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Global stability of a stage-structured predator-prey model with prey dispersal ☆

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Abstract

A delayed Lotka–Volterra type predator-prey model with stage structure for predator and prey dispersal in two-patch environments is investigated. It is assumed that immature individuals and mature individuals of predator species are divided by a fixed age, and that immature predators do not feed on prey and do not have the ability to reproduce; on the other hand, it is assumed that the prey species can disperse between one patch with a low level of food and without predation and one patch with a higher level of food but with predation. By means of two different kinds of Lyapunov functionals, sufficient conditions are derived respectively for the global asymptotic stability of a positive equilibrium of the model. By analyzing the characteristic equation, criterion is established for the local stability of the positive equilibrium. Numerical simulations are presented to illustrate our main results.

Keywords: Stage structure; Time delay; Dispersal; Permanence; Global stability

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1. Introduction

Interest has been growing in the study of mathematical models of populations dispersing among patches in a heterogeneous environment(see, for example, [1–15], and references cited therein). Many of the existing models deal with a single population dispersing among patches. Some of them deal with competition and predator-prey interactions in patchy environments. The analysis of these models has been centered around the coexistence of populations and the stability of equilibria. These works indicate that a diffusion process in an ecological system is often considered to have a stabilizing influence on the system (see, for example, [6,11]), but is also probably destabilizing the system (see, for example, [9,10]). In [2], Beretta et al. discussed a predator-prey model where the prey can diffuse between one patch with a low level of food and without predation and one patch with higher level of food but with predation. By homotopy techniques they proved that if the prey diffusion is weak enough, then a nonzero globally stable equilibrium exists. By assuming that the predator density is regulated only by predation (the intra-specific competition rate is equal to zero), they proved the existence of a Hopf bifurcating orbit from a positive equilibrium. We note that it is assumed in [2] that each individual predator admits the same ability to feed on 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 recent years. The pioneering work of Aiello and Freedman [16] on a single species growth model with stage structure represents a mathematically more careful and biologically meaningful formulation approach. In [16], a model of single species population growth incorporating stage structure as a reasonable generalization of the classical logistic model was formulated and discussed. This model assumes an average age to maturity which appears as a constant time delay reflecting a delayed birth of immatures and a reduced survival of immatures to their maturity. The model takes the form

$$
\begin{aligned}
\dot{x}_i(t) &= \alpha x_m(t) - \gamma x_i(t) - \alpha e^{-\gamma\tau} x_m(t-\tau),\\
\dot{x}_m(t) &= \alpha e^{-\gamma\tau} x_m(t-\tau) - \beta x_m^2(t), \quad t > \tau,
\end{aligned}
\tag{1.1}
$$

where $x_i(t)$ denotes the immature population density, $x_m(t)$ represents the mature population density, $\alpha > 0$ represents the birth rate, $\gamma > 0$ is the immature death rate, $\beta > 0$ is the mature death and overcrowding rate, τ is the time to maturity. The term $\alpha e^{-\gamma\tau} x_m(t-\tau)$ represents the immatures who were born at time $t-\tau$ and survive at time t (with the immature death rate γ), and therefore represents the transformation of immatures to matures. Recently, many authors proposed and discussed different models with stage structure, and some excellent work was done for the global dynamics of stage-structured models (see, for example, [16–27]).

Motivated by the recent work of Aiello and Freedman [16] and Beretta et al [2], in the present paper we are concerned with the combined effects of stage structure for predator and prey dispersal on the global dynamics of Lotka–Volterra type predator-prey system. To do so, we study the following delayed differential system

$$\begin{cases} \dot{x}_1(t) = x_1(t)(r_1 - a_{11}x_1(t) - a_{13}y_1(t)) + D_1(x_2(t) - x_1(t)), \\ \dot{x}_2(t) = x_2(t)(r_2 - a_{22}x_2(t)) + D_2(x_1(t) - x_2(t)), \\ \dot{y}_1(t) = \alpha e^{-\gamma\tau}x_1(t-\tau)y_1(t-\tau) - r_3y_1(t) - a_{33}y_1^2(t), \\ \dot{y}_2(t) = \alpha x_1(t)y_1(t) - \gamma y_2(t) - \alpha e^{-\gamma\tau}x_1(t-\tau)y_1(t-\tau), \end{cases} \tag{1.2}$$

where $x_i(t)$ denotes the density of species x in patch i ($i = 1, 2$) at time t, and $y_1(t)$ and $y_2(t)$ represent the densities of immature and mature individual predators at time t, respectively. a_{11}, a_{13}, a_{22}, a_{33}, r_1, r_2, r_3, D_1, D_2, α, γ and τ are positive constants. The model is derived under the following assumptions.

(A1) *The prey population*: the prey can live in two patches. In patch 2 there is less food without predation; in patch 1 there is more food but risk of predation. r_i is the intrinsic growth rate of the prey in patch i, $i = 1, 2$; a_{ii} ($i = 1, 2$) are the intra-specific competition rates of the prey in patch i. D_i is the dispersion rate of prey species between two patches. To model the different levels of food supply, we suppose that the carrying capacity r_1/a_{11} in patch 1 is greater than the carrying capacity r_2/a_{22} in patch 2.

(A2) *The predator population*: a_{13} is the capturing rate of mature predator, α/a_{13} is the conversion rate of nutrients into the reproduction of the mature predator, r_3 is the death rate of the mature predator, a_{33} is the intra-specific competition rate of the mature predators. The death rate of the immature population is proportional to the existing immature population with a proportionality constant $\gamma > 0$. The term $\alpha e^{-\gamma\tau}x_1(t-\tau)y_1(t-\tau)$ represents the number of immature predators that were born at time $t-\tau$ which still survive at time t and are transferred from the immature stage to the mature stage at time t. It is assumed in (1.2) that the mature and immature predators cannot disperse into patch 2, and immature individual predators do not feed on prey and do not have the ability to reproduce.

The initial conditions for system (1.2) take the form of

$$\begin{aligned} &x_i(\theta) = \phi(\theta), \quad y_i(\theta) = \psi_i(\theta), \\ &\phi_i(0) > 0, \quad \psi_i(0) > 0, \quad i = 1, 2, \end{aligned} \tag{1.3}$$

where $(\phi_1(\theta), \phi_2(\theta), \psi_1(\theta), \psi_2(\theta)) \in C([-\tau, 0], R^4_{+0})$, the Banach space of continuous functions mapping the interval $[-\tau, 0]$ into R^4_{+0}, where $R^4_{+0} = \{(x_1, x_2, x_3, x_4) : x_i \geqslant 0, i = 1, 2, 3, 4\}$.

For continuity of the initial conditions, we further require

$$y_2(0) = \int_{-\tau}^{0} \alpha e^{\gamma s} \phi_1(s) \psi_1(s)\, ds. \tag{1.4}$$

The paper is organized as follows. In the next section, we will discuss the permanence of system (1.2). In Section 3, we are concerned with the global stability of a positive equilibrium of system (1.2) by constructing two different kinds of Lyapunov functionals, respectively. By analyzing the characteristic equation, criterion is derived for the local stability of the positive equilibrium of system (1.2). Numerical simulations are presented to illustrate our main results. A brief discussion is given in Section 4 to conclude this work.

2. Permanence

In this section, we are concerned with the permanence of system (1.2). To this end, we first need to show the positivity of solutions to system (1.2) with initial conditions (1.3) and (1.4).

Lemma 2.1. *Solutions of system* (1.2) *with initial conditions* (1.3) *and* (1.4) *are positive for all* $t \geqslant 0$.

Proof. Let $(x_1(t), x_2(t), y_1(t), y_2(t))$ be a solution of system (1.2) with initial conditions (1.3) and (1.4). Let us first consider $y_1(t)$ for $t \in [0, \tau]$. It follows from the third equation of system (1.2) that

$$\dot{y}_1(t) = \alpha e^{-\gamma\tau} \phi_1(t-\tau)\psi_1(t-\tau) - r_3 y_1(t) - a_{33} y_1^2(t) \geqslant -r_3 y_1(t) - a_{33} y_1^2(t)$$

since $\phi_1(\theta) \geqslant 0$, $\psi_1(\theta) \geqslant 0$ for $\theta \in [-\tau, 0]$. Therefore, a standard comparison argument shows that

$$y_1(t) \geqslant \frac{r_3 y_1(0)}{a_{33} y_1(0)(e^{r_3 t} - 1) + r_3} > 0.$$

We derive from the first and the second equations of system (1.2) that for $t \in [0, \tau]$,

$$\dot{x}_1(t)|_{x_1=0} = D_1(t) x_2 > 0 \quad \text{for } x_2 > 0,$$

$$\dot{x}_2(t)|_{x_2=0} = D_2(t) x_1 > 0 \quad \text{for } x_1 > 0.$$

Thus, it follows that $x_1(t) > 0$, $x_2(t) > 0$ for $t \in [0, \tau]$.

In a similar way we treat the intervals $[\tau, 2\tau], \ldots, [n\tau, (n+1)\tau]$, $n \in N$. Thus, $x_1(t) > 0$, $x_2(t) > 0$ and $y_1(t) > 0$ for all $t \geqslant 0$.

By (1.4) and the fourth equation of system (1.2) we obtain that

$$y_2(t) = \int_{t-\tau}^{t} \alpha e^{-\gamma(t-s)} x_1(s) y_1(s)\,ds. \tag{2.1}$$

Therefore, the positivity of $y_2(t)$ for $t \geqslant 0$ follows. The proof is complete. □

In order to discuss the permanence of system (1.2), we need the following result from [23].

Lemma 2.2. *Consider the following equation*

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

where a, b, c *and* τ *are positive constants*, $x(t) > 0$ *for* $t \in [-\tau, 0]$. *We have*

(i) *If* $a > b$, *then* $\lim_{t\to+\infty} x(t) = (a-b)/c$;
(ii) *If* $a < b$, *then* $\lim_{t\to+\infty} x(t) = 0$.

We are now able to state and prove our permanence result for system (1.2).

Theorem 2.1. *Let* $r_1/a_{11} \geqslant r_2/a_{22}$. *Assume further that*

(H1) $r_1\alpha e^{-\gamma\tau} - r_3 a_{11} > 0$,
(H2) $r_2 - D_2 > 0$,
(H3) $(r_1\alpha e^{-\gamma\tau} - r_3 a_{11})\left(1 - \frac{a_{13}\alpha e^{-\gamma\tau}}{a_{11}a_{33}}\right) - D_1 \alpha e^{-\gamma\tau} > 0$.

Then system (1.2) *is permanent.*

Proof. Suppose $(x_1(t), x_2(t), y_1(t), y_2(t))$ is a positive solution of system (1.2) with initial conditions (1.3) and (1.4).

Define

$$\rho(t) = \max\{x_1(t), x_2(t)\}.$$

Using a similar argument in the proof of Lemma 2.1 in [15] we derive that

$$\limsup_{t\to+\infty} \rho(t) \leqslant \max\left\{\frac{r_1}{a_{11}}, \frac{r_2}{a_{22}}\right\} = \frac{r_1}{a_{11}}.$$

Therefore, for $\varepsilon > 0$ sufficiently small there is a $T_{11} > 0$ such that if $t > T_{11}$,

$$x_1(t) \leqslant \frac{r_1}{a_{11}} + \varepsilon := M_1, \quad x_2(t) \leqslant \frac{r_1}{a_{11}} + \varepsilon := M_1. \tag{2.2}$$

It follows from the third equation of system (1.2) that for $t > T_{11} + \tau$,

$$\dot{y}_1(t) \leqslant \alpha e^{-\gamma\tau}\left(\frac{r_1}{a_{11}} + \varepsilon\right)y_1(t-\tau) - r_3 y_1(t) - a_{33}y_1^2(t).$$

Consider the following auxiliary equation

$$\dot{u}(t) = \alpha e^{-\gamma\tau}\left(\frac{r_1}{a_{11}} + \varepsilon\right)u(t-\tau) - r_3 u(t) - a_{33}u^2(t).$$

By Lemma 2.2, we obtain that

$$\lim_{t\to+\infty} u(t) = \frac{\alpha e^{-\gamma\tau}\left(\frac{r_1}{a_{11}} + \varepsilon\right) - r_3}{a_{33}}.$$

A standard comparison argument shows that

$$\limsup_{t\to+\infty} y_1(t) \leqslant \frac{\alpha e^{-\gamma\tau}\left(\frac{r_1}{a_{11}} + \varepsilon\right) - r_3}{a_{33}}.$$

Since $\varepsilon > 0$ is arbitrary and sufficiently small, we can conclude that

$$\limsup_{t\to+\infty} y_1(t) \leqslant \frac{r_1\alpha e^{-\gamma\tau} - r_3 a_{11}}{a_{11}a_{33}}.$$

Hence, for $\varepsilon > 0$ sufficiently small there is a $T_{12} > T_{11} + \tau$ such that

$$y_1(t) \leqslant \frac{r_1\alpha e^{-\gamma\tau} - r_3 a_{11}}{a_{11}a_{33}} + \varepsilon := M_2. \tag{2.3}$$

Setting $T_1 = T_{12} + \tau$, it then follows from (2.1) that for $t > T_1$,

$$y_2(t) \leqslant \frac{\alpha}{\gamma}M_1 M_2(1 - e^{-\gamma\tau}) := M_3.$$

Again, we derive from (1.2) that for $t > T_1$,

$$\begin{aligned} &\dot{x}_1(t) > x_1(t)(r_1 - D_1 - a_{13}M_2 - a_{11}x_1(t)),\\ &\dot{x}_2(t) > x_2(t)(r_2 - D_2 - a_{22}x_2(t)). \end{aligned} \tag{2.4}$$

By comparison we derive from the first inequality of (2.4) that

$$\liminf_{t\to+\infty} x_1(t) \geqslant \frac{r_1 - D_1 - a_{13}\left(\frac{r_1\alpha e^{-\gamma\tau} - r_3 a_{11}}{a_{11}a_{33}} + \varepsilon\right)}{a_{11}}.$$

Since $\varepsilon > 0$ is arbitrary and sufficiently small, we conclude that

$$\liminf_{t\to+\infty} x_1(t) \geqslant \frac{r_1 - D_1 - a_{13}\frac{r_1\alpha e^{-\gamma\tau} - r_3 a_{11}}{a_{11}a_{33}}}{a_{11}}.$$

Hence, for $\varepsilon > 0$ sufficiently small there is a $T_2 > T_1$ such that if $t > T_2$,

$$x_1(t) > \frac{r_1 - D_1 - a_{13}\frac{r_1\alpha e^{-\gamma\tau} - r_3 a_{11}}{a_{11}a_{33}}}{a_{11}} - \varepsilon := m_1. \tag{2.5}$$

Similarly, it follows from the second inequality of (2.4) that

$$\liminf_{t\to+\infty} x_2(t) \geqslant \frac{r_2 - D_2}{a_{22}}.$$

Therefore, for $\varepsilon > 0$ sufficiently small there exists a $T_3 > T_2$ such that if $t > T_3, x_2(t) > \frac{r_2 - D_2}{a_{22}} - \varepsilon$.

It follows from the third equation of system (1.2) that for $t > T_3 + \tau$,

$$\dot{y}_1(t) \geqslant \alpha e^{-\gamma\tau} m_1 y_1(t-\tau) - r_3 y_1(t) - a_{33} y_1^2(t).$$

Consider the following equation

$$\dot{u}(t) = \alpha e^{-\gamma\tau} m_1 u(t-\tau) - r_3 u(t) - a_{33} u^2(t).$$

By Lemma 2.2 we derive that

$$\lim_{t\to+\infty} u(t) = \frac{1}{a_{33}}\left[\alpha e^{-\gamma\tau}\left(\frac{r_1 - D_1 - a_{13}\frac{r_1\alpha e^{-\gamma\tau} - r_3 a_{11}}{a_{11}a_{33}}}{a_{11}} - \varepsilon\right) - r_3\right].$$

By comparison it follows that

$$\liminf_{t\to+\infty} y_1(t) \geqslant \frac{1}{a_{33}}\left[\alpha e^{-\gamma\tau}\left(\frac{r_1 - D_1 - a_{13}\frac{r_1\alpha e^{-\gamma\tau} - r_3 a_{11}}{a_{11}a_{33}}}{a_{11}} - \varepsilon\right) - r_3\right].$$

Since $\varepsilon > 0$ is arbitrary and sufficiently small, we conclude that

$$\liminf_{t\to+\infty} y_1(t) \geqslant \frac{1}{a_{33}}\left[\left(\frac{r_1\alpha e^{-\gamma\tau}}{a_{11}} - r_3\right)\left(1 - \frac{a_{13}\alpha e^{-\gamma\tau}}{a_{11}a_{33}}\right) - \frac{D_1\alpha e^{-\gamma\tau}}{a_{11}}\right].$$

Therefore, for $\varepsilon > 0$ sufficiently small there is a $T > T_3 + \tau$ such that if $t > T$,

$$y_1(t) > \frac{1}{a_{33}}\left[\left(\frac{r_1\alpha e^{-\gamma\tau}}{a_{11}} - r_3\right)\left(1 - \frac{a_{13}\alpha e^{-\gamma\tau}}{a_{11}a_{33}}\right) - \frac{D_1\alpha e^{-\gamma\tau}}{a_{11}}\right] - \varepsilon := m_2. \tag{2.6}$$

It follows from (2.1) that for $t > T + \tau$

$$y_2(t) \geqslant \frac{\alpha}{\gamma} m_1 m_2 (1 - e^{-\gamma\tau}) > 0.$$

The proof is complete. □

We now give a result on the extinction of the mature and immature predator.

Theorem 2.2. *The mature and immature predator population will go to extinction if the following holds*:

(H4) $r_1\alpha e^{-\gamma\tau} < r_3a_{11}$.

Proof. Let $(x_1(t), x_2(t), y_1(t), y_2(t))$ be a positive solution of system (1.2) with initial conditions (1.3) and (1.4). Choose $\varepsilon > 0$ sufficiently small such that

$$\alpha e^{-\gamma\tau}\left(\frac{r_1}{a_{11}} + \varepsilon\right) - r_3 < 0. \tag{2.7}$$

By Theorem 2.1 for $\varepsilon > 0$ sufficiently small satisfying (2.7) there is a $T_1 > 0$ such that if $t > T_1$,

$$x_1(t) \leqslant \frac{r_1}{a_{11}} + \varepsilon.$$

It therefore follows from the third equation of system (1.2) that for $t > T_1 + \tau$,

$$\dot{y}_1(t) \leqslant \alpha e^{-\gamma\tau}\left(\frac{r_1}{a_{11}} + \varepsilon\right)y_1(t-\tau) - r_3y_1(t) - a_{33}y_1^2(t).$$

Consider the following equation

$$\dot{u}(t) = \alpha e^{-\gamma\tau}\left(\frac{r_1}{a_{11}} + \varepsilon\right)u(t-\tau) - r_3u(t) - a_{33}u^2(t). \tag{2.8}$$

By Lemma 2.2 we derive from (2.7) and (2.8) that

$$\lim_{t\to+\infty} u(t) = 0.$$

A standard comparison argument shows that

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

Therefore, $\forall\varepsilon > 0$, there is a $T_4 > T_3$ such that if $t > T_4$, $0 < y_1(t) < \frac{\gamma\varepsilon}{2\alpha M_1(1-e^{-\gamma\tau})}$. In addition, it follows from (2.2) that $0 < x_1(t) \leqslant M_1$ for $t > T_4 > T_3$. Thus, we derive from (2.1) that for $t > T_4 + \tau$,

$$y_2(t) = \int_{t-\tau}^{t} \alpha e^{-\gamma(t-s)}x_1(s)y_1(s)\,ds \leqslant \int_{t-\tau}^{t} \alpha e^{-\gamma(t-s)}M_1\frac{\gamma\varepsilon}{2\alpha M_1(1-e^{-\gamma\tau})}\,ds < \varepsilon.$$

We therefore obtain that

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

This completes the proof. □

3. Global stability

In this section, we discuss the global asymptotic stability of a positive equilibrium of system (1.2). The strategy of the proofs is to construct appropriate Lyapunov functionals.

By Theorem 2.1 we see that if (H1)–(H3) hold, system (1.2) is permanent, which implies that system (1.2) must have at least one positive equilibrium (see, for example, [7]). In the following we always assume that such a positive equilibrium exists and denote it by $E^*(x_1^*, x_2^*, y_1^*, y_2^*)$.

Theorem 3.1. *Let* (H1)–(H3) *hold. Assume further that*

(H5) $A_i > 0$, $i = 1, 2$, *where*

$$\begin{aligned} A_1 &= a_{11} - \frac{a_{13}^2 \alpha e^{-\gamma\tau}}{a_{11}a_{33}}, \\ A_2 &= \frac{1}{2} - \frac{a_{13}\alpha e^{-\gamma\tau}}{a_{11}a_{33}} - \frac{\alpha e^{-\gamma\tau}}{2a_{33}} - \frac{D_1 \alpha e^{-\gamma\tau}}{r_1 \alpha e^{-\gamma\tau} - r_3 a_{11}}. \end{aligned} \tag{3.1}$$

Then the positive equilibrium $E^*(x_1^*, x_2^*, y_1^*, y_2^*)$ *of system* (1.2) *is globally asymptotically stable.*

Proof. We first consider the following subsystem:

$$\begin{aligned} \dot{x}_1(t) &= x_1(t)(r_1 - a_{11}x_1(t) - a_{13}y_1(t)) + D_1(x_2(t) - x_1(t)), \\ \dot{x}_2(t) &= x_2(t)(r_2 - a_{22}x_2(t)) + D_2(x_1(t) - x_2(t)), \\ \dot{y}_1(t) &= \alpha e^{-\gamma\tau} x_1(t-\tau)y_1(t-\tau) - r_3 y_1(t) - a_{33}y_1^2(t). \end{aligned} \tag{3.2}$$

Noting that $E_1^*(x_1^*, x_2^*, y_1^*)$ is a positive equilibrium of system (3.2), we may rewrite system (3.2) as

$$\begin{aligned} \dot{x}_1(t) =& x_1(t)[-a_{11}(x_1(t) - x_1^*) - a_{13}(y_1(t) - y_1^*)] \\ & - \frac{D_1}{x_1^*} x_2(t)(x_1(t) - x_1^*) + \frac{D_1}{x_1^*} x_1(t)(x_2(t) - x_2^*), \\ \dot{x}_2(t) =& - a_{22}x_2(t)(x_2(t) - x_2^*) \\ & - \frac{D_2}{x_2^*} x_1(t)(x_2(t) - x_2^*) + \frac{D_2}{x_2^*} x_2(t)(x_1(t) - x_1^*), \\ \dot{y}_1(t) =& \alpha e^{-\gamma\tau} y_1(t-\tau)(x_1(t-\tau) - x_1^*) + \alpha e^{-\gamma\tau} x_1^*(y_1(t-\tau) - y_1^*) \\ & - r_3(y_1(t) - y_1^*) - a_{33}(y_1(t) + y_1^*)(y_1(t) - y_1^*). \end{aligned} \tag{3.3}$$

Define

$$V_1(t) = \sum_{i=1}^{2} c_i\left(x_i(t) - x_i^* - x_i^* \ln\frac{x_i(t)}{x_i^*}\right) + \frac{1}{2}c_3(y_1(t) - y_1^*)^2. \tag{3.4}$$

Calculating the derivative of $V_1(t)$ along solutions of system (1.2), it follows that

$$\begin{aligned}\frac{\mathrm{d}V_1(t)}{\mathrm{d}t} &= \sum_{i=1}^{2} c_i(x_i(t) - x_i^*)\frac{\dot{x}_i(t)}{x_i(t)} + c_3(y_1(t) - y_1^*)\dot{y}_1(t)\\ &= -c_1a_{11}(x_1(t) - x_1^*)^2 - c_1a_{13}(x_1(t) - x_1^*)(y_1(t) - y_1^*) - \frac{c_1D_1}{x_1^*}\\ &\quad\times\frac{x_2(t)}{x_1(t)}(x_1(t) - x_1^*)^2 + \frac{c_1D_1}{x_1^*}(x_1(t) - x_1^*)(x_2(t) - x_2^*)\\ &\quad - c_2a_{22}(x_2(t) - x_2^*)^2 - \frac{c_2D_2}{x_2^*}\frac{x_1(t)}{x_2(t)}(x_2(t) - x_2^*)^2 + \frac{c_2D_2}{x_2^*}\\ &\quad\times(x_1(t) - x_1^*)(x_2(t) - x_2^*) + c_3\alpha e^{-\gamma\tau}y_1(t-\tau)(x_1(t-\tau)\\ &\quad - x_1^*)(y_1(t) - y_1^*) + c_3\alpha e^{-\gamma\tau}x_1^*(y_1(t) - y_1^*)(y_1(t-\tau) - y_1^*)\\ &\quad - c_3r_3(y_1(t) - y_1^*)^2 - c_3a_{33}(y_1(t) + y_1^*)(y_1(t) - y_1^*)^2.\end{aligned} \tag{3.5}$$

Setting $c_1 = 1$, $c_2 = D_1x_2^*/(D_2x_1^*)$, we derive from (3.5) that

$$\begin{aligned}\frac{\mathrm{d}V_1(t)}{\mathrm{d}t} &= -a_{11}(x_1(t) - x_1^*)^2 - \frac{a_{22}D_1x_2^*}{D_2x_1^*}(x_2(t) - x_2^*)^2 - a_{13}(x_1(t) - x_1^*)\\ &\quad\times(y_1(t) - y_1^*) - \frac{D_1}{x_1^*}\left[\sqrt{\frac{x_2(t)}{x_1(t)}}(x_1(t) - x_1^*) - \sqrt{\frac{x_1(t)}{x_2(t)}}(x_2(t) - x_2^*)\right]^2\\ &\quad + c_3\alpha e^{-\gamma\tau}y_1(t-\tau)(x_1(t-\tau) - x_1^*)(y_1(t) - y_1^*)\\ &\quad + c_3\alpha e^{-\gamma\tau}x_1^*(y_1(t) - y_1^*)(y_1(t-\tau) - y_1^*) - c_3r_3(y_1(t) - y_1^*)^2\\ &\quad - c_3a_{33}(y_1(t) + y_1^*)(y_1(t) - y_1^*)^2\\ &\leqslant -a_{11}(x_1(t) - x_1^*)^2 - \frac{a_{22}D_1x_2^*}{D_2x_1^*}(x_2(t) - x_2^*)^2 - a_{13}(x_1(t) - x_1^*)\\ &\quad\times(y_1(t) - y_1^*) + c_3\alpha e^{-\gamma\tau}y_1(t-\tau)(x_1(t-\tau) - x_1^*)(y_1(t) - y_1^*)\\ &\quad + c_3\alpha e^{-\gamma\tau}x_1^*(y_1(t) - y_1^*)(y_1(t-\tau) - y_1^*) - c_3r_3(y_1(t) - y_1^*)^2\\ &\quad - c_3a_{33}(y_1(t) + y_1^*)(y_1(t) - y_1^*)^2.\end{aligned} \tag{3.6}$$

By using the inequality $ab \leqslant \frac{1}{2}ka^2 + \frac{1}{2k}b^2$, it follows from (3.6) that

$$\begin{aligned}\frac{\mathrm{d}V_1(t)}{\mathrm{d}t} \leqslant & -a_{11}(x_1(t)-x_1^*)^2 - \frac{a_{22}D_1x_2^*}{D_2x_1^*}(x_2(t)-x_2^*)^2 \\ & + a_{13}\left\{\frac{1}{2}A(x_1(t)-x_1^*)^2 + \frac{1}{2A}(y_1(t)-y_1^*)^2\right\} + c_3\alpha \mathrm{e}^{-\gamma\tau}y_1(t-\tau) \\ & \times \left\{\frac{1}{2}B(x_1(t-\tau)-x_1^*)^2 + \frac{1}{2B}(y_1(t)-y_1^*)^2\right\} \\ & + c_3\alpha \mathrm{e}^{-\gamma\tau}x_1^*\left\{\frac{1}{2}C(y_1(t)-y_1^*)^2 + \frac{1}{2C}(y_1(t-\tau)-y_1^*)^2\right\} \\ & - c_3r_3(y_1(t)-y_1^*)^2 - c_3a_{33}(y_1(t)+y_1^*)(y_1(t)-y_1^*)^2, \end{aligned} \tag{3.7}$$

where parameters A, B, C are positive constants to be determined.

Define

$$\begin{aligned} V(t) = & V_1(t) + \frac{1}{2}c_3\alpha \mathrm{e}^{-\gamma\tau}B\int_{t-\tau}^{t} y_1(s)(x_1(s)-x_1^*)^2\mathrm{d}s + \frac{1}{2C}c_3\alpha \mathrm{e}^{-\gamma\tau}x_1^* \\ & \times \int_{t-\tau}^{t}(y_1(s)-y_1^*)^2\mathrm{d}s. \end{aligned} \tag{3.8}$$

Then it follows from (3.7) and (3.8) that

$$\begin{aligned}\frac{\mathrm{d}V(t)}{\mathrm{d}t} \leqslant & -a_{11}(x_1(t)-x_1^*)^2 - \frac{a_{22}D_1x_2^*}{D_2x_1^*}(x_2(t)-x_2^*)^2 \\ & + a_{13}\left\{\frac{1}{2}A(x_1(t)-x_1^*)^2 + \frac{1}{2A}(y_1(t)-y_1^*)^2\right\} \\ & + \frac{1}{2}c_3\alpha B\mathrm{e}^{-\gamma\tau}y_1(t)(x_1(t)-x_1^*)^2 + \frac{1}{2B}c_3\alpha \mathrm{e}^{-\gamma\tau}y_1(t-\tau)(y_1(t)-y_1^*)^2 \\ & + c_3\alpha \mathrm{e}^{-\gamma\tau}x_1^*\left(\frac{1}{2}C + \frac{1}{2C}\right)(y_1(t)-y_1^*)^2 - c_3r_3(y_1(t)-y_1^*)^2 \\ & - c_3a_{33}(y_1(t)+y_1^*)(y_1(t)-y_1^*)^2. \end{aligned} \tag{3.9}$$

Setting $A = \frac{a_{11}}{a_{13}}$, $B = C = 1$, $c_3 = \frac{a_{13}^2}{r_1\alpha \mathrm{e}^{-\gamma\tau} - r_3a_{11}}$, we derive from (3.9) that for $t > T + \tau$,

$$\begin{aligned}\frac{\mathrm{d}V(t)}{\mathrm{d}ct} \leqslant & -\frac{1}{2}[a_{11} - c_3\alpha \mathrm{e}^{-\gamma\tau}y_1(t)](x_1(t)-x_1^*)^2 - \frac{a_{22}D_1x_2^*}{D_2x_1^*}(x_2(t)-x_2^*)^2 \\ & - \left[c_3a_{33}y_1(t) - \frac{a_{13}^2}{2a_{11}} - \frac{1}{2}c_3\alpha \mathrm{e}^{-\gamma\tau}y_1(t-\tau)\right](y_1(t)-y_1^*)^2 \\ \leqslant & -\bar{A}_1(x_1(t)-x_1^*)^2 - \bar{A}_2(x_2(t)-x_2^*)^2 - \bar{A}_3(y_1(t)-y_1^*)^2, \end{aligned} \tag{3.10}$$

where

$$\begin{aligned}\bar{A}_1 &= \frac{1}{2}\left(a_{11} - \frac{a_{13}^2\alpha e^{-\gamma\tau}}{r_1\alpha e^{-\gamma\tau} - r_3 a_{11}} M_2\right), \quad \bar{A}_2 = \frac{a_{22}D_1 x_2^*}{D_2 x_1^*},\\ \bar{A}_3 &= \frac{a_{13}^2 a_{33} m_2}{r_1\alpha e^{-\gamma\tau} - r_3 a_{11}} - \frac{a_{13}^2}{2a_{11}} - \frac{a_{13}^2\alpha e^{-\gamma\tau} M_2}{2(r_1\alpha e^{-\gamma\tau} - r_3 a_{11})},\end{aligned} \tag{3.11}$$

M_2 and m_2 are defined in (2.3) and (2.6), respectively.

If (H1)–(H3) and (H5) hold and $\varepsilon > 0$ is sufficiently small, we have $\bar{A}_1 > 0$, $\bar{A}_3 > 0$. We therefore conclude from the Lyapunov Theorem (see, for example, [28, Corollary 5.2]) that the positive equilibrium $E_1^*(x_1^*, x_2^*, y_1^*)$ of system (3.2) is globally asymptotically stable. Thus, we have

$$\lim_{t\to+\infty} x_1(t) = x_1^*, \quad \lim_{t\to+\infty} x_2(t) = x_2^*, \quad \lim_{t\to+\infty} y_1(t) = y_1^*. \tag{3.12}$$

By using L'Hospital's rule, it follows from (2.1) and (3.12) that

$$\begin{aligned}\lim_{t\to+\infty} y_2(t) &= \lim_{t\to+\infty} \frac{\alpha[e^{\gamma t}x_1(t)y_1(t) - e^{\gamma_1(t-\tau)}x_1(t-\tau)y_1(t-\tau)]}{\gamma e^{\gamma t}}\\ &= \frac{\alpha}{\gamma}\lim_{t\to+\infty}\{x_1(t)y_1(t) - e^{-\gamma\tau}x_1(t-\tau)y_1(t-\tau)\}\\ &= \frac{\alpha x_1^* y_1^*}{\gamma}(1 - e^{-\gamma\tau}) = y_2^*.\end{aligned} \tag{3.13}$$

This completes the proof. □

In the following, we give another result on the global stability of the positive equilibrium $E^*(x_1^*, x_2^*, y_1^*, y_2^*)$ of system (1.2) by constructing a different Lyapunov functional.

Theorem 3.2. *Let* (H1)–(H3) *hold. Then the positive equilibrium* $E^*(x_1^*, x_2^*, y_1^*, y_2^*)$ *of system* (1.2) *is globally asymptotically stable provided that*

(H6) $\alpha_i > 0$, $i = 1, 2, 3$, *where*

$$\begin{aligned}\alpha_1 &= \frac{\alpha e^{-\gamma\tau}a_{11}}{a_{13}} - \frac{1}{2m_2}\alpha e^{-\gamma\tau}M_1M_2\tau\left(a_{11} + \frac{D_1}{x_1^*} + \alpha e^{-\gamma\tau}\right),\\ \alpha_2 &= \frac{D_1}{x_1^*}\left(\frac{\alpha a_{22}x_2^* e^{-\gamma\tau}}{a_{13}D_2} - \frac{1}{2m_2}\alpha e^{-\gamma\tau}M_1M_2\tau\right),\\ \alpha_3 &= a_{33} - \frac{2}{m_2}\alpha^2 M_1 x_1^*\tau e^{-2\gamma\tau} - \frac{1}{2m_2}M_1M_2\alpha\tau e^{-\gamma\tau}\\ &\quad\times\left(a_{11} + 2a_{13} + \frac{2D_1}{x_1^*} + \alpha e^{-\gamma\tau} + 2a_{33}\right),\end{aligned} \tag{3.14}$$

in which M_i *and* m_i *are defined in* (2.2), (2.3), (2.5) *and* (2.6), *respectively.*

Proof. We first consider the following subsystem

$$\begin{aligned}\dot{x}_1(t) &= x_1(t)(r_1 - a_{11}x_1(t) - a_{13}y_1(t)) + D_1(x_2(t) - x_1(t)),\\ \dot{x}_2(t) &= x_2(t)(r_2 - a_{22}x_2(t)) + D_2(x_1(t) - x_2(t)),\\ \dot{y}_1(t) &= \alpha e^{-\gamma\tau}x_1(t-\tau)y_1(t-\tau) - r_3y_1(t) - a_{33}y_1^2(t).\end{aligned} \tag{3.15}$$

System (3.15) can be rewritten as

$$\begin{aligned}\dot{x}_1(t) =& x_1(t)(r_1 - a_{11}x_1(t) - a_{13}y_1(t)) + D_1(x_2(t) - x_1(t)),\\ \dot{x}_2(t) =& x_2(t)(r_2 - a_{22}x_2(t)) + D_2(x_1(t) - x_2(t)),\\ \dot{y}_1(t) =& y_1(t)(-r_3 + \alpha e^{-\gamma\tau}x_1(t) - a_{33}y_1(t))\\ & - \alpha e^{-\gamma\tau}\int_{t-\tau}^{t} y_1(u)\{x_1(u)(r_1 - a_{11}x_1(u) - a_{13}y_1(u)) + D_1(x_2(u) - x_1(u))\}\mathrm{d}u\\ & - \alpha e^{-\gamma\tau}\int_{t-\tau}^{t} x_1(u)\{\alpha e^{-\gamma\tau}x_1(u-\tau)y_1(u-\tau) - r_3y_1(u) - a_{33}y_1^2(u)\}\mathrm{d}u.\end{aligned} \tag{3.16}$$

Noting that if (H1)–(H3) hold, $E_1^*(x_1^*, x_2^*, y_1^*)$ is a positive equilibrium of system (3.15), we therefore rewrite system (3.16) into

$$\begin{aligned}\dot{x}_1(t) =& x_1(t)[-a_{11}(x_1(t) - x_1^*) - a_{13}(y_1(t) - y_1^*)]\\ & - \frac{D_1}{x_1^*}x_2(t)(x_1(t) - x_1^*) + \frac{D_1}{x_1^*}x_1(t)(x_2(t) - x_2^*),\\ \dot{x}_2(t) =& -a_{22}x_2(t)(x_2(t) - x_2^*) - \frac{D_2}{x_2^*}x_1(t)(x_2(t) - x_2^*) + \frac{D_2}{x_2^*}x_2(t)(x_1(t) - x_1^*),\\ \dot{y}_1(t) =& y_1(t)[\alpha e^{-\gamma\tau}(x_1(t) - x_1^*) - a_{33}(y_1(t) - y_1^*)]\\ & - \alpha e^{-\gamma\tau}\int_{t-\tau}^{t} y_1(u)\Big\{x_1(u)[-a_{11}(x_1(u) - x_1^*) - a_{13}(y_1(u) - y_1^*)]\\ & - \frac{D_1}{x_1^*}x_2(u)(x_1(u) - x_1^*) + \frac{D_1}{x_1^*}x_1(u)(x_2(u) - x_2^*)\Big\}\mathrm{d}u\\ & - \alpha e^{-\gamma\tau}\int_{t-\tau}^{t} x_1(u)\{\alpha e^{-\gamma\tau}[y_1(u-\tau)(x_1(u-\tau) - x_1^*)\\ & + x_1^*(y_1(u-\tau) - y_1^*) - x_1^*(y_1(u) - y_1^*)] - a_{33}y_1(u)(y_1(u) - y_1^*)\}\mathrm{d}u.\end{aligned} \tag{3.17}$$

Let

$$V_1(t) = \sum_{i=1}^{2} c_i\left(x_i(t) - x_i^* - x_i^* \ln\frac{x_i(t)}{x_i^*}\right), \tag{3.18}$$

where c_1 and c_2 are positive constants to be determined.

Calculating the derivative of $V_1(t)$ along solutions of system (1.2), it follows from (3.17) and (3.18) that

$$\begin{aligned}\frac{\mathrm{d}V_1(t)}{\mathrm{d}t} &= c_1(x_1(t)-x_1^*)\frac{\dot{x}_1(t)}{x_1(t)} + c_2(x_2(t)-x_2^*)\frac{\dot{x}_2(t)}{x_2(t)} \\ &= -c_1a_{11}(x_1(t)-x_1^*)^2 - c_1a_{13}(x_1(t)-x_1^*)(y_1(t)-y_1^*) - \frac{c_1D_1}{x_1^*}\frac{x_2(t)}{x_1(t)} \\ &\quad \times (x_1(t)-x_1^*)^2 + \frac{c_1D_1}{x_1^*}(x_1(t)-x_1^*)(x_2(t)-x_2^*) \\ &\quad - c_2a_{22}(x_2(t)-x_2^*)^2 - \frac{c_2D_2}{x_2^*}\frac{x_1(t)}{x_2(t)}(x_2(t)-x_2^*)^2 \\ &\quad + \frac{c_2D_2}{x_2^*}(x_1(t)-x_1^*)(x_2(t)-x_2^*). \end{aligned} \tag{3.19}$$

Setting $c_1 = \alpha e^{-\gamma\tau}/a_{13}$, $c_2 = \alpha D_1x_2^*e^{-\gamma\tau}/(a_{13}D_2x_1^*)$, we derive from (3.19) that

$$\begin{aligned}\frac{\mathrm{d}V_1(t)}{\mathrm{d}t} &= -\frac{\alpha e^{-\gamma\tau}a_{11}}{a_{13}}(x_1(t)-x_1^*)^2 - \alpha e^{-\gamma\tau}(x_1(t)-x_1^*)(y_1(t)-y_1^*) \\ &\quad - \frac{\alpha a_{22}D_1x_2^*e^{-\gamma\tau}}{a_{13}D_2x_1^*}(x_2(t)-x_2^*)^2 \\ &\quad - \frac{\alpha D_1e^{-\gamma\tau}}{a_{13}x_1^*}\left[\sqrt{\frac{x_2(t)}{x_1(t)}}(x_1(t)-x_1^*) - \sqrt{\frac{x_1(t)}{x_2(t)}}(x_2(t)-x_2^*)\right]^2 \\ &\leqslant -\frac{\alpha e^{-\gamma\tau}a_{11}}{a_{13}}(x_1(t)-x_1^*)^2 - \alpha e^{-\gamma\tau}(x_1(t)-x_1^*)(y_1(t)-y_1^*) \\ &\quad - \frac{\alpha a_{22}D_1x_2^*e^{-\gamma\tau}}{a_{13}D_2x_1^*}(x_2(t)-x_2^*)^2. \end{aligned} \tag{3.20}$$

Next, let

$$V_{21}(t) = y_1(t) - y_1^* - y_1^*\ln\frac{y_1(t)}{y_1^*}. \tag{3.21}$$

Calculating the derivative of $V_{21}(t)$ along solutions of system (1.2), it follows from (3.17) and (3.21) that

$$\begin{aligned}\frac{\mathrm{d}V_{21}(t)}{\mathrm{d}t} &= (y_1(t)-y_1^*)\frac{\dot{y}_1(t)}{y_1(t)} \\ &= -a_{33}(y_1(t)-y_1^*)^2 + \alpha e^{-\gamma\tau}(x_1(t)-x_1^*)(y_1(t)-y_1^*) - \alpha e^{-\gamma\tau} \\ &\quad \times \frac{1}{y_1(t)}(y_1(t)-y_1^*)\int_{t-\tau}^{t} y_1(u)\Big\{x_1(u)[-a_{11}(x_1(u)-x_1^*) - a_{13}(y_1(u)-y_1^*)] \\ &\quad - \frac{D_1}{x_1^*}x_2(u)(x_1(u)-x_1^*) + \frac{D_1}{x_1^*}x_1(u)(x_2(u)-x_2^*)\Big\}\mathrm{d}u - \alpha e^{-\gamma\tau}\frac{1}{y_1(t)}(y_1(t)-y_1^*) \\ &\quad \times \int_{t-\tau}^{t} x_1(u)\{\alpha e^{-\gamma\tau}[y_1(u-\tau)(x_1(u-\tau)-x_1^*) + x_1^*(y_1(u-\tau)-y_1^*) \\ &\quad - x_1^*(y_1(u)-y_1^*)] - a_{33}y_1(u)(y_1(u)-y_1^*)\}\mathrm{d}u. \end{aligned} \tag{3.22}$$

Using the inequality $a^2 + b^2 \geqslant 2ab$, we derive from (3.22) that

$$\begin{aligned}\frac{\mathrm{d}V_{21}(t)}{\mathrm{d}t} \leqslant & -a_{33}(y_1(t)-y_1^*)^2 + \alpha \mathrm{e}^{-\gamma\tau}(x_1(t)-x_1^*)(y_1(t)-y_1^*) + \alpha \mathrm{e}^{-\gamma\tau}\frac{1}{2y_1(t)} \\ & \times (y_1(t)-y_1^*)^2 \int_{t-\tau}^{t} y_1(u)\left\{x_1(u)(a_{11}+a_{13}) + \frac{D_1}{x_1^*}x_2(u)\right. \\ & \left. + \frac{D_1}{x_1^*}x_1(u)\right\}\mathrm{d}u + \alpha \mathrm{e}^{-\gamma\tau}\frac{1}{2y_1(t)}\int_{t-\tau}^{t} y_1(u)\left\{x_1(u)[a_{11}(x_1(u)-x_1^*)^2\right. \\ & + a_{13}(y_1(u)-y_1^*)^2] + \frac{D_1}{x_1^*}x_2(u)(x_1(u)-x_1^*)^2 \\ & \left. + \frac{D_1}{x_1^*}x_1(u)(x_2(u)-x_2^*)^2\right\}\mathrm{d}u + \alpha \mathrm{e}^{-\gamma\tau}\frac{1}{2y_1(t)}(y_1(t)-y_1^*)^2 \\ & \times \int_{t-\tau}^{t} x_1(u)\{\alpha \mathrm{e}^{-\gamma\tau}(y_1(u-\tau)+2x_1^*) + a_{33}y_1(u)\}\mathrm{d}u \\ & + \alpha \mathrm{e}^{-\gamma\tau}\frac{1}{2y_1(t)}\int_{t-\tau}^{t} x_1(u)\left\{\alpha \mathrm{e}^{-\gamma\tau}[y_1(u-\tau)(x_1(u-\tau)-x_1^*)^2\right. \\ & \left. + x_1^*(y_1(u-\tau)-y_1^*)^2 + x_1^*(y_1(u)-y_1^*)^2] + a_{33}y_1(u)(y_1(u)-y_1^*)^2\right\}\mathrm{d}u. \end{aligned} \tag{3.23}$$

By Theorem 2.1, there is a $T > 0$ such that if $t > T$, $m_1 < x_i(t) < M_1$ $(i = 1, 2)$, $m_2 < y_1(t) < M_2$. It therefore follows from (3.23) that for $t > T + \tau$,

$$\begin{aligned}\frac{\mathrm{d}V_{21}(t)}{\mathrm{d}t} \leqslant & -a_{33}(y_1(t)-y_1^*)^2 + \alpha \mathrm{e}^{-\gamma\tau}(x_1(t)-x_1^*)(y_1(t)-y_1^*) \\ & + \frac{1}{2m_2}M_1M_2\alpha\tau \mathrm{e}^{-\gamma\tau}\left(a_{11}+a_{13}+\frac{2D_1}{x_1^*}\right)(y_1(t)-y_1^*)^2 \\ & + \alpha \mathrm{e}^{-\gamma\tau}\frac{1}{2m_2}\int_{t-\tau}^{t} M_2\left\{M_1[a_{11}(x_1(u)-x_1^*)^2 + a_{13}(y_1(u)-y_1^*)^2]\right. \\ & \left. + \frac{D_1}{x_1^*}M_1(x_1(u)-x_1^*)^2 + \frac{D_1}{x_1^*}M_1(x_2(u)-x_2^*)^2\right\}\mathrm{d}u \\ & + \frac{1}{2m_2}M_1\alpha\tau \mathrm{e}^{-\gamma\tau}[\alpha \mathrm{e}^{-\gamma\tau}(M_2+2x_1^*) \\ & + a_{33}M_2](y_1(t)-y_1^*)^2 + \alpha \mathrm{e}^{-\gamma\tau}\frac{1}{2m_2}\int_{t-\tau}^{t} M_1\{\alpha \mathrm{e}^{-\gamma\tau}[M_2(x_1(u-\tau)-x_1^*)^2 \\ & + x_1^*(y_1(u-\tau)-y_1^*)^2 + x_1^*(y_1(u)-y_1^*)^2] \\ & + a_{33}M_2(y_1(u)-y_1^*)^2\}\mathrm{d}u. \end{aligned} \tag{3.24}$$

Define

$$V_{22}(t) = \frac{1}{2m_2}\alpha M_1 M_2 e^{-\gamma\tau} \int_{t-\tau}^{t} \int_{s}^{t} \left\{ a_{11}(x_1(u) - x_1^*)^2 + a_{13}(y_1(u) - y_1^*)^2 \right.$$
$$\left. + \frac{D_1}{x_1^*}(x_1(u) - x_1^*)^2 + \frac{D_1}{x_1^*}(x_2(u) - x_2^*)^2 \right\} du\, ds + \frac{1}{2m_2}\alpha M_1 e^{-\gamma\tau}$$
$$\times \int_{t-\tau}^{t} \int_{s}^{t} \{\alpha e^{-\gamma\tau}[M_2(x_1(u-\tau) - x_1^*)^2 + x_1^*(y_1(u-\tau) - y_1^*)^2$$
$$+ x_1^*(y_1(u) - y_1^*)^2] + a_{33}M_2(y_1(u) - y_1^*)^2\} du\, ds. \tag{3.25}$$

We derive from (3.24) and (3.25) that for $t > T + \tau$,

$$\frac{dV_{21}(t)}{dt} + \frac{dV_{22}(t)}{dt} \leqslant -a_{33}(y_1(t) - y_1^*)^2 + \alpha e^{-\gamma\tau}(x_1(t) - x_1^*)(y_1(t) - y_1^*)$$
$$+ \frac{1}{2m_2} M_1 M_2 \alpha\tau e^{-\gamma\tau}\left(a_{11} + a_{13} + \frac{2D_1}{x_1^*}\right)(y_1(t) - y_1^*)^2$$
$$+ \frac{1}{2m_2}\alpha e^{-\gamma\tau} M_2 \tau \left\{ M_1[a_{11}(x_1(t) - x_1^*)^2 + a_{13}(y_1(t) - y_1^*)^2] \right.$$
$$\left. + \frac{D_1}{x_1^*} M_1 (x_1(t) - x_1^*)^2 + \frac{D_1}{x_1^*} M_1 (x_2(t) - x_2^*)^2 \right\}$$
$$+ \frac{1}{2m_2} M_1 \alpha\tau e^{-\gamma\tau}[\alpha e^{-\gamma\tau}(M_2 + 2x_1^*) + a_{33}M_2](y_1(t) - y_1^*)^2$$
$$+ \frac{1}{2m_2}\alpha M_1 \tau e^{-\gamma\tau}\{\alpha e^{-\gamma\tau}[M_2(x_1(t-\tau) - x_1^*)^2$$
$$+ x_1^*(y_1(t-\tau) - y_1^*)^2 + x_1^*(y_1(t) - y_1^*)^2]$$
$$+ a_{33}M_2(y_1(t) - y_1^*)^2\}. \tag{3.26}$$

Define

$$V_2(t) = V_{21}(t) + V_{22}(t) + \frac{1}{2m_2}\alpha^2 M_1 \tau e^{-2\gamma\tau} \int_{t-\tau}^{t} [M_2(x_1(l) - x_1^*)^2$$
$$+ x_1^*(y_1(l) - y_1^*)^2] dl. \tag{3.27}$$

It follows from (3.26) and (3.27) that for $t > T + \tau$,

$$\begin{aligned}\frac{dV_2(t)}{dt} \leqslant & -a_{33}(y_1(t)-y_1^*)^2 + \alpha e^{-\gamma\tau}(x_1(t)-x_1^*)(y_1(t)-y_1^*) \\ & + \frac{1}{2m_2} M_1 M_2 \alpha\tau e^{-\gamma\tau}\left(a_{11} + a_{13} + \frac{2D_1}{x_1^*}\right)(y_1(t)-y_1^*)^2 \\ & + \frac{1}{2m_2}\alpha e^{-\gamma\tau} M_2 \tau \Big\{ M_1[a_{11}(x_1(t)-x_1^*)^2 + a_{13}(y_1(t)-y_1^*)^2] \\ & + \frac{D_1}{x_1^*} M_1 (x_1(t)-x_1^*)^2 + \frac{D_1}{x_1^*} M_1 (x_2(t)-x_2^*)^2 \Big\} \\ & + \frac{1}{2m_2} M_1 \alpha\tau e^{-\gamma\tau}[\alpha e^{-\gamma\tau}(M_2 + 2x_1^*) + a_{33}M_2](y_1(t)-y_1^*)^2 \\ & + \frac{1}{2m_2}\alpha M_1 \tau e^{-\gamma\tau}\{\alpha e^{-\gamma\tau}[M_2(x_1(t)-x_1^*)^2 + 2x_1^*(y_1(t)-y_1^*)^2] \\ & + a_{33}M_2(y_1(t)-y_1^*)^2\}. \end{aligned} \tag{3.28}$$

Finally, we define

$$V(t) = V_1(t) + V_2(t). \tag{3.29}$$

Then we obtain from (3.20), (3.28) and (3.29) that for $t > T + \tau$,

$$\frac{dV(t)}{dt} \leqslant -\alpha_1(x_1(t)-x_1^*)^2 - \alpha_2(x_2(t)-x_2^*)^2 - \alpha_3(y_1(t)-y_1^*)^2,$$

where α_i is defined in (3.14). We therefore conclude from the Lyapunov Theorem (see, for example, [28, Corollary 5.2]) that the positive equilibrium $E_1^*(x_1^*, x_2^*, y_1^*)$ of system (3.15) is globally asymptotically stable. Thus, we have

$$\lim_{t\to+\infty} x_i(t) = x_i^* \quad (i = 1, 2), \qquad \lim_{t\to+\infty} y_1(t) = y_1^*.$$

By the same argument as in (3.13) it follows from (2.1) that $\lim_{t\to+\infty} y_2(t) = y_2^*$. This completes the proof. □

It is interesting to discuss the local stability of the positive equilibrium $E^*(x_1^*, x_2^*, y_1^*, y_2^*)$ of system (1.2).

The characteristic equation of the positive equilibrium E^* of (1.2) is of the form

$$(\lambda + \gamma)[P(\lambda) + Q(\lambda)e^{-\lambda\tau}] = 0,$$

where

$$P(\lambda) = \lambda^3 + a_2\lambda^2 + a_1\lambda + a_0,$$
$$Q(\lambda) = b_2\lambda^2 + b_1\lambda + b_0,$$

here

$$
\begin{aligned}
a_0 =&(r_3 + 2a_{33}y_1^*)\left[\left(a_{11}x_1^* + D_1\frac{x_2^*}{x_1^*}\right)\left(a_{22}x_2^* + D_2\frac{x_1^*}{x_2^*}\right) - D_1D_2\right],\\
a_1 =&(r_3 + 2a_{33}y_1^*)\left(a_{11}x_1^* + D_1\frac{x_2^*}{x_1^*} + a_{22}x_2^* + D_2\frac{x_1^*}{x_2^*}\right)\\
&+\left(a_{11}x_1^* + D_1\frac{x_2^*}{x_1^*}\right)\left(a_{22}x_2^* + D_2\frac{x_1^*}{x_2^*}\right) - D_1D_2,\\
a_2 =&a_{11}x_1^* + D_1\frac{x_2^*}{x_1^*} + a_{22}x_2^* + D_2\frac{x_1^*}{x_2^*} + r_3 + 2a_{33}y_1^*,\\
b_0 =&\alpha e^{-\gamma\tau}x_1^*\left[-\left(a_{11}x_1^* + D_1\frac{x_2^*}{x_1^*}\right)\left(a_{22}x_2^* + D_2\frac{x_1^*}{x_2^*}\right) + a_{13}y_1^*\left(a_{22}x_2^* + D_2\frac{x_1^*}{x_2^*}\right) + D_1D_2\right],\\
b_1 =& -\alpha e^{-\gamma\tau}x_1^*\left[a_{11}x_1^* + D_1\frac{x_2^*}{x_1^*} + a_{22}x_2^* + D_2\frac{x_1^*}{x_2^*} - a_{13}y_1^*\right],\\
b_2 =& -\alpha e^{-\gamma\tau}x_1^*.
\end{aligned}
$$

Clearly, $\lambda = -\gamma$ is a negative eigenvalue. Noting that $a_i > 0$ $(i = 0, 1, 2)$ and $a_1a_2 - a_0 > 0$, by Routh–Hurwitz Theorem the positive equilibrium E^* of system (1.2) is locally asymptotically stable when $\tau = 0$.

Let

$$
\begin{aligned}
F(y) &= |P(iy)|^2 - |Q(iy)|^2\\
&= y^6 + (a_2^2 - 2a_1 - b_2^2)y^4 + (a_1^2 - 2a_0a_2 + 2b_2b_0 - b_1^2)y^2 + a_0^2 - b_0^2.
\end{aligned}
$$

It is easy to show that

$$
\begin{aligned}
a_0 + b_0 = a_{33}y_1^*&\left[\left(a_{11}x_1^* + D_1\frac{x_2^*}{x_1^*}\right)\left(a_{22}x_2^* + D_2\frac{x_1^*}{x_2^*}\right) - D_1D_2\right]\\
&+ a_{13}y_1^*(r_3 + a_{33}y_1^*)\left(a_{22}x_2^* + D_2\frac{x_1^*}{x_2^*}\right) > 0,
\end{aligned}
$$

$$
\begin{aligned}
a_2^2 - 2a_1 - b_2^2 = &\left(a_{11}x_1^* + D_1\frac{x_2^*}{x_1^*}\right)^2 + \left(a_{22}x_2^* + D_2\frac{x_1^*}{x_2^*}\right)^2 + 2D_1D_2\\
&+ a_{33}y_1^*(2r_3 + 3a_{33}y_1^*) > 0.
\end{aligned}
$$

By the general theory on characteristic equations of delay differential equations (see, for example, [28, Theorem 4.1]), we therefore derive the following results on the stability of the positive equilibrium E^*.

Theorem 3.3. *Suppose that system (1.2) admits a positive equilibrium* $E^*(x_1^*, x_2^*, y_1^*, y_2^*)$.

(1) *If* $a_0 > b_0, a_1^2 - 2a_0a_2 + 2b_2b_0 - b_1^2 > 0$, *then the positive equilibrium* E^* *of system* (1.2) *is locally asymptotically stable.*
(2) *If* $a_0 < b_0$, *then there exists a positive number* τ_0 *such that the positive equilibrium* E^* *of system* (1.2) *is locally asymptotically stable if* $0 < \tau < \tau_0$ *and is locally unstable if* $\tau > \tau_0$.

We now give two examples to illustrate our main results in Theorems 3.1 and 3.3.

Example 1. As an example, we consider the following system:

$$\begin{cases} \dot{x}_1(t) = x_1(t)(8 - 2x_1(t) - 2y_1(t)) + 0.01(x_2(t) - x_1(t)), \\ \dot{x}_2(t) = x_2(t)(1 - 2x_2(t)) + 0.01(x_1(t) - x_2(t)), \\ \dot{y}_1(t) = 2e^{-\tau}x_1(t-\tau)y_1(t-\tau) - 0.1y_1(t) - 8y_1^2(t), \\ \dot{y}_2(t) = 2x_1(t)y_1(t) - y_2(t) - 2e^{-\tau}x_1(t-\tau)y_1(t-\tau), \end{cases} \tag{3.30}$$

where the parameter τ is a positive constant.

It is easy to show that if $\tau < 4$, then (H1)–(H3) and (H5) hold for system (3.30). By Theorem 2.1 we see that system (3.30) is permanent when $\tau < 4$.

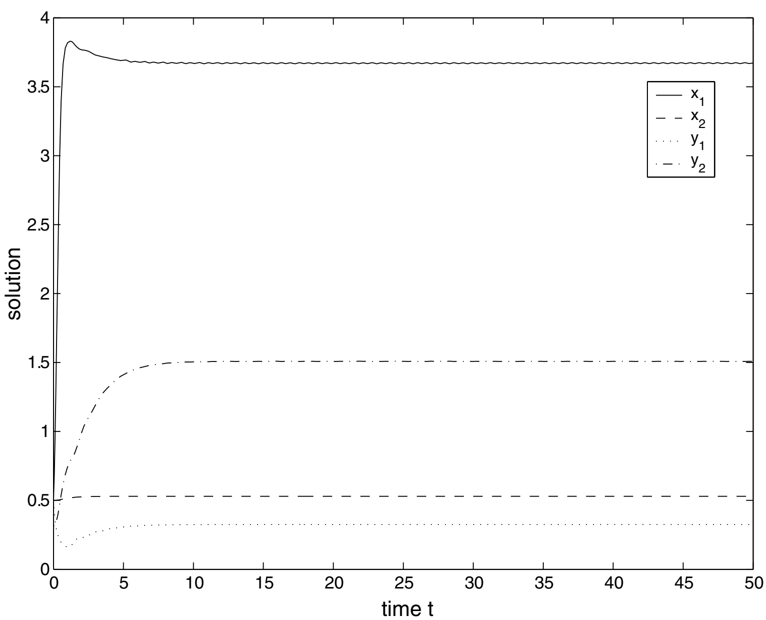

Fig. 1. The temporal solution found by numerical integration of system (3.30) with $\tau = 1$ and $(\phi_1(\theta), \phi_2(\theta), \psi_1(\theta), \psi_2(\theta)) \equiv (0.5, 0.5, 0.5, 0.5(1 - e^{-1}))$.

By Theorem 3.1 we see that the positive equilibrium of system (3.30) is globally asymptotically stable. Numerical integration can be carried out using standard MATLAB algorithm. Numerical simulation also confirms the fact above (see Fig. 1).

Example 2. Consider the following system

$$\begin{cases} \dot{x}_1(t) = x_1(t)(8 - x_1(t) - 5y_1(t)) + 5(x_2(t) - x_1(t)), \\ \dot{x}_2(t) = x_2(t)(1 - 0.5x_2(t)) + 10(x_1(t) - x_2(t)), \\ \dot{y}_1(t) = 3\mathrm{e}^{-1}x_1(t-1)y_1(t-1) - 0.5y_1(t) - 0.01y_1^2(t), \\ \dot{y}_2(t) = 3x_1(t)y_1(t) - y_2(t) - 3\mathrm{e}^{-1}x_1(t-1)y_1(t-1). \end{cases} \tag{3.31}$$

System (3.31) has a unique positive equilibrium $E^*(0.4674, 0.5052, 1.5873, 1.4069)$. It is easy to show that $a_0 = 3.0881 < b_0 = 35.9172$. Numerical simulation shows that the positive equilibrium E^* of system (3.31) is locally unstable (see Fig. 2).

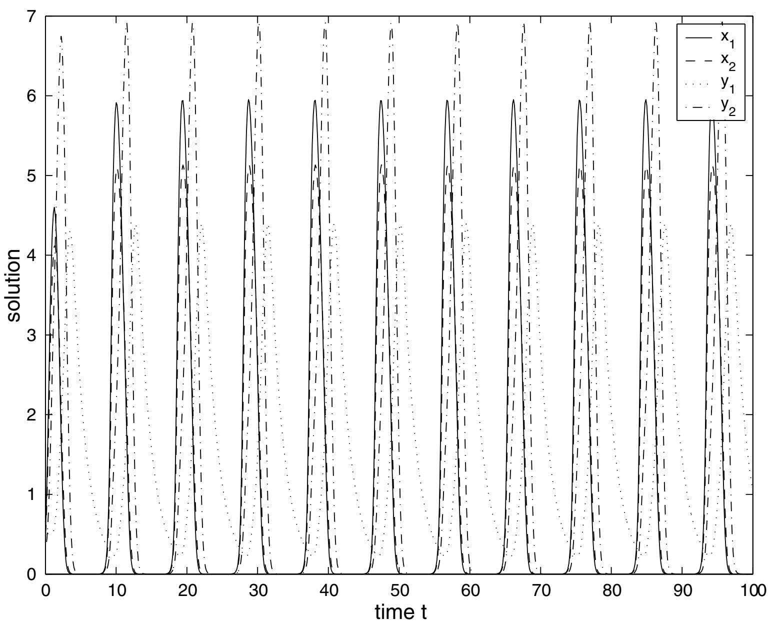

Fig. 2. The temporal solution found by numerical integration of system (3.31) with $(\phi_1(\theta), \phi_2(\theta), \psi_1(\theta), \psi_2(\theta)) \equiv (0.5, 0.5, 0.5, 0.5(1 - \mathrm{e}^{-1}))$.

4. Discussion

In this paper, motivated by the work of Aiello and Freedman [16] and Beretta et al [2], we discussed a Lotka–Volterra type predator-prey model with stage structure for predator and prey dispersal in two-patch environments. By using comparison arguments we established sufficient conditions for system (1.2) to be permanent. By constructing two different kinds of Lyapunov functionals, sufficient conditions are derived for the global asymptotic stability of the positive equilibrium of system (1.2). Theorem 3.1 gives a result for the global stability of the positive equilibrium of system (1.2) with a longer delay. By Theorem 3.1 we see that if the intra-specific competition rates of prey in two patches and the intrinsic growth rate of the prey in patch 1 are high and the dispersion rate is low satisfying (H1)–(H3) and (H5), the positive equilibrium of system (1.2) is globally asymptotically stable. On the other hand, Theorem 3.2 shows that if the time delay due to maturity is sufficiently small, the positive equilibrium of system (1.2) is globally asymptotically stable. By Theorem 2.2 we see that if the intrinsic growth rate of the prey species in patch 1 and the transformation rate of immatures to matures are low and the death rate of the mature predator and the intra-specific competition rate of the prey species in patch 1 are high enough satisfying (H4), the predator population will go to extinction.

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