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Research Article

Permanence and Stability of an Age-Structured Prey-Predator System with Delays

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An age-structured prey-predator model with delays is proposed and analyzed. Mathematical analyses of the model equations with regard to boundedness of solutions, permanence, and stability are analyzed. By using the persistence theory for infinite-dimensional systems, the sufficient conditions for the permanence of the system are obtained. By constructing suitable Lyapunov functions and using an iterative technique, sufficient conditions are also obtained for the global asymptotic stability of the positive equilibrium of the model.

1. Introduction

The classic Lotka-Volterra-type prey-predator system is an important population model and has been studied by some authors (see [1–5]). It is assumed that each individual prey admits the same risk to be attacked by predator. However, these assumptions provide only an idealization of the natural world. In the natural world, there are many species who go through two or more life stages while they proceed from birth to death. Different life stages usually have different physical behaviors. Age-structured ecological models have received much attention in recent years. This is not only because they are simpler than the models governed by partial differential equations, but also they can exhibit phenomena similar to those of partial differential models, and many important physiological parameters can be incorporated (see [6]). Recently, papers [7–12] have studied the age-structured population model with or without time delays. They study the effect of age structure on the dynamical behavior of prey-predator system. In addition, a good overview on age-structured models can be found in the recent book by Murdoch et al. [13, Chapter 5 in particular].

Motivated by recent works of Gourley and Kuang [9] and Zhang et al. [12], in this paper, we consider the following plausible age-structured prey-predator interaction model:

$$\begin{aligned}\frac{dx_j(t)}{dt} &= \alpha x(t) - \gamma x_j(t) - \alpha e^{-\gamma\tau}x(t-\tau),\\ \frac{dx(t)}{dt} &= \alpha e^{-\gamma\tau}x(t-\tau) - \mu_1 x(t) - mx^2(t) - \beta x(t)y(t),\\ \frac{dy(t)}{dt} &= b\beta x(t-\sigma)y(t-\sigma) - \mu_2 y(t) - \omega y^2(t),\end{aligned} \tag{1.1}$$

where $x_j(t)$ and $x(t)$ represent, respectively, the juvenile and adult prey densities at time t; $y(t)$ represents the predator density at time t. α, μ_1, γ, μ_2, β, τ, σ, m and ω are positive constants.

The model is derived under the following assumptions.

(A_1) We first assume that the life history of prey species is divided into two stages: juvenile and adult. The delay τ denotes the time from birth to maturity of prey species. We then assume that the juvenile prey reproduction rate is proportional to the existing adult prey population with a proportionality constant α; γ is the death rate of the juvenile populations. Finally, we assume that the juvenile preys born at time $t-\tau$ that survive to time t exit from the the juvenile population and enter the the mature population at time t. The term $\alpha e^{-\gamma\tau}x(t-\tau)$ represents the the juvenile prey individuals who were born at time $t-\tau$ and still survive at time t, and represents the transformation of the juvenile prey population to the adult prey population.

(A_2) We assume that the adult prey species have death and intraspecific competition rate constants μ_1 and m, respectively. μ_2 and ω are, respectively, death and intraspecific competition rate constants of the predator, β is the predation coefficient, and b ($0 \le b \le 1$) is the coefficient in conversing prey into predator. It seems reasonable to assume that the reproduction of predator after predating the prey will not be instantaneous, but mediated by some discrete time delay required for gestation of predator (see [8, 14]). σ ($\sigma > 0$) is the time required for the gestation of the predator.

(A_3) It seems reasonable for many species of mammals, where immature preys concealed in the mountain cave are raised by their parents; they do not necessarily go out to seek food, so they are not attacked by the predators and the rate at which the predators attack can be ignored.

The initial conditions for system (1.1) take the form of

$$\begin{gathered} x_j(\theta) = \varphi_j(\theta) \ge 0, \quad x(\theta) = \varphi(\theta) \ge 0, \quad y(\theta) = \psi(\theta) \ge 0, \quad \theta \in [-h,0],\\ \varphi_j(0) > 0, \qquad \varphi(0) > 0, \qquad \psi(0) > 0,\end{gathered} \tag{1.2}$$

where $h = \max\{\tau,\sigma\}$, $\Phi = (\varphi_j(\theta),\varphi(\theta),\psi(\theta)) \in C([-h,0],\mathbb{R}^3_{+0})$, the Banach space of continuous functions mapping the interval $[-h,0]$ into $\mathbb{R}^3_{+0}$, where $\mathbb{R}^3_{+0} = \{(x_j,x,y) : x_j \ge 0,\ x \ge 0,\ y \ge 0\}$.

The first equation of system (1.1) with initial conditions (1.2) can be rewritten as

$$x_j(t) = \int_{t-\tau}^{t} \alpha e^{-\gamma(t-\theta)} x(\theta)d\theta. \tag{1.3}$$

For continuity of the initial conditions, we further require $x_j(0) = \int_{-\tau}^{0} \alpha e^{\gamma\theta}\varphi(\theta)d\theta$.

Thus, $x_j(t)$ can be completely determined by $x(t)$, $y(t)$, respectively. Therefore, the dynamics of system (1.1) are completely determined by the second and third equations. In the rest of this paper, we will consider the following subsystem:

$$\begin{aligned}\frac{dx(t)}{dt} &= \alpha e^{-\gamma\tau}x(t-\tau) - \mu_1 x(t) - mx^2(t) - \beta x(t)y(t),\\ \frac{dy(t)}{dt} &= b\beta x(t-\sigma)y(t-\sigma) - \mu_2 y(t) - \omega y^2(t).\end{aligned} \tag{1.4}$$

In this paper, we will perform a global analysis for the age-structured prey-predator model (1.4) to show the combined effects of age structure for prey and delay due to the gestation of the predator on the dynamics of the model.

The organization of this paper is as follows. In the next section, stability of boundary equilibria of the system is discussed. In Section 3, the sufficient conditions for the permanence of the system are obtained. In Section 4, global stability of the positive equilibrium is also discussed. The paper ends with brief remarks.

2. Stability of boundary equilibria

In this section, we first show the existence of equilibria and the local stability of boundary equilibria for system (1.4).

Except for equilibrium $E_0(0,0)$, system (1.4) has also equilibria $E_1(x^0,0)$, $E^*(x^*,y^*)$, where

$$x^0 = \frac{\alpha e^{-\gamma\tau} - \mu_1}{m}, \qquad x^* = \frac{\omega(\alpha e^{-\gamma\tau} - \mu_1) + \beta\mu_2}{m\omega + b\beta^2}, \qquad y^* = \frac{b\beta(\alpha e^{-\gamma\tau} - \mu_1) - m\mu_2}{m\omega + b\beta^2}. \tag{2.1}$$

The boundary equilibrium $E_1(x^0,0)$ exists if $\alpha e^{-\gamma\tau} > \mu_1$, and the existence condition for the positive equilibrium $E^*(x^*,y^*)$ is $b\beta(\alpha e^{-\gamma\tau} - \mu_1) > m\mu_2$.

Theorem 2.1. (1) *The equilibrium E_0 of system (1.4) is stable if $\alpha e^{-\gamma\tau} < \mu_1$ and unstable if $\alpha e^{-\gamma\tau} > \mu_1$.*

(2) *The equilibrium E_1 of system (1.4) is locally asymptotically stable if $b\beta(\alpha e^{-\gamma\tau} - \mu_1) < m\mu_2$ and unstable if $b\beta(\alpha e^{-\gamma\tau} - \mu_1) > m\mu_2$.*

Proof. (1) The characteristic equation of the equilibrium $E_0(0,0)$ is

$$(\lambda - \alpha e^{-(\gamma+\lambda)\tau} + \mu_1)(\lambda + \mu_2) = 0. \tag{2.2}$$

Clearly, $\lambda = -\mu_2$ is a negative eigenvalue, while the other eigenvalue is given by the solutions of $\lambda = \alpha e^{-(\gamma+\lambda)\tau} - \mu_1$. If $\alpha e^{-\gamma\tau} > \mu_1$, we claim that the solutions of $\lambda = \alpha e^{-(\gamma+\lambda)\tau} - \mu_1$

have only negative real parts. Suppose that $\text{Re}\lambda \geq 0$. By computing the real parts of λ, we get

$$\text{Re}\lambda = \alpha e^{-\gamma\tau} e^{-\tau \text{Re}\lambda} \cos(\tau \,\text{Im}\lambda) - \mu_1 \leq \alpha e^{-\gamma\tau} - \mu_1 < 0, \tag{2.3}$$

a contradiction. Thus we have $\text{Re}\lambda < 0$.

If $\alpha e^{-\gamma\tau} > \mu_1$, we claim that $\lambda = \alpha e^{-(\gamma+\lambda)\tau} - \mu_1$ has at least a positive solution. In fact, set

$$f(\lambda) = \lambda - \alpha e^{-(\gamma+\lambda)\tau} + \mu_1. \tag{2.4}$$

We have $f(0) = \mu_1 - \alpha e^{-\gamma\tau} < 0$ and $f(+\infty) = +\infty$. Hence, $f(\lambda)$ has at least one positive root and E_0 is unstable.

(2) The characteristic equation of the equilibrium $E_1(x^0, 0)$ is

$$G(\lambda) \overset{\text{def}}{=} (\lambda - \alpha e^{-\gamma\tau} e^{-\lambda\tau_1} + \mu_1 + 2mx^0)(\lambda - b\beta x^0 e^{-\lambda\sigma} + \mu_2) = 0. \tag{2.5}$$

Thus, all eigenvalues are given by the solutions $\lambda = \alpha e^{-\gamma\tau} e^{-\lambda\tau_1} - \mu_1 - 2mx^0$ and $\lambda = b\beta x^0 e^{-\lambda\sigma} - \mu_2$, respectively. Similar to the above arguments, if $b\beta(\alpha e^{-\gamma\tau} - \mu_1) < m\mu_2$, we obtain that all the roots for the equation $G(\lambda)$ have only negative real parts, and E_1 is stable. Otherwise, E_1 is unstable. The proof is complete. □

Similar to the arguments of paper [10, 15], we have the following lemmas.

Lemma 2.2. *Let $x(\theta), y(\theta) \geq 0$, on $-h \leq \theta < 0$, and $x(0), y(0) > 0$. Then solutions of system (1.4) are positive for all $t \geq 0$.*

Lemma 2.3. *Consider the following equation:*

$$\dot{x}(t) = ax(t-\tau) - bx(t) - cx^2(t), \tag{2.6}$$

where $a, b, c, \tau > 0$; $x(t) > 0$, for $-\tau \leq t \leq 0$. One has the following.

(i) *If $a > b$, then $\lim_{t\to\infty} x(t) = (a-b)/c$.*

(ii) *If $a < b$, then $\lim_{x\to\infty} x(t) = 0$.*

Lemma 2.4. *Assume that $b\beta(\alpha e^{-\gamma\tau} - \mu_1) > m\mu_2$. Then all solutions of system (1.4) with initial conditions are bounded for all $t \geq 0$.*

Proof. Noting that $b\beta(\alpha e^{-\gamma\tau} - \mu_1) > m\mu_2$, there exists an ϵ such that $b\beta((\alpha e^{-\gamma\tau} - \mu_1)/m + \epsilon) > \mu_2$. From the first equation of system (1.4), we have

$$\frac{dx(t)}{dt} \leq \alpha e^{-\gamma\tau} x(t-\tau) - \mu_1 x(t) - mx^2(t). \tag{2.7}$$

Since $\alpha e^{-\gamma\tau} > \mu_1$, by Lemma 2.3 and comparison, we have $\lim_{t\to+\infty} x(t) \leq (\alpha e^{-\gamma\tau} - \mu_1)/m$. Thus, there exists a $T_\epsilon > 0$ such that $x(t) \leq (\alpha e^{-\gamma\tau} - \mu_1)/m + \epsilon$ for $t > T_\epsilon$. From the second equation of system (1.4), we obtain that for $t > T_\epsilon + \sigma$,

$$\frac{dy(t)}{dt} \leq b\beta\left(\frac{\alpha e^{-\gamma\tau} - \mu_1}{m} + \epsilon\right) y(t-\sigma) - \mu_2 y(t) - \omega y^2(t). \tag{2.8}$$

Since $b\beta((\alpha e^{-\gamma\tau}-\mu_1)/m+\epsilon)>\mu_2$, by Lemma 2.3 and comparison, it is easy to obtain that $\lim_{t\to+\infty} y(t)\le(\alpha e^{-\gamma\tau}-\mu_1)/m\omega+\epsilon$. The proof is complete. □

Similar to the arguments of Lemma 2.4, it is easy to obtain the following conclusion.

Theorem 2.5. *Assume that* $\alpha e^{-\gamma\tau}<\mu_1$. *Then solutions of system (1.4) satisfy* $x(t)\to 0$, $y(t)\to 0$ *as* $t\to\infty$.

Now we give the sufficient conditions for the global stability of the boundary equilibrium $(x,y)=(x^0,0)$. The biological meaning of the condition is obvious: if the predators recruitment rate $b\beta$ at the peak of adult prey abundance is no more than their death rate μ_2, then the predators face extinction.

Theorem 2.6. *Assume that* $0<b\beta((\alpha e^{-\gamma\tau}-\mu_1)/m)<\mu_2$. *Then the solutions of system (1.4) satisfy* $x(t)\to x^0$, $y(t)\to 0$ *as* $t\to\infty$.

Proof. Noting that $0<b\beta((\alpha e^{-\gamma\tau}-\mu_1)/m)<\mu_2$, thus there exists an ϵ' such that $b\beta((\alpha e^{-\gamma\tau}-\mu_1)/m+\epsilon')<\mu_2$. It follows from the first equation of system (1.4) that

$$\frac{dx(t)}{dt}\le\alpha e^{-\gamma\tau}x(t-\tau)-\mu_1 x(t)-mx^2(t). \tag{2.9}$$

Since $\alpha e^{-\gamma\tau}>\mu_1$, by Lemma 2.3 and comparison, we have $\lim_{t\to+\infty}x(t)=(\alpha e^{-\gamma\tau}-\mu_1)/m$. Thus, there exists $T_{\epsilon'}>0$ such that $x(t)\le(\alpha e^{-\gamma\tau}-\mu_1)/m+\epsilon'$, for all $t>T_{\epsilon'}>0$. Then for $t>T_{\epsilon'}+\sigma$, we have

$$\frac{dy}{dt}\le b\beta\left(\frac{\alpha e^{-\gamma\tau}-\mu_1}{m}+\epsilon'\right)y(t-\sigma)-\mu_2 y(t)-\omega y^2(t). \tag{2.10}$$

Therefore, by Lemma 2.3 and comparison, we have $y(t)\to 0$.

In the following, we will show that $\lim_{t\to\infty}x(t)=x^0$, we consider two cases.

Case 1. $x(t)$ is oscillatory about x^0. Then for the bounded $x(t)$, there must exist a sequence $\{t_k\}$, such that $\lim_{k\to\infty}t_k=\infty$, and $x(t_k)$ is a local maximum. That is, $\dot{x}(t_k)=0$, $\ddot{x}(t_k)<0$. Let

$$\tilde{x}=\limsup_{k\to\infty}\{x(t_k)\}. \tag{2.11}$$

We have $0<\tilde{x}<+\infty$ and $\lim_{k\to\infty}\sup x(t)=\tilde{x}$. We claim that $\tilde{x}\le(\alpha e^{-\gamma\tau}-\mu_1)/m$. Otherwise,

$$\tilde{x}>\frac{\alpha e^{-\gamma\tau}-\mu_1}{m}. \tag{2.12}$$

From the first equation of system (1.4), we obtain that at t_k,

$$0=\dot{x}(t_k)=\alpha e^{-\gamma\tau}x(t_k-\tau)-\mu_1 x(t_k)-mx^2(t_k)-\beta x(t_k)y(t_k), \tag{2.13}$$

Let $\hat{x}=\lim_{k\to\infty}\sup\{x(t_k-\tau)\}$.

We take a subsequence of $\{t_k\}$ and, without loss generality, rewrite $\{t_k\}$ such that $t_{k+1}>t_k+\tau$, $\lim_{t_k\to\infty}x(t_k)=\tilde{x}$, $\lim_{t_k\to\infty}x(t_k)=\hat{x}$. Thus, taking lim both sides of (2.13), and incorporating $\lim_{t\to\infty} y(t) = 0$ and (2.12), we obtain that

$$0 = \alpha e^{-\gamma\tau}\hat{x} - \mu_1\tilde{x} - m\widetilde{x^2} < \alpha e^{-\gamma\tau}(\hat{x} - \tilde{x}). \tag{2.14}$$

Therefore, we have $\hat{x} > \tilde{x}$. This is a contradiction to the definition of t_k and (2.11). Hence, we have $\tilde{x} \le (\alpha e^{-\gamma\tau} - \mu_1)/m$. That is, $\lim_{t\to\infty}\sup x(t) \le (\alpha e^{-\gamma\tau} - \mu_1)/m$. Similar to the above arguments, we can obtain $\lim_{t\to\infty}\inf x(t) \ge (\alpha e^{-\gamma\tau} - \mu_1)/m$. Therefore, we have $\lim_{t\to\infty} x(t) = (\alpha e^{-\gamma\tau} - \mu_1)/m$.

Case 2. $x(t)$ is nonoscillatory. Then $x(t)$ is eventually monotone. Thus for the bounded $x(t)$, there exists $\bar{x}$, $0 < \bar{x} < +\infty$, such that $\lim_{t\to\infty} x(t) = \bar{x}$. It follows from the first equation of the system that $\lim_{t\to\infty} \dot{x}(t)$ exists. As a consequence, [16] implies that $\lim_{t\to\infty} \dot{x}(t) = 0$. Taking lim both sides of the first equation for system (1.4) and incorporating $\lim_{t\to\infty} y(t) = 0$ give $0 = \bar{x}(\alpha e^{-\gamma\tau} - \mu_1 - m\bar{x})$. That is, $\bar{x} = (\alpha e^{-\gamma\tau} - \mu_1)/m$.

The proof is complete. □

By Theorems 2.1-2.6, we directly obtain the following corollaries.

Corollary 2.7. *The equilibrium $E_0(0,0)$ of system (1.4) is globally asymptotically stable if $\alpha e^{-\gamma\tau} < \mu_1$ holds true.*

Corollary 2.8. *The equilibrium $E_1(x^0,0)$ of system (1.4) is globally asymptotically stable if $0 < b\beta(\alpha e^{-\gamma\tau} - \mu_1) < m\mu_2$ holds true.*

3. Permanence of system (1.4)

In this section, we will apply the permanent theory for infinite-dimensional system from [17] to obtain the permanence of system (1.4).

Lemma 3.1 (see [17, page 392]). *Suppose that $T(t)$ satisfies (H_1) and the following conditions hold:*

(i) *there is a $t_0 \ge 0$ such that $T(t)$ is compact for $t > t_0$;*
(ii) *$T(t)$ is point dissipative in X;*
(iii) *$\widetilde{A_b} = \bigcup_{x\in A_b}\omega(x)$ is isolated and has an acyclic covering $\widetilde{M}$, where*

$$\widetilde{M} = \{A_1, A_2, \dots, A_n\}; \tag{3.1}$$

(iv) *$W^s(A_i) \cap X_0 = \phi$, for $i = 1,2,\dots,n$. Then X_0 is a uniform repeller with respect to X^0, that is, there is an $\epsilon > 0$ such that for $x \in X^0$, $\liminf_{t\to+\infty} d(T(t)x, X_0) \ge \epsilon$, where d is the distance of $T(t)x$ from X_0.*

Theorem 3.2. *Assume that $b\beta(\alpha e^{-\gamma\tau} - \mu_1) > m\mu_2$. Then system (1.4) is permanent.*

Proof. We first begin by showing that the boundary planes of $\mathbb{R}_+^2 = \{(x,y) : x \ge 0,\ y \ge 0\}$ repel the positive solutions to system (1.4) uniformly. Let us define

$$\begin{aligned} C_1 &= \{(\varphi,\psi) \in C([-h,0],\mathbb{R}_+^2) : \varphi(\theta) \equiv 0,\ \theta \in [-h,0]\}, \\ C_2 &= \{(\varphi,\psi) \in C([-h,0],\mathbb{R}_+^2) : \varphi(\theta) > 0,\ \psi(\theta) \equiv 0,\ \theta \in [-h,0]\}, \end{aligned} \tag{3.2}$$

where $C([-h,0],\mathbb{R}_+^2)$ is the space of continuous functions mapping $[-h,0]$ into $\mathbb{R}_+^2$. Set $C_0 = C_1 \bigcup C_2$, $X = C([-h,0],\mathbb{R}_+^2)$. Thus $X^0 = IntC([-h,0],\mathbb{R}_+^2)$, $C_0 = \partial X^0$.

We now verify that the conditions of Lemma 3.1 are satisfied.

By the definition of X^0, ∂X^0, and system (1.4), it is easy to see that X^0 and ∂X^0 are invariant, hence (H_1) is satisfied. System (1.4) possesses two constant solutions in $C_0 = \partial X^0 : A_1 \in C_1$, $A_2 \in C_2$ with

$$\begin{aligned} A_1 &= \{(\varphi,\psi) \in C([-\tau,0],\mathbb{R}_+^2) : \varphi(\theta) \equiv \psi \equiv 0,\ \theta \in [-\tau,0]\}, \\ A_2 &= \{(\varphi,\psi) \in C([-\tau,0],\mathbb{R}_+^2) : \varphi(\theta) \equiv x^0,\ \psi(\theta) \equiv 0,\ \theta \in [-\tau,0]\}. \end{aligned} \tag{3.3}$$

By Lemmas 2.2 and 2.4, conditions (i) and (ii) of Lemma 3.1 are clearly satisfied.

Consider condition (iii) of Lemma 3.1. We have $\dot{x}(t)|_{(\varphi,\psi)\in C_1} \equiv 0$, then we get $x(t)|_{(\varphi,\psi)\in C_1} \equiv 0$, for all $t \geq 0$. Using the second equation of system (1.4), we have $\dot{y}(t)|_{(\varphi,\psi)\in C_1} = -\mu_2 y(t) - \omega y^2(t) \leq 0$, hence all points in C_1 approach A_1, that is, $C_1 = W^s(A_1)$. On the other hand, note that $\dot{y}(t)|_{(\varphi,\psi)\in C_1} = 0$, and thus $y(t)|_{(\varphi,\psi)\in C_1} = 0$ for all $t \geq 0$. Accordingly, we have $\dot{x}(t)|_{(\varphi,\psi)\in C_2} = \alpha e^{-\gamma\tau}x(t-\tau) - \mu_1 x(t) - mx^2(t)$. By Lemma 2.3, we have $\lim_{t\to\infty} x(t) = (\alpha e^{-\gamma\tau} - \mu_1)/m$. It is obvious that we have that all points in C_2 approach A_2, that is, $C_2 = W^s(A_2)$. Hence $\widetilde{M} = \{A_1, A_2\}$, and clearly it is isolated. Noting that $C_1 \cap C_2 = \phi$, it follows from these structural features that the flow in $\widetilde{M}$ is acyclic, satisfying condition(iii) of Lemma 3.1. Now we show that $W^s(A_i) \cap X^0 = \phi$, $i = 1,2$. Since Lemmas 2.2 and 2.4 indicate that $W^s(A_1) \cap X^0 = \phi$, we only need to prove that $W^s(A_2) \cap X^0 = \phi$.

Assume the contrary, that is, $W^s(A_2) \cap X^0 \neq \phi$, thus there exists a positive solution $(x(t), y(t))$ to system (1.4) with $\lim_{t\to\infty}(x(t), y(t)) = (x^0, 0)$. Then for the sufficiently small ϵ with $(b\beta(\alpha e^{-\gamma\tau} - \mu_1) - m\mu_2)/(b\beta + \omega)m\omega > \epsilon$, there exists a positive constant $T = T(\epsilon)$ such that $x(t) > (\alpha e^{-\gamma\tau} - \mu_1)/m - \epsilon$, $y(t) < \epsilon$, for all $t \geq T$. By the second equation of system (1.4), we have

$$\frac{dy}{dt} > b\beta\left(\frac{\alpha e^{-\gamma\tau} - \mu_1}{m} - \epsilon\right)y(t-\sigma) - \mu_2 y(t) - \omega y^2(t), \quad t \geq T + \tau. \tag{3.4}$$

By Lemma 2.3 and comparison, we have $\lim_{t\to\infty} y(t) > u^*$, where

$$u^* = \frac{b\beta(\alpha e^{-\gamma\tau} - \mu_1) - mb\beta\epsilon - m\mu_2}{m\omega} > \epsilon. \tag{3.5}$$

This is a contradiction to $y(t) < \varepsilon$. Therefore, the condition $W^s(A_i) \cap X^0 = \phi$, $i = 1,2$, of Lemma 3.1 holds. Thus system (1.4) satisfies all conditions of Lemma 3.1. Accordingly, system (1.4) is uniformly persistent, that is, there exist positive constants ε and $T = T(\varepsilon)$ such that the solutions $x(t)$, $y(t)$ of system (1.4) satisfy $x(t), y(t) \geq \epsilon$ for all $t \geq T$. Furthermore, Lemma 2.4 shows that $(x(t), y(t))$ are ultimately bounded. That is, system (1.4) is dissipative, and this proves the permanence of system (1.4). □

4. Global stability of the positive equilibrium

In the following, we first discuss the local asymptotic stability of the positive equilibrium $E^*(x^*,y^*)$ of system (1.4). Based on the permanence of solutions of system (1.4), we will use the method of Lyapunov functionals.

Theorem 4.1. *The positive equilibrium E^* of system (1.4) is locally asymptotically stable provided that (H_2): $\theta_1>0$, $\theta_2>0$, where*

$$\theta_1 = \frac{by^*}{x^*}\{2mx^* - \alpha e^{-\gamma\tau}\tau[4\alpha e^{-\gamma\tau}+(2m+\beta)x^*] - \beta\sigma x^*[2\alpha e^{-\gamma\tau}+(b\beta+m)x^*]\},$$
$$\theta_1 = \mu_2+2\omega y^* - \alpha e^{-\gamma\tau}b\beta y^*\tau - b\beta\sigma\{[2\alpha e^{-\gamma\tau}+(m+2\beta+b\beta)x^*]y^*+2x^*(2\beta x^*+\omega y^*)\}. \tag{4.1}$$

Proof. Let us linearize system (1.4) at $E^*(x^*,y^*)$. Setting $x=x^*+w$, $y=y^*+z$, where w and z are small, and linearizing give

$$\begin{aligned}\dot{w}(t) &= Aw(t-\tau)+A_1w(t)+Bz(t),\\ \dot{z}(t) &= Cw(t-\sigma)+Dz(t-\sigma)+D_1z(t),\end{aligned} \tag{4.2}$$

where

$$\begin{gathered}A=\alpha e^{-\gamma\tau}, \qquad A_1=-\mu_1-2mx^*-\beta y^*, \qquad B=-\beta x^*,\\ C=b\beta y^*, \qquad D=b\beta x^*, \qquad D_1=-\mu_2-2\omega y^*.\end{gathered} \tag{4.3}$$

The first equation of (4.2) can be rewritten as

$$\dot{w}(t) = (A+A_1)w(t)+Bz(t)-A\int_{t-\tau}^{t}[Aw(u-\tau)+A_1w(u)+Bz(u)]du. \tag{4.4}$$

Set

$$V_{11}(t)=w^2(t). \tag{4.5}$$

Calculating the derivation of $V_{11}(t)$ along solutions of (4.2), and using the inequality $2ab\le(a^2+b^2)$, we have

$$\begin{aligned}\dot{V}_{11}(t) \le{}& 2(A+A_1)w^2(t)+2Bw(t)z(t)+A(A-A_1-B)\tau w^2(t)\\ &+A\int_{t-\tau}^{t}[Aw^2(u-\tau)-A_1w^2(u)-Bz^2(u)]du.\end{aligned} \tag{4.6}$$

Set

$$V_{12}(t)=A\int_{t-\tau}^{t}\int_{v}^{t}[Aw^2(u-\tau)-A_1w^2(u)-Bz^2(u)]du\,dv. \tag{4.7}$$

It follows from (4.6) and (4.7) that

$$\begin{aligned}\frac{d(V_{11}(t)+V_{12}(t))}{dt} \le{}& 2(A+A_1)w^2(t)+2Bw(t)z(t)+A(A-A_1-B)\tau\\ &\times w^2(t)+A\tau[Aw^2(t-\tau)-A_1w^2(t)-Bz^2(t)]du.\end{aligned} \tag{4.8}$$

Set

$$V_1(t) = V_{11}(t) + V_{12}(t) + V_{13}(t), \tag{4.9}$$

where

$$V_{13} = A^2\tau \int_{t-\tau}^{t} w^2(u)du. \tag{4.10}$$

It follows from (4.8) and (4.10) that

$$\dot{V}_1(t) \le [2(A+A_1) + A(2A - 2A_1 - B)\tau]w^2(t) - AB\tau z^2(t) + 2Bw(t)z(t). \tag{4.11}$$

Similarly, the second equation of (4.2) can be written as

$$\begin{aligned}\dot{z}(t) = (D+D_1)z(t) + Cw(t) - C\int_{t-\sigma}^{t}[Aw(u-\tau) + A_1w(u) + Bz(u)]du \\ - D\int_{t-\sigma}^{t}[Cw(u-\sigma) + Dz(u-\sigma) + D_1z(u)]du.\end{aligned} \tag{4.12}$$

Set

$$V_{21}(t) = z^2(t). \tag{4.13}$$

Then along the solutions of system (4.2), using the inequality $2ab \le a^2 + b^2$, we have

$$\begin{aligned}\dot{V}_{21}(t) \le\ & 2(D+D_1)z^2(t) + 2Cw(t)z(t) + C(A - A_1 - B)\sigma z^2(t) \\ & + D(C + D - D_1)\sigma z^2(t) + C\int_{t-\sigma}^{t}[Aw^2(u-\tau) - A_1w^2(u) - Bz^2(u)]du \\ & + D\int_{t-\sigma}^{t}[Cw^2(u-\sigma) + Dz^2(u-\sigma) - D_1z^2(u)]du.\end{aligned} \tag{4.14}$$

Set

$$\begin{aligned}V_{22}(t) = C\int_{t-\sigma}^{t}\int_{v}^{t}[Aw^2(u-\tau) - A_1w^2(u) - Bz^2(u)]du\,dv \\ + D\int_{t-\sigma}^{t}\int_{v}^{t}[Cw^2(u-\sigma) + Dz^2(u-\sigma) - D_1z^2(u)]du\,dv.\end{aligned} \tag{4.15}$$

It follows from (4.14) and (4.15) that

$$\begin{aligned}\frac{d(V_{21}(t) + V_{22}(t))}{dt} \le\ & 2(D+D_1)z^2(t) + 2Cw(t)z(t) + C(A - A_1 - B) \\ & \times \sigma z^2(t) + D(C + D - D_1)\sigma z^2(t) \\ & + C\sigma[Aw^2(t-\tau) - A_1w^2(t) - Bz^2(t)] \\ & + D\sigma[Cw^2(t-\sigma) + Dw^2(t-\sigma) - D_1w^2(t)].\end{aligned} \tag{4.16}$$

Set

$$V_2(t) = V_{21}(t) + V_{22}(t) + V_{23}(t), \tag{4.17}$$

where

$$V_{23}(t) = AC\sigma \int_{t-\tau}^{t} w^2(u)du + D\sigma \int_{t-\sigma}^{t} [Cw^2(u) + Dz^2(u)]du. \tag{4.18}$$

Then it follows from (4.16), (4.17), and (4.18) that

$$\begin{aligned}\dot{V}_2(t) \le{}& 2(D+D_1)z^2(t) + 2Cw(t)z(t) + C(A-A_1-2B)\sigma z^2(t)\\ &+ D(C+2D-2D_1)\sigma z^2(t) + C\sigma(D+A-A_1)w^2(t).\end{aligned} \tag{4.19}$$

Set

$$V(t) = -\frac{C}{B}V_1(t) + V_2(t). \tag{4.20}$$

Then it follows from (4.11), (4.19), and (4.20) that

$$\begin{aligned}\dot{V}(t) \le{}& -\frac{C}{B}\{[2(A+A_1) + A(2A-2A_1-B)\tau]w^2(t) - AB\tau z^2(t) + 2Bw(t)z(t)\}\\ &+ 2(D+D_1)z^2(t) + 2Cw(t)z(t) + C(A-A_1-2B)\sigma z^2(t)\\ &+ D(C+2D-2D_1)\sigma z^2(t) + C\sigma(D+A-A_1)w^2(t)\\ =:{}& -\theta_1 w^2(t) - \theta_2 z^2(t).\end{aligned} \tag{4.21}$$

By assumption (H_2), we have $\theta_1 > 0$, $\theta_2 > 0$. According to the Lyapunov theorem (see [12]), we can derive that the zero solution of (4.2) is uniformly asymptotically stable. Accordingly, the positive equilibrium E^* of system (1.4) is uniformly asymptotically stable. □

Remark 4.2. From Theorem 4.1, it is easy to see that the positive instantaneous equilibrium (i.e., when $\tau = 0$, $\sigma = 0$) of the system (1.4) is locally uniformly asymptotically stable. Then the local uniform asymptotic stability of E^* for the delayed model (1.4) is preserved for small τ and σ satisfying (H_2).

Now we show the global attractivity of E^* by using an iterative technique.

THEOREM 4.3. *Assume that $b\beta\omega(\alpha e^{-\gamma\tau} - \mu_1) > m\omega\mu_2 > b\beta^2\mu_2$ holds. Then solutions of system (1.4) satisfy $x(t) \to x^*$, $y(t) \to y^*$ as $t \to \infty$.*

Proof. It follows from $b\beta\omega(\alpha e^{-\gamma\tau} - \mu_1) > m\omega\mu_2 > b\beta^2\mu_2$ that $\alpha e^{-\gamma\tau} - \mu_1 > 0$, $\sum_{k=0}^{n}(m\omega)^k(-b\beta^2)^{n-k} > 0$ $(n = 1, 2, 3, \ldots)$ and the unique positive equilibrium (x^*, y^*) exists.

From the first equation of system (1.4), we obtain $\dot{x}(t) \le \alpha e^{-\gamma\tau}x(t-\tau) - \mu_1 x(t) - mx^2(t)$. Consider the following auxiliary equation:

$$\frac{du(t)}{dt} = \alpha e^{-\gamma\tau}u(t-\tau) - \mu_1 u(t) - mu^2(t), \quad \text{satisfying } u(0) = y(0). \tag{4.22}$$

Let $P_1 = m^{-1}(\alpha e^{-\gamma\tau} - \mu_1)$. By Lemma 2.3, we have $\lim_{t\to+\infty} u(t) = P_1$. By comparison, there are a $T_{11} > 0$ and sufficiently small $\epsilon_1 > 0$ such that $x(t) \le u(t) \le P_1 + \epsilon_1$, $t > T_{11}$. Thus, for $t > T_{11} + \sigma$, we have

$$\dot{y}(t) \le b\beta(P_1 + \epsilon_1)y(t-\sigma) - \mu_2 y(t) - \omega y^2(t). \tag{4.23}$$

Let

$$Q_1 = \frac{b\beta(P_1+\epsilon_1) - \mu_1}{\omega} = \frac{b\beta(\alpha e^{-\gamma\tau} - \mu_1) - m\mu_2}{m\omega} + \frac{b\beta\epsilon_1}{\omega} > 0. \tag{4.24}$$

By Lemma 2.3 and comparison, for the above ϵ_1, there exists $T_{21} > T_{11}$, such that $y(t) \le Q_1 + \epsilon_1$, $t > T_{21}$. Then we have

$$\dot{x}(t) \ge \alpha e^{-\gamma\tau}x(t-\tau) - \mu_1 x(t) - \beta(Q_1+\epsilon_1)x(t) - mx^2(t). \tag{4.25}$$

Let

$$\begin{aligned} P_2 &= \frac{\alpha e^{-\gamma\tau} - \mu_1 - \beta(Q_1+\epsilon_1)}{m} \\ &= \frac{(m\omega - b\beta^2)(\alpha e^{-\gamma\tau} - \mu_1) + m\beta\mu_2}{\omega m^2} - \frac{b\beta^2 + \omega\beta}{m\omega}\epsilon_1 > 0. \end{aligned} \tag{4.26}$$

By Lemma 2.3 and comparison, for the above ϵ_1, there is $T_{22} > T_{21}$, such that $x(t) \ge P_2 - \epsilon_1$, for $t > T_{22}$. Therefore, we obtain for $t > T_{22} + \sigma$ that

$$\dot{y}(t) \ge b\beta(P_2 - \epsilon_1)y(t-\sigma) - \mu_2 y(t) - \omega y^2(t). \tag{4.27}$$

Let

$$\begin{aligned} Q_2 &= \frac{b\beta(P_2 - \epsilon_1) - \mu_2}{\omega} \\ &= \frac{(m\omega - b\beta^2)(b\beta(\alpha e^{-\gamma\tau} - \mu_1) - m\mu_2)}{m^2\omega^2} - \frac{b\beta(b\beta^2 + b\beta + m\omega)}{m\omega^2}\epsilon_1 > 0. \end{aligned} \tag{4.28}$$

By Lemma 2.3 and comparison, for the above ϵ_1, there is $T_{31} > T_{22}$, such that $y(t) \ge Q_2 - \epsilon_1$, $t > T_{31}$. We obtain that for $t > T_{31} + \tau$,

$$\dot{x}(t) \le \alpha e^{-\gamma\tau}x(t-\tau) - \mu_1 x(t) - \beta(Q_2 - \epsilon_1)x(t) - mx_2^2(t). \tag{4.29}$$

Let

$$\begin{aligned} P_3 &= \frac{\alpha e^{-\gamma\tau} - \mu_1 - \beta Q_2 + \beta\epsilon_1}{m} \\ &= \frac{(m^2\omega^2 - m\omega b\beta^2 + b\beta^4)(\alpha e^{-\gamma\tau} - \mu_1) + m\beta\mu_2(m\omega - b\beta^2)}{m^3\omega^2} \\ &\quad + \frac{\beta(b\beta^2 + m\omega)(b\beta + \omega)}{m^2\omega^2}\epsilon_1 > 0. \end{aligned} \tag{4.30}$$

By Lemma 2.3 and comparison, for the above ϵ_1, there is $T_{32} > T_{31}$, such that $x(t) \leq P_3 + \epsilon_1$, for $t > T_{32}$. Thus, for $t > T_{32} + \sigma$, we have

$$\dot{y}(t) \leq b\beta(P_3 + \epsilon_1)y(t-\sigma) - \mu_2 y(t) - \omega y^2(t)). \tag{4.31}$$

Let

$$\begin{aligned} Q_3 &= \frac{b\beta(P_3+\epsilon_1) - \mu_2}{\omega} \\ &= \frac{\sum_{k=0}^{2}(m\omega)^k(-b\beta^2)^{2-k}(b\beta(\alpha e^{-\gamma\tau} - \mu_1) - m\mu_2)}{m^3\omega^3} \\ &\quad + \frac{mb\beta[b^2\beta^4 + \omega b\beta^2 + m^2\omega^2 + \beta\omega(b\beta^2 + m\omega)]}{m^2\omega^3}\epsilon_1 > 0. \end{aligned} \tag{4.32}$$

By Lemma 2.3 and comparison, for the above ϵ_1, there is $T_{41} > T_{32}$, such that $y(t) \leq Q_3 + \epsilon_1$, $t > T_{41}$. Then, for $t > T_{41} + \tau$, we have

$$\dot{x}(t) \geq \alpha e^{-\gamma\tau}x(t-\tau) - \mu_1 x(t) - \beta(Q_3 + \epsilon_1)x(t) - mx^2(t). \tag{4.33}$$

Continuing this process and by induction, we obtain

$$\begin{aligned} x(t) &\leq P_{2s-1} + \epsilon_{2s-1} \\ &= \frac{(\alpha e^{-\gamma\tau} - \mu_1)\sum_{k=0}^{2s-2}(m\omega)^k(-b\beta^2)^{2s-2-k} + m\beta\mu_2\sum_{k=0}^{2s-3}(m\omega)^k(-b\beta^2)^{2s-3-k}}{m^{2s-1}\omega^{2s-2}} \\ &\quad + \epsilon_{2s-1}, \quad \text{for } t > T_{2s-1\ s}, \\ y(t) &\leq Q_{2s-1} + \epsilon'_{2s-1} \\ &= \frac{[b\beta(\alpha e^{-\gamma\tau} - \mu_1) - m\mu_2]\sum_{k=0}^{2s-2}(m\omega)^k(-b\beta^2)^{2s-2-k}}{m^{2s-1}\omega^{2s-1}} \\ &\quad + \epsilon'_{2s-1}, \quad \text{for } t > T_{2s\ 1} > T_{2s-1\ s}, \\ x(t) &\geq P_{2s} - \epsilon_{2s} \\ &= \frac{(\alpha e^{-\gamma\tau} - \mu_1)\sum_{k=0}^{2s-1}(m\omega)^k(-b\beta^2)^{2s-1-k} + m\beta\mu_2\sum_{k=0}^{2s-2}(m\omega)^k(-b\beta^2)^{2s-2-k}}{m^{2s}\omega^{2s-1}} \\ &\quad - \epsilon_{2s}, \quad \text{for } t > T_{2s\ 2} > T_{2s\ 1}, \\ y(t) &\geq Q_{2s} - \epsilon'_{2s} = \frac{[b\beta(\alpha e^{-\gamma\tau} - \mu_1) - m\mu_2]\sum_{k=0}^{2s-1}(m\omega)^k(-b\beta^2)^{2s-1-k}}{m^{2s}\omega^{2s}} \\ &\quad - \epsilon'_{2s}, \quad \text{for } t > T_{2s+1\ 2s-1} > T_{2s\ 2}\ (s = 2,3,4,\ldots), \end{aligned} \tag{4.34}$$

where

$$\begin{aligned} \epsilon_n &= \frac{\beta(m\omega + bm\beta)\sum_{k=0}^{s-2}(m\omega)^k(b\beta^2)^{s-2-k}}{m^n\omega^{n-1}}\epsilon_1 + \epsilon_1 \quad (n = 2s-1,\ 2s), \\ \epsilon'_n &= \frac{bm\beta\left(\sum_{k=0}^{n-1}(m\omega)^k(b\beta^2)^{s-1-k} + \beta\omega\sum_{k=0}^{s-2}(m\omega)^k(b\beta^2)^{s-2-k}\right)}{\omega^n m^n}\epsilon_1 + \epsilon_1. \end{aligned} \tag{4.35}$$

Therefore, we obtain

$$\begin{aligned} P_{2s} - \epsilon_{2s} \le x(t) \le P_{2s-1} + \epsilon_{2s-1}, \\ Q_{2s} - \epsilon'_{2s} \le y(t) \le Q_{2s-1} + \epsilon'_{2s-1}, \end{aligned} \quad \text{for } t > T_{2s+1\ 2s-1}. \tag{4.36}$$

By direct calculation, we obtain

$$\begin{aligned}
&\lim_{s\to+\infty} P_{2s-1} \\
&\quad = \lim_{s\to+\infty} \frac{(\alpha e^{-\gamma\tau} - \mu_1)\sum_{k=0}^{2s-2}(m\omega)^k(-b\beta^2)^{2s-2-k} + m\beta\mu_2\sum_{k=0}^{2s-3}(m\omega)^k(-b\beta^2)^{2s-3-k}}{\omega^{2s-2}m^{2s-1}} \\
&\quad = \lim_{s\to+\infty} \frac{\omega(\alpha e^{-\gamma\tau} - \mu_1)[(m\omega)^{2s-1} - (-b\beta^2)^{2s-1}] + m\omega\mu_2\beta[(m\omega)^{2s-2} - (-b\beta^2)^{2s-2}]}{\omega^{2s-1}m^{2s-1}(m\omega + b\beta^2)} \\
&\quad = \lim_{s\to+\infty} \frac{\omega(\alpha e^{-\gamma\tau} - \mu_1)(q^{2s-1} - 1) + m\omega\mu_2\beta(-b\beta^2)^{-1}(q^{2s-2} - 1)}{q^{2s-1}(m\omega + b\beta^2)} \\
&\quad = \frac{\omega(\alpha e^{-\gamma\tau} - \mu_1) + \beta\mu_2}{m\omega + b\beta^2} \qquad \left(|q| = \frac{m\omega}{b\beta^2} > 1\right), \\
&\lim_{s\to+\infty} \epsilon_{2s-1} \\
&\quad = \lim_{s\to+\infty} \left(\frac{\beta(m\omega + bm\beta)\sum_{k=0}^{2s-3}(m\omega)^k(b\beta^2)^{2s-3-k}}{b^{2s-2}m^{2s-1}}\epsilon_1 + \epsilon_1\right) \\
&\quad = \frac{\beta(mn + b\beta^2)}{\omega(m\omega - b\beta^2)}\epsilon_1 + \epsilon_1.
\end{aligned} \tag{4.37}$$

Similarly, we have

$$\begin{aligned} \lim_{s\to+\infty} P_{2s} &= \frac{\omega(\alpha e^{-\gamma\tau} - \mu_1) + \beta\mu_2}{m\omega + b\beta^2}, \\ \lim_{m\to+\infty} \epsilon_{2s} &= \frac{\beta(m\omega + b\beta^2)}{m(m\omega - b\beta^2)}\epsilon_1 + \epsilon_1. \end{aligned} \tag{4.38}$$

Hence, we obtain

$$\lim_{t\to+\infty} x(t) = \frac{\omega(\alpha e^{-\gamma\tau} - \mu_1) + \beta\mu_2}{m\omega + b\beta^2} = x^*. \tag{4.39}$$

By similar calculations, we can obtain

$$\lim_{t\to+\infty} y(t) = \frac{b\beta(\alpha e^{-\gamma\tau} - \mu_1) - m\mu_2}{m\omega + b\beta^2} = y^*. \tag{4.40}$$

The proof is complete. □

By Theorems 4.1-4.3, we directly obtain the following corollary.

Corollary 4.4. *Let (H_2) hold. Then the equilibrium $E^*(x^*, y^*)$ of system (1.4) is globally asymptotically stable provided that $b\beta\omega(\alpha e^{-\gamma\tau} - \mu_1) > m\omega\mu_2 > b\beta^2\mu_2$.*

5. Concluding remarks

In this paper, by introducing the duration times of immature individuals into the classical Lotka-Volterra prey-predator model [1], we have performed a global analysis of age-structured prey-predator system (1.4). By using the persistence theory for infinite-dimensional systems, the sufficient conditions for the permanence of the system are obtained. By constructing suitable Lyapunov functions and using an iterative technique, verifiable sufficient conditions are also obtained for the global asymptotic stability of the positive equilibrium of the model. Our results (Corollaries 2.7-2.8) extend the classical Lotka-Volterra prey-predator model [1], which suggests that system (1.4) has similar asymptotic behavior to those of the model [1]. Therefore, there is a good continuity between the age-structured system (1.4) and the classical Lotka-Volterra prey-predator model [1]. Our results also show the negative effect of age structure on the permanence of species: suppose $b\beta(\alpha e^{-\gamma\tau} - \mu_1) > m\mu_2$ holds (i.e., the unique positive equilibrium E^* exists). Then Theorem 3.2 shows that all the populations in (1.4) can coexist. Now if we enlarge the degree of age structure d ($d \overset{\text{def}}{=} \gamma\tau$) of the prey species gradually while keeping all the other coefficients fixed, we will find that once d reaches large enough values, conditions of Corollary 2.8 will be satisfied. This shows that a sufficient increase of the degree of age structure for the prey species will lead to the predator's extinction.

Here, we will point out that we are unable to show that system (1.4) admits periodic solutions (or limit cycles) when the delays change. This is known to be true for the delayed system (see [5, 13, 18]). We leave this for future investigations.

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