y_1(\theta) &= \psi_1(\theta), \\ y_2(\theta) &= \psi_2(\theta), \\ \phi(\theta) &\geq 0, & \psi_1(\theta) &\geq 0, & \psi_2(\theta) &\geq 0, \\ \theta &\in [-\tau, 0), \\ \phi(0) &> 0, & \psi_1(0) &> 0, & \psi_2(0) &> 0, \end{aligned} \tag{1.3}$$

where $(\phi(\theta), \psi_1(\theta), \psi_2(\theta)) \in C([-\tau, 0], \mathbb{R}_{+0}^3)$, the Banach space of continuous functions mapping the interval $[-\tau, 0]$ into \mathbb{R}_{+0}^3 , where $\mathbb{R}_{+0}^3 = \{(x_1, x_2, x_3) : x_i \geq 0, i = 1, 2, 3\}$.

It is well known by the fundamental theory of functional differential equations [9], system (1.2) has a unique solution $(x(t), y_1(t), y_2(t))$ satisfying initial conditions (1.3). It is easy to show that all solutions of system (1.2) corresponding to initial conditions (1.3) 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, by analyzing the corresponding characteristic equations, the local stability of a predator-extinction equilibrium and a coexistence equilibrium

of system (1.2) is discussed and the existence of Hopf bifurcations at the coexistence equilibrium is established. In Sect. 3, by means of the persistence theory on infinite dimensional systems, we prove that system (1.2) is permanent when the coexistence equilibrium exists. In Sect. 4, by using Lyapunov functionals and the LaSalle invariance principle, we show 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 (1.2). A brief remark is given in Sect. 5 to conclude this work.

2 Local stability and Hopf bifurcation

In this section, we study the local stability of each of feasible equilibria of system (1.2) and the existence of Hopf bifurcations at the coexistence equilibrium.

System (1.2) always has a trivial equilibrium $E_0(0, 0, 0)$ and a predator-extinction equilibrium $E_1(r/a, 0, 0)$. Further, if the following holds:

$$(H1) \quad a_2rD > r_2(a + mr)(D + r_1),$$

then system (1.2) has a unique coexistence equilibrium $E^*(x^*, y_1^*, y_2^*)$, where

$$\begin{aligned} x^* &= \frac{r_2(D + r_1)}{a_2D - mr_2(D + r_1)}, & y_1^* &= \frac{r_2}{D}y_2^*, \\ y_2^* &= \frac{a_2D[a_2rD - r_2(a + mr)(D + r_1)]}{a_1[a_2D - mr_2(D + r_1)]^2}. \end{aligned} \tag{2.1}$$

It is easy to show that the trivial equilibrium $E_0(0, 0, 0)$ is always unstable.

The characteristic equation of system (1.2) at the predator-extinction equilibrium E_1 takes the form

$$(\lambda + r)[\lambda^2 + P_1\lambda + P_0 + Q_0e^{-\lambda\tau}] = 0, \tag{2.2}$$

where

$$P_0 = r_2(D + r_1), \quad P_1 = D + r_1 + r_2, \tag{2.3}$$

$$Q_0 = -\frac{a_2rD}{a + mr}.$$

Clearly, (2.2) has a negative real root $\lambda = -r$, other roots are determined by the following equation:

$$\lambda^2 + P_1\lambda + P_0 + Q_0e^{-\lambda\tau} = 0. \tag{2.4}$$

Let

$$f(\lambda) = \lambda^2 + P_1\lambda + P_0 + Q_0e^{-\lambda\tau}.$$

If (H1) holds, it is easy to show that, for λ real,

$$f(0) = -\frac{a_2rD - r_2(a + mr)(D + r_1)}{a + mr} < 0,$$

$$\lim_{\lambda \rightarrow +\infty} f(\lambda) = +\infty.$$

Hence, $f(\lambda) = 0$ has at least one positive real root. Therefore, if (H1) holds, the equilibrium E_1 is unstable.

If $a_2rD < r_2(a + mr)(D + r_1)$, it is readily seen from (2.4) that E_1 is locally asymptotically stable when $\tau = 0$. In this case, it is easy to show that

$$P_1^2 - 2P_0 = (D + r_1)^2 + r_2^2 > 0,$$

$$\begin{aligned} P_0^2 - Q_0^2 &= \left[r_2(D + r_1) + \frac{a_2rD}{a + mr} \right] \\ &\times \left[r_2(D + r_1) - \frac{a_2rD}{a + mr} \right] > 0. \end{aligned}$$

By Theorem 3.4.1 in Kuang [12], we see that if $a_2rD < r_2(a + mr)(D + r_1)$, E_1 is locally asymptotically stable for all $\tau \geq 0$.

The characteristic equation of system (1.2) at the coexistence equilibrium E^* is of the form

$$\lambda^3 + p_2\lambda^2 + p_1\lambda + p_0 + (q_1\lambda + q_0)e^{-\lambda\tau} = 0, \tag{2.5}$$

where

$$p_0 = \frac{r_2x^*}{1 + mx^*}(D + r_1)(a - mr + 2amx^*),$$

$$\begin{aligned} p_1 &= r_2(D + r_1) + \frac{x^*}{1 + mx^*}(D + r_1 + r_2) \\ &\times (a - mr + 2amx^*), \end{aligned}$$

$$p_2 = D + r_1 + r_2 + \frac{x^*}{1 + mx^*} \tag{2.6}$$

$$\times (a - mr + 2amx^*),$$

$$q_0 = -r_2(D + r_1)(-r + 2ax^*),$$

$$q_1 = -r_2(D + r_1).$$

When $\tau = 0$, (2.5) becomes

$$\lambda^3 + p_2\lambda^2 + (p_1 + q_1)\lambda + p_0 + q_0 = 0. \tag{2.7}$$

It is easy to show that

$$p_0 + q_0 = \frac{a_1 r_2 (D + r_1) y_2^*}{(1 + m x^*)^2},$$

$$p_1 + q_1 = (D + r_1 + r_2) \frac{x^* (a - m r + 2 a m x^*)}{1 + m x^*}.$$

Hence, by the Routh–Hurwitz theorem, the equilibrium E^* of system (1.2) is locally asymptotically stable when $\tau = 0$ if the following holds:

$$(H2) \quad x^* (D + r_1 + r_2) (a - m r + 2 a m x^*) \times \left[\frac{x^* (a - m r + 2 a m x^*)}{1 + m x^*} + D + r_1 + r_2 \right] > \frac{a_1 r_2 (D + r_1) y_2^*}{1 + m x^*},$$

and E^* is unstable if the inequality in (H2) is reversed.

If $i\omega$ ($\omega > 0$) is a solution of (2.5), separating real and imaginary parts, we have

$$-\omega^3 + p_1 \omega = q_0 \sin \omega \tau - q_1 \omega \cos \omega \tau, \tag{2.8}$$

$$p_2 \omega^2 - p_0 = q_0 \cos \omega \tau + q_1 \omega \sin \omega \tau.$$

Squaring and adding the two equations of (2.8), it follows that

$$\omega^6 + (p_2^2 - 2p_1)\omega^4 + (p_1^2 - 2p_0p_2 - q_1^2)\omega^2 + p_0^2 - q_0^2 = 0. \tag{2.9}$$

It is easy to show that

$$p_2^2 - 2p_1 = \frac{x^{*2} (a - m r + 2 a m x^*)^2}{(1 + m x^*)^2} + (D + r_1)^2 + r_2^2,$$

$$p_1^2 - 2p_0p_2 - q_1^2 = \frac{x^{*2} (a - m r + 2 a m x^*)^2}{(1 + m x^*)^2} \times [(D + r_1)^2 + r_2^2],$$

$$p_0 - q_0 = \frac{r_2 (D + r_1)}{1 + m x^*} \times [r - a x^* + 2(2 a x^* - r)(1 + m x^*)].$$

Hence, if $p_0 > q_0$, (2.9) has no positive real roots. Accordingly, if (H2) and $p_0 > q_0$ hold, then the equilibrium E^* is locally asymptotically stable for all $\tau \geq 0$. If $p_0 < q_0$, then (2.9) has a unique positive root ω_0 ,

that is, (2.5) has a pair of purely imaginary roots of the form $\pm i\omega_0$. Denote

$$\tau_{0n} = \frac{1}{\omega_0} \arccos \frac{q_0 (p_2 \omega_0^2 - p_0) + q_1 \omega_0 (\omega_0^3 - p_1 \omega_0)}{q_0^2 + q_1^2 \omega_0^2} + \frac{2n\pi}{\omega_0}, \quad n = 0, 1, 2, \dots$$

Noting that if (H2) holds, E^* is locally stable when $\tau = 0$, by the general theory on characteristic equations of delay differential equations from [12] (Theorem 3.4.1), E^* remains stable for $\tau < \tau_0$, where $\tau_0 = \tau_{00}$.

We now claim that

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

This will show 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 [9] are then satisfied yielding a periodic solution. To this end, differentiating (2.5) with respect τ , it follows that

$$(3\lambda^2 + 2p_2\lambda + p_1) \frac{d\lambda}{d\tau} + q_1 e^{-\lambda\tau} \frac{d\lambda}{d\tau} - \tau (q_1\lambda + q_0) e^{-\lambda\tau} \frac{d\lambda}{d\tau} = \lambda (q_1\lambda + q_0) e^{-\lambda\tau},$$

which yields

$$\left(\frac{d\lambda}{d\tau} \right)^{-1} = \frac{3\lambda^2 + 2p_2\lambda + p_1}{-\lambda(\lambda^3 + p_2\lambda^2 + p_1\lambda + p_0)} + \frac{q_1}{\lambda(q_1\lambda + q_0)} - \frac{\tau}{\lambda}.$$

Hence, a direct calculation shows that

$$\operatorname{sgn} \left\{ \frac{d(\operatorname{Re} \lambda)}{d\tau} \right\}_{\lambda=i\omega_0} = \operatorname{sgn} \left\{ \operatorname{Re} \left(\frac{d\lambda}{d\tau} \right)^{-1} \right\}_{\lambda=i\omega_0} = \operatorname{sgn} \left\{ - \frac{(p_1 - 3\omega_0^2)(\omega_0^2 - p_1) + 2p_2(p_0 - p_2\omega_0^2)}{(\omega_0^3 - p_1\omega_0)^2 + (p_0 - p_2\omega_0^2)^2} - \frac{q_1^2}{q_0^2 + q_1^2\omega_0^2} \right\}.$$

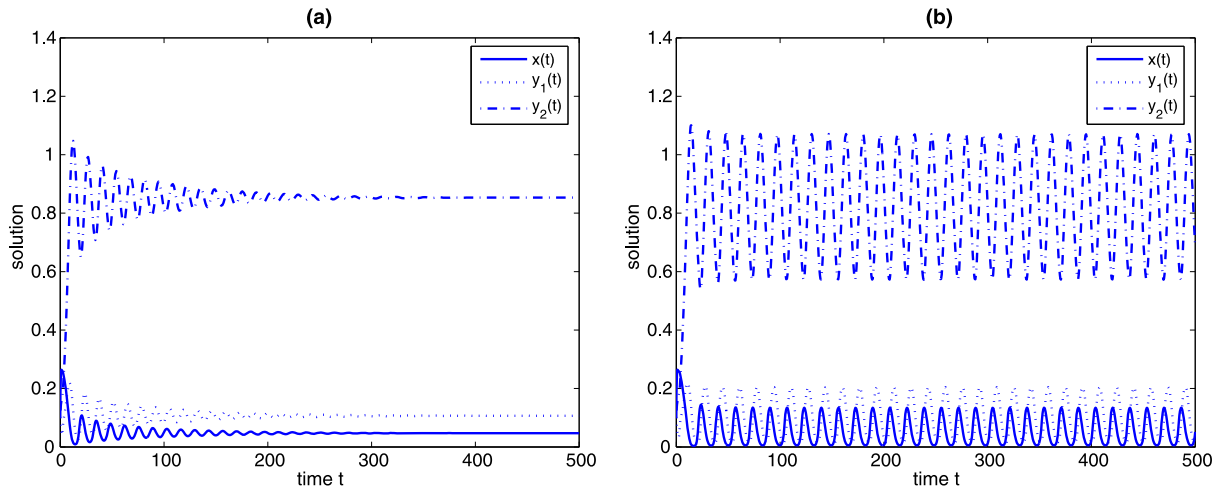


Fig. 1 The temporal solution found by numerical integration of system (1.2) with $r = 5, a = 16, a_1 = 5, a_2 = 3, D = 1, m = 1/10, r_1 = r_2 = 1/8$, (a) $\tau = 1.5$, (b) $\tau = 2.3$; $(\phi, \psi_1, \psi_2) \equiv (0.1, 0.1, 0.1)$

It follows from (2.8) that

$$(\omega_0^3 - p_1\omega_0)^2 + (p_0 - p_2\omega_0^2)^2 = q_0^2 + q_1^2\omega_0^2.$$

Hence, we derive that

$$\begin{aligned} & \operatorname{sgn} \left\{ \frac{d(\operatorname{Re} \lambda)}{d\tau} \right\}_{\lambda=i\omega_0} \\ &= \operatorname{sgn} \left\{ \frac{3\omega_0^4 + 2(p_2^2 - 2p_1)\omega_0^2 + p_1^2 - 2p_0p_2 - q_1^2}{q_0^2 + q_1^2\omega_0^2} \right\} \\ &> 0. \end{aligned}$$

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

We conclude the discussions above as follows.

Theorem 2.1 For system (1.2), we have the following:

- (i) The equilibrium $E_0(0, 0, 0)$ is always unstable.
- (ii) If $a_2rD < r_2(a + mr)(D + r_1)$, then the predator-extinction equilibrium $E_1(r/a, 0, 0)$ is locally asymptotically stable; if $a_2rD > r_2(a + mr) \times (D + r_1)$, then E_1 is unstable.
- (iii) Let (H1) and (H2) hold. If $ax^* + (2ax^* - r) \times (1 + 2mx^*) > 0$, then the coexistence equilibrium $E^*(x^*, y_1^*, y_2^*)$ is locally asymptotically stable for all $\tau \geq 0$; if $ax^* + (2ax^* - r)(1 + 2mx^*) < 0$, 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 (1.2) undergoes a Hopf bifurcation at E^* when $\tau = \tau_0$.

We now give an example to illustrate the result in Theorem 2.1.

Example 1 In (1.2), let $r = 5, a = 16, a_1 = 5, a_2 = 3, D = 1, r_1 = r_2 = 1/8, m = 1/10$. It is easy to show that system (1.2) has a unique coexistence equilibrium $E^*(0.0471, 0.1067, 0.8533)$. By calculation, we have $p_0 - q_0 \approx -0.3880 < 0, p_2(p_1 + q_1) - (p_0 + q_0) \approx 1.2247, \tau_0 \approx 1.6856$. By Theorem 2.1, E^* is locally asymptotically stable if $0 < \tau < \tau_0$ and is unstable if $\tau > \tau_0$, and system (1.2) undergoes a Hopf bifurcation at E^* when $\tau = \tau_0$. Numerical simulation illustrates this fact (see Fig. 1).

3 Permanence

In this section, we are concerned with the permanence of system (1.2).

Definition 3.1 System (1.2) is said to be permanent (uniformly persistent) if there are positive constants m_1, m_2, M_1 , and M_2 such that each positive solution $(x(t), y_1(t), y_2(t))$ of system (1.2) satisfies

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

In order to study the permanence of system (1.2), we refer to the persistence theory on infinite dimensional systems developed by Hale and Waltman in [10].

Let X be a complete metric space with metric d . Suppose that T is a continuous semiflow on X , i.e., a continuous mapping $T : [0, \infty) \times X \rightarrow X$ with the following properties:

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

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 $\gamma^+(x)$ through x is defined as $\gamma^+(x) = \bigcup_{t \geq 0} \{T(t)x\}$, and its ω -limit set is $\omega(x) = \bigcap_{s \geq 0} \overline{\bigcup_{t \geq s} \{T(t)x\}}$. Define $W^s(A)$ the strong stable set of a compact invariant set A as

$$W^s(A) = \{x : x \in X, \omega(x) \neq \emptyset, \omega(x) \subset A\}.$$

(C1) 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

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

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

Lemma 3.1 (Hale & Waltman [10]) *Suppose that $T(t)$ satisfies (C1) 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) *\hat{A}_b is isolated and has an acyclic covering \hat{M} , where*

$$\hat{M} = \{\tilde{M}_1, \tilde{M}_2, \dots, \tilde{M}_n\};$$

- (iv) *$W^s(\tilde{M}_i) \cap X^0 = \emptyset$ 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 $x \in X^0$, $\liminf_{t \rightarrow +\infty} d(T(t)x, X_0) \geq \varepsilon$.

Lemma 3.2 *There are positive constants M_1 and M_2 such that for any positive solution $(x(t), y_1(t), y_2(t))$*

of system (1.2),

$$\begin{aligned} \limsup_{t \rightarrow +\infty} x(t) &< M_1, & \limsup_{t \rightarrow +\infty} y_1(t) &< M_2, \\ \limsup_{t \rightarrow +\infty} y_2(t) &< M_2. \end{aligned} \tag{3.1}$$

Proof Let $(x(t), y_1(t), y_2(t))$ be any positive solution of system (1.2) with initial conditions (1.3). Denote $r_0 = \min\{r_1, r_2\}$. Define

$$V(t) = \frac{a_2}{a_1}x(t - \tau) + y_1(t) + y_2(t).$$

Calculating the derivative of $V(t)$ along positive solutions of system (1.2), it follows that

$$\begin{aligned} \frac{d}{dt}V(t) &= \frac{a_2}{a_1}x(t - \tau)(r - ax(t - \tau)) \\ &\quad - r_1y_1(t) - r_2y_2(t) \\ &= -r_0x(t) - r_1y_1(t) - r_2y_2(t) \\ &\quad + \frac{a_2}{a_1}x(t - \tau)(r + r_0 - ax(t - \tau)) \\ &\leq -r_0V(t) + \frac{a_2(r + r_0)^2}{4aa_1}, \end{aligned}$$

which yields

$$\limsup_{t \rightarrow +\infty} V(t) \leq \frac{a_2(r + r_0)^2}{4aa_1r_0}.$$

Letting $M_1 = (r + r_0)^2/(4ar_0), M_2 = a_2(r + r_0)^2/(4aa_1r_0)$, then (3.1) follows. This completes the proof. \square

We are now able to state and prove the result on the permanence of system (1.2).

Theorem 3.1 *If (H1) holds, then system (1.2) is permanent.*

Proof We need only to show that the boundaries of \mathbb{R}^3_{+0} repel positive solutions of system (1.2) uniformly.

Let $C^+([-\tau, 0], \mathbb{R}^3_{+0})$ denote the space of continuous functions mapping $[-\tau, 0]$ into \mathbb{R}^3_{+0} . Define

$$C_1 = \{(\phi, \psi_1, \psi_2) \in C^+([-\tau, 0], \mathbb{R}^3_{+0}) : \phi(\theta) \equiv 0, \theta \in [-\tau, 0]\},$$

$$C_2 = \{(\phi, \psi_1, \psi_2) \in C^+([-\tau, 0], \mathbb{R}^3_{+0}) : \phi(\theta) > 0, \psi_i(\theta) \equiv 0, \theta \in [-\tau, 0], i = 1, 2\}.$$

Denote $C_0 = C_1 \cup C_2$, $X = C^+([-\tau, 0], \mathbb{R}_{+0}^3)$ and $C^0 = \text{int}C^+([-\tau, 0], \mathbb{R}_{+0}^3)$.

In the following, we show that the conditions in Lemma 3.1 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 3.1 are clearly satisfied. Thus, we need only to show that the conditions (iii) and (iv) hold. Clearly, corresponding to $x(t) = y_1(t) = y_2(t) = 0$ and $x(t) = r/a$, $y_1(t) = y_2(t) = 0$, respectively, there are two constant solutions in C_0 : $\tilde{E}_0 \in C_1$, $\tilde{E}_1 \in C_2$ satisfying

$$\begin{aligned} \tilde{E}_0 &= \{(\phi, \psi_1, \psi_2) \in ([-\tau, 0], \mathbb{R}_{+0}^3) : \\ &\quad \phi(\theta) \equiv 0, \psi_1(\theta) \equiv 0, \psi_2(\theta) \equiv 0, \theta \in [-\tau, 0]\}, \\ \tilde{E}_1 &= \{(\phi, \psi_1, \psi_2) \in ([-\tau, 0], \mathbb{R}_{+0}^3) : \phi(\theta) \equiv r/a, \\ &\quad \psi_1(\theta) \equiv 0, \psi_2(\theta) \equiv 0, \theta \in [-\tau, 0]\}. \end{aligned}$$

We now verify the condition (iii) of Lemma 3.1. If $(x(t), y_1(t), y_2(t))$ is a solution of system (1.2) initiating from C_1 , then $\dot{y}_1(t) = -(D + r_1)y_1(t)$, $\dot{y}_2(t) = Dy_1(t) - r_2y_2(t)$, which yields $y_1(t) \rightarrow 0$, $y_2(t) \rightarrow 0$ as $t \rightarrow +\infty$. If $(x(t), y_1(t), y_2(t))$ is a solution of system (1.2) initiating from C_2 with $\phi(0) > 0$, then it follows from the first equation of system (1.2) that $\dot{x}(t) = x(t)(r - ax(t))$ which yields $x(t) \rightarrow r/a$ as $t \rightarrow +\infty$. Noting that $C_1 \cap C_2 = \phi$, 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 3.1.

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

Since (H1) holds, we can choose $\varepsilon > 0$ sufficiently small such that

$$\frac{a_2D(r/a - \varepsilon)}{1 + m(r/a - \varepsilon)} > r_2(D + r_1). \tag{3.2}$$

Since $\lim_{t \rightarrow +\infty} x(t) = r/a$, for $\varepsilon > 0$ sufficiently small satisfying (3.2), there is a $t_0 > 0$ such that, if $t > t_0$,

$$\frac{r}{a} - \varepsilon < x(t) < \frac{r}{a} + \varepsilon.$$

For $\varepsilon > 0$ sufficiently small satisfying (3.2), it follows from the second and the third equations of system (1.2)

that, for $t > t_0 + \tau$,

$$\begin{aligned} \dot{y}_1(t) &\geq \frac{a_2D(r/a - \varepsilon)}{1 + m(r/a - \varepsilon)}y_2(t - \tau) \\ &\quad - (D + r_1)y_1(t), \end{aligned} \tag{3.3}$$

$$\dot{y}_2(t) = Dy_1(t) - r_2y_2(t).$$

Consider the following auxiliary equations:

$$\begin{aligned} \dot{u}_1(t) &= \frac{a_2D(r/a - \varepsilon)}{1 + m(r/a - \varepsilon)}u_2(t - \tau) \\ &\quad - (D + r_1)u_1(t), \end{aligned} \tag{3.4}$$

$$\dot{u}_2(t) = Du_1(t) - r_2u_2(t),$$

with initial conditions (1.3).

Define

$$A_\varepsilon = \begin{pmatrix} -(D + r_1) & \frac{a_2D(r/a - \varepsilon)}{1 + m(r/a - \varepsilon)} \\ D & -r_2 \end{pmatrix}.$$

Since A_ε has positive off-diagonal elements, by the Perron–Frobenius theorem, there is a positive eigenvector v for the maximum eigenvalue α of A_ε . Noting that (3.2) holds, a direct calculation shows that $\alpha > 0$. Using a similar argument as that in the proof of Theorem 2.1 in [15], one can show that $\lim_{t \rightarrow +\infty} u_i(t) = +\infty (i = 1, 2)$. By comparison, it follows that $\lim_{t \rightarrow +\infty} y_i(t) = +\infty (i = 1, 2)$. This contradicts Lemma 3.2. Hence, we have $W^s(\tilde{E}_1) \cap C^0 = \phi$. By Lemma 3.1, we conclude that C_0 repels positive solutions of system (1.2) uniformly. Therefore, system (1.2) is permanent. The proof is complete. \square

4 Global stability

In this section, we study the global stability of the predator-extinction equilibrium E_1 and the coexistence equilibrium E^* of system (1.2), respectively. The strategy of proofs is to use Lyapunov functionals and the LaSalle invariance principle.

Theorem 4.1 *If $a_2rD < r_2(a + mr)(D + r_1)$, then the predator-extinction equilibrium $E_1(r/a, 0, 0)$ of system (1.2) is globally asymptotically stable.*

Proof Let $(x(t), y_1(t), y_2(t))$ be any positive solution of system (1.2) with initial conditions (1.3). Denote $x_0 = r/a$.

Define

$$V_{11}(t) = x - x_0 - x_0 \ln \frac{x}{x_0} + c_1 y_1 + c_2 y_2, \tag{4.1}$$

where $c_1 = a_1(1 + mx_0)/a_2$, $c_2 = c_1(D + r_1)/D$.

Calculating the derivative of $V_{11}(t)$ along positive solutions of system (1.2), it follows that

$$\begin{aligned} \frac{d}{dt} V_{11}(t) &= \left(1 - \frac{x_0}{x}\right) \left[x(t)(r - ax(t)) \right. \\ &\quad \left. - \frac{a_1 x(t) y_2(t)}{1 + mx(t)} \right] \\ &\quad + c_1 \left[\frac{a_2 x(t - \tau) y_2(t - \tau)}{1 + mx(t - \tau)} \right. \\ &\quad \left. - r_1 y_1(t) - D y_1(t) \right] \\ &\quad + c_2 [D y_1 - r_2 y_2]. \end{aligned} \tag{4.2}$$

On substituting $r = ax_0$ into (4.2), we obtain that

$$\begin{aligned} \frac{d}{dt} V_{11}(t) &= \left(1 - \frac{x_0}{x}\right) \left[-ax(t)(x(t) - x_0) \right. \\ &\quad \left. - \frac{a_1 x(t) y_2(t)}{1 + mx(t)} \right] \\ &\quad + c_1 \left[\frac{a_2 x(t - \tau) y_2(t - \tau)}{1 + mx(t - \tau)} \right. \\ &\quad \left. - r_1 y_1(t) - D y_1(t) \right] \\ &\quad + c_2 [D y_1(t) - r_2 y_2(t)] \\ &= -a(x(t) - x_0)^2 - a_1(1 + mx_0) \\ &\quad \times \frac{x(t) y_2(t)}{1 + mx(t)} + c_1 a_2 \frac{x(t - \tau) y_2(t - \tau)}{1 + mx(t - \tau)} \\ &\quad + \frac{a_1}{aa_2 D} [a_2 r D - r_2(D + r_1) \\ &\quad \times (a + mr)] y_2(t). \end{aligned} \tag{4.3}$$

Define

$$V_1(t) = V_{11}(t) + c_1 a_2 \int_{t-\tau}^t \frac{x(s) y_2(s)}{1 + mx(s)} ds. \tag{4.4}$$

We derive from (4.3) and (4.4) that

$$\frac{d}{dt} V_1(t) = -a(x(t) - x_0)^2$$

$$\begin{aligned} &+ \frac{a_1}{aa_2 D} [a_2 r D - r_2(D + r_1) \\ &\quad \times (a + mr)] y_2(t). \end{aligned} \tag{4.5}$$

If $a_2 r D < r_2(a + mr)(D + r_1)$, it then follows from (4.5) that $V_1'(t) \leq 0$. By Theorem 5.3.1 in [9], solutions limit to \mathcal{M} , the largest invariant subset of $\{V_1'(t) = 0\}$. Clearly, we see from (4.5) that $V_1'(t) = 0$ if and only if $x = x_0, y_2 = 0$. Noting that \mathcal{M} is invariant, for each element in \mathcal{M} , we have $x(t) = x_0, y_2(t) = 0$. It therefore follows from the third equation of system (1.2) that

$$0 = \dot{y}_2(t) = D y_1(t),$$

which yields $y_1(t) = 0$. Hence, $V_1'(t) = 0$ if and only if $(x, y_1, y_2) = (x_0, 0, 0)$. Accordingly, the global asymptotic stability of E_1 follows from LaSalle's invariance principle. This completes the proof. \square

We are now in a position to state and prove our result on the global asymptotic stability of the coexistence equilibrium $E^*(x^*, y_1^*, y_2^*)$ of system (1.2).

Theorem 4.2 *Let (H1) hold. Then the coexistence equilibrium $E^*(x^*, y_1^*, y_2^*)$ of system (1.2) is globally asymptotically stable provided that*

$$(H3) \quad \underline{x} > r/(2a).$$

Here, $\underline{x} > 0$ is the persistency constant for x satisfying $\liminf_{t \rightarrow +\infty} x(t) \geq \underline{x}$.

Proof Assume that $(x(t), y_1(t), y_2(t))$ is any positive solution of system (1.2) with initial conditions (1.3). Since $\underline{x} > r/(2a)$, it is seen that there is a $T > 0$ such that $x(t) > r/(2a)$ for all $t \geq T$ and also that $x^* > r/(2a)$. Consequently, by Theorem 2.1, E^* is locally asymptotically stable for all $\tau \geq 0$.

Define

$$\begin{aligned} V_{21}(t) &= x - x^* - x^* \ln \frac{x}{x^*} \\ &\quad + k_1 \left(y_1 - y_1^* - y_1^* \ln \frac{y_1}{y_1^*} \right) \\ &\quad + k_2 \left(y_2 - y_2^* - y_2^* \ln \frac{y_2}{y_2^*} \right), \end{aligned} \tag{4.6}$$

where $k_1 = a_1(1 + mx^*)/a_2$, $k_2 = k_1(D + r_1)/D$. Calculating the derivative of $V_{21}(t)$ along positive solu-

tions of system (1.2), it follows that

$$\begin{aligned} \frac{d}{dt} V_{21}(t) = & \left(1 - \frac{x^*}{x}\right) \left[x(t)(r - ax(t)) \right. \\ & \left. - \frac{a_1 x(t)y_2(t)}{1 + mx(t)} \right] \\ & + k_1 \left(1 - \frac{y_1^*}{y_1}\right) \left[\frac{a_2 x(t - \tau)y_2(t - \tau)}{1 + mx(t - \tau)} \right. \\ & \left. - r_1 y_1(t) - Dy_1(t) \right] \\ & + k_2 \left(1 - \frac{y_2^*}{y_2}\right) [Dy_1(t) - r_2 y_2(t)]. \end{aligned} \tag{4.7}$$

On substituting $r = ax^* + a_1 y_2^*/(1 + mx^*)$ into (4.7), we derive that

$$\begin{aligned} \frac{d}{dt} V_{21}(t) = & \left(1 - \frac{x^*}{x}\right) \left[x(r - ax) - x^*(r - ax^*) \right. \\ & \left. + \frac{a_1 x^* y_2^*}{1 + mx^*} \right] \\ & - a_1 \left[1 + mx^* - \frac{x^*(1 + mx)}{x} \right] \\ & \times \frac{x(t)y_2(t)}{1 + mx(t)} \\ & + k_1 \left(1 - \frac{y_1^*}{y_1}\right) \left[\frac{a_2 x(t - \tau)y_2(t - \tau)}{1 + mx(t - \tau)} \right. \\ & \left. - r_1 y_1(t) - Dy_1(t) \right] \\ & + k_2 \left(1 - \frac{y_2^*}{y_2}\right) [Dy_1(t) - r_2 y_2(t)] \\ = & \left(1 - \frac{x^*}{x}\right) \left[x(r - ax) - x^*(r - ax^*) \right. \\ & \left. + \frac{a_1 x^* y_2^*}{1 + mx^*} \right] \\ & - a_1 (1 + mx^*) \frac{x(t)y_2(t)}{1 + mx(t)} \\ & + k_1 a_2 \frac{x(t - \tau)y_2(t - \tau)}{1 + mx(t - \tau)} \\ & - k_1 a_2 \frac{y_1^* x(t - \tau)y_2(t - \tau)}{y_1(t)(1 + mx(t - \tau))} \end{aligned}$$

$$\begin{aligned} & + k_1 (D + r_1) y_1^* \\ & - k_2 D y_1^* \frac{y_2^* y_1(t)}{y_1^* y_2(t)} + k_2 r_2 y_2^*. \end{aligned} \tag{4.8}$$

Define

$$\begin{aligned} V_2(t) = & V_{21}(t) + k_1 a_2 \int_{t-\tau}^t \left[\frac{x(s)y_2(s)}{1 + mx(s)} \right. \\ & \left. - \frac{x^* y_2^*}{1 + mx^*} - \frac{x^* y_2^*}{1 + mx^*} \right. \\ & \left. \times \ln \frac{(1 + mx^*)x(s)y_2(s)}{x^* y_2^* (1 + mx(s))} \right] ds. \end{aligned} \tag{4.9}$$

It follows from (4.8) and (4.9) that

$$\begin{aligned} \frac{d}{dt} V_2(t) = & \left(1 - \frac{x^*}{x}\right) \left[x(r - ax) - x^*(r - ax^*) \right. \\ & \left. + \frac{a_1 x^* y_2^*}{1 + mx^*} \right] - k_1 a_2 \\ & \times \frac{x^* y_2^* y_1^* (1 + mx^*) x(t - \tau) y_2(t - \tau)}{1 + mx^* x^* y_2^* y_1(t) (1 + mx(t - \tau))} \\ & + k_1 (D + r_1) y_1^* - k_2 D y_1^* \frac{y_2^* y_1(t)}{y_1^* y_2(t)} \\ & + k_2 r_2 y_2^* + k_1 a_2 \frac{x^* y_2^*}{1 + mx^*} \\ & \times \ln \frac{(1 + mx(t))x(t - \tau)y_2(t - \tau)}{x(t)y_2(t)(1 + mx(t - \tau))}. \end{aligned} \tag{4.10}$$

Noting that

$$\begin{aligned} k_2 r_2 y_2^* = & k_2 D y_1^* = k_1 (D + r_1) y_1^* \\ = & k_1 a_2 \frac{x^* y_2^*}{1 + mx^*} = a_1 x^* y_2^*, \end{aligned}$$

and

$$\frac{a_1 x^* y_2^*}{1 + mx^*} \left(1 - \frac{x^*}{x}\right) = a_1 x^* y_2^* \left(1 - \frac{x^*(1 + mx)}{(1 + mx^*)x}\right),$$

we derive from (4.10) that

$$\begin{aligned} \frac{d}{dt} V_2(t) = & \frac{(x - x^*)^2}{x} [r - a(x + x^*)] \\ & - a_1 x^* y_2^* \left[\frac{x^*(1 + mx)}{(1 + mx^*)x} - 1 \right. \\ & \left. - \ln \frac{x^*(1 + mx)}{(1 + mx^*)x} \right] \end{aligned}$$

$$\begin{aligned}
 & -a_1x^*y_2^*\left[\frac{y_2^*y_1(t)}{y_1^*y_2(t)} - 1 - \ln \frac{y_2^*y_1(t)}{y_1^*y_2(t)}\right] \\
 & -a_1x^*y_2^*\left[\frac{y_1^*(1+mx^*)x(t-\tau)y_2(t-\tau)}{x^*y_2^*y_1(t)(1+mx(t-\tau))}\right. \\
 & \left. - 1 - \ln \frac{y_1^*(1+mx^*)x(t-\tau)y_2(t-\tau)}{x^*y_2^*y_1(t)(1+mx(t-\tau))}\right].
 \end{aligned}
 \tag{4.11}$$

If $x(t) > r/(2a)$ for $t \geq T$, we have

$$\frac{(x - x^*)^2}{x} [r - a(x + x^*)] \leq 0,$$

with equality if and only if $x = x^*$. This, together with (4.11), implies that if $x(t) > r/(2a)$ for $t \geq T$, $V_2'(t) \leq 0$, with equality if and only if $x = x^*$, $\frac{y_1^*(1+mx^*)x(t-\tau)y_2(t-\tau)}{x^*y_2^*y_1(t)(1+mx(t-\tau))} = \frac{y_2^*y_1(t)}{y_1^*y_2(t)} = 1$. We now look for the invariant subset \mathcal{M} within the set

$$\begin{aligned}
 M = & \left\{ (x, y_1, y_2) : x = x^*, \right. \\
 & \left. \frac{y_1^*(1+mx^*)x(t-\tau)y_2(t-\tau)}{x^*y_2^*y_1(t)(1+mx(t-\tau))} \right. \\
 & \left. = \frac{y_2^*y_1(t)}{y_1^*y_2(t)} = 1 \right\}.
 \end{aligned}$$

Since $x = x^*$ on \mathcal{M} and consequently, $0 = \dot{x}(t) = x^*(r - ax^* - \frac{a_1y_2(t)}{1+mx^*})$, which yields $y_2(t) = y_2^*$. It follows from the third equation of system (1.2) that $0 = \dot{y}_2(t) = Dy_1(t) - r_2y_2^*$, which leads to $y_1 = y_1^*$. Hence, the only invariant set in M is $\mathcal{M} = \{(x^*, y_1^*, y_2^*)\}$. Using the LaSalle invariance principle, the global asymptotic stability of E^* follows. This completes the proof. \square

We now give an example to illustrate the result in Theorem 4.2.

Example 2 In (1.2), let $r = 3.5, a = 16, a_1 = 5, a_2 = 1, D = 1, m = 1/10, r_1 = r_2 = 1/8$. By calculation, we derive that $a_2rD - r_2(a + mr)(D + r_1) \approx 1.2008 > 0$. Hence, by Theorem 3.1, system (1.2) is permanent. It is easy to show that system (1.2) has a unique coexistence equilibrium $E^*(0.1426, 0.0309, 0.2471)$. From the proof of Lemma 3.2, we have $\limsup_{t \rightarrow +\infty} y_2(t) \leq M_2 := a_2(r + r_0)^2/(4aa_1r_0)$. Hence, for $\varepsilon > 0$ sufficiently small, there is a $T_1 > 0$

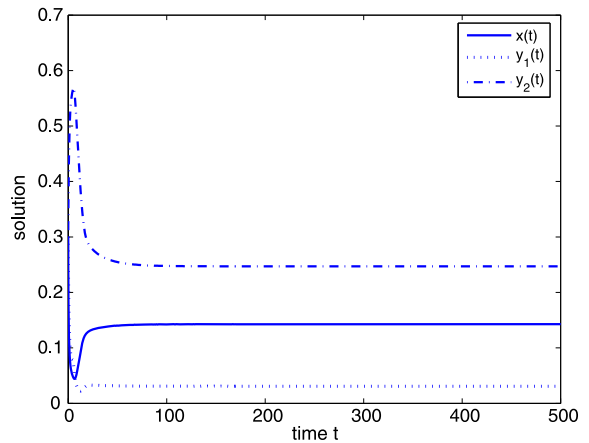


Fig. 2 The temporal solution found by numerical integration of system (1.2) with $r = 3.5, a = 16, a_1 = 5, a_2 = 1, D = 1, m = 1/10, r_1 = r_2 = 1/8, \tau = 5, (\phi, \psi_1, \psi_2) \equiv (0.3, 0.3, 0.3)$

such that if $t > T_1, y_2(t) < M_2 + \varepsilon$. It follows from the first equation of system (1.2) that, for $t > T_1$,

$$\dot{x}(t) > x(t)[r - ax(t) - a_1(M_2 + \varepsilon)],$$

which yields

$$\liminf_{t \rightarrow +\infty} x(t) \geq \frac{r - a_1M_2}{a} := \underline{x}.$$

By calculation, we derive that $\underline{x} \approx 0.1161, r/(2a) \approx 0.1094$. By Theorem 4.2, we see that the coexistence equilibrium E^* is globally asymptotically stable. Numerical simulation illustrates the result above (see Fig. 2).

5 Concluding remark

In this paper, the global dynamics of a delayed predator-prey model with stage structure for the predator and Holling type-II functional response was investigated using Lyapunov functionals and LaSalle’s invariance principle. It has been shown that, under hypothesis guaranteeing the uniform persistence of the system, a priori lower bound condition on the density of the prey population ensures the global asymptotic stability of the coexistence equilibrium. That is, if the prey is always abundant enough, the coexistence equilibrium is a global attractor of the system. On the other hand, it has been shown that under some conditions, the time delay due to the gestation of the mature predator may destabilize the coexistence equilibrium of the system and cause the population to fluctuate.

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