Acta Mathematicae Applicatae Sinica, English Series
Vol. 19, No. 2 (2003) 317–332

Acta Mathematicae Applicatae Sinica, English Series

Attractivity in a Delayed Three-species Ratio-dependent Predator-prey System without Dominating Instantaneous Negative Feedback

Rui Xu[1], **Lan-sun Chen**[2], **M.A.J. Chaplain**[3]

[1]Department of Mathematics, Mechanical Engineering College, Shijiazhuang 050003, China
[2]Institute of Mathematics, Academy of Mathematics and System Sciences, Chinese Academy of Sciences, Beijing 100080, China
[3]Department of Mathematics, University of Dundee, Dundee DD1 4HN, UK

Abstract A delayed three-species ratio-dependent predator-prey food-chain model without dominating instantaneous negative feedback is investigated. It is shown that the system is permanent under some appropriate conditions, and sufficient conditions are derived for the global attractivity of the positive equilibrium of the system.

Keywords Time delay, uniform persistence, global attractivity
2000 MR Subject Classification 34

1 Introduction

An important and ubiquitous problem in predator-prey theory and related topics in mathematical ecology, concerns the long term coexistence (or persistence) of species. Standard Lotka-Volterra type models, on which a large proportion of existing predator-prey theory is built, assume that the per capita rate of predation depends on the prey numbers only. Recently, there is growing explicit biological and physiological evidence (cf. [2–4, 12]) that in many situations, especially when predators have to search for food (and therefore have to share or compete for food), a more suitable general predator-prey theory should be based on the so-called "ratio-dependent" theory. This roughly states that the per capita predator growth rate should be a function of the ratio of prey to predator abundance. That is, as the numbers of predators change slowly (relative to prey change), there is often competition among the predators, and the per capita rate of predation depends on the numbers of both prey and predator, most likely and simply on their ratio. These hypotheses are strongly supported by numerous field and laboratory experiment and observations (cf. [1–3, 13]).

A generic ratio-dependent predator-prey model takes the form

$$\begin{cases} \dot{x} = xf(x) - yp(x/y), \\ \dot{y} = cyq(x/y) - dy, \end{cases} \tag{1.1}$$

where x, y denote the prey and predator density respectively. The functions $p(x)$ (the so-called

Manuscript received September 7, 2001. Revised November 21, 2002.
Supported by (Grant DMS-9803323).

predator functional response) and $q(x)$ satisfy the standard properties such as being nonnegative and increasing, and equal to zero at zero.

On the other hand, it is well known that time delays in ecological system can have a considerable influence on the qualitative behavior of these systems. It is generally recognized that some kinds of time delays are inevitable in population interactions and tend to be destabilizing in the sense that longer delays may destroy the stability of positive equilibrium (see [8, 14] and the references cited therein). The effect of time delays on the asymptotic behavior of populations has been studied by a number of authors (see for example, [5, 9, 10, 15]). It has been found that "continuously distributed" delay models are more realistic (see [7]) and "continuously distributed" delays are more accurate than instantaneous time lags (see [6]). Since the traditional Lotka-Volterra type predator-prey model with Michaelis-Menten type functional response received great attention among theoretical and mathematical biologists, we will focus our attention here on the ratio-dependent type predator-prey model with Michaelis-Menten type functional response.

In this paper we incorporate distributed time delays due to gestation and negative feedback into the ratio-dependent predator-prey system. For the three-species ratio-dependent predator-prey food-chain model with Michaelis-Menten type functional response, this results in the following delayed system

$$\begin{cases} \dot{x}_1(t) = x_1(t)\Big(a_1 - a_{11}\displaystyle\int_0^\infty K_1(s)x_1(t-s)ds - \frac{a_{12}x_2(t)}{m_{12}x_2(t)+x_1(t)}\Big), \\ \dot{x}_2(t) = x_2(t)\Big(-a_2 + a_{21}\displaystyle\int_0^\infty K_2(s)\frac{x_1(t-s)}{m_{12}x_2(t-s)+x_1(t-s)}ds - \frac{a_{23}x_3(t)}{m_{23}x_3(t)+x_2(t)}\Big), \\ \dot{x}_3(t) = x_3(t)\Big(-a_3 + a_{32}\displaystyle\int_0^\infty K_3(s)\frac{x_2(t-s)}{m_{23}x_3(t-s)+x_2(t-s)}ds\Big) \end{cases} \tag{1.2}$$

with initial conditions

$$x_i(s) = \phi_i(s), \qquad s \in (-\infty, 0], \qquad \phi_i(0) > 0, \qquad i = 1, 2, 3, \tag{1.3}$$

where $x_i(t)$ represents the densities of the prey, predator and the top predator population respectively, $i = 1, 2, 3$. ϕ_i $(i = 1, 2, 3)$ are continuous bounded functions; $a_1, a_2, a_3, a_{12}, a_{21}, a_{23}, a_{32}, m_{12}$ and m_{23} are positive constants. $K_i(t) : [0, \infty) \mapsto [0, \infty)$ is piecewise continuous and normalized function such that

$$\int_0^\infty K_i(s)ds = 1; \qquad \sigma_i = \int_0^\infty sK_i(s)ds < \infty, \qquad i = 1, 2, 3. \tag{1.4}$$

We adopt the following notations and concepts throughout this paper.

Let $R^3_+ = \{x \in R^3 : x_i \geq 0, i = 1, 2, 3\}$. For ecological reasons, we consider system (1.2), only in $\text{Int}R^3_+$.

Definition 1.1. *System (1.2) is said to be uniformly persistent if there exists a compact region $D \subset \text{Int}R^3_+$ such that every solution $x(t) = \big(x_1(t), x_2(t), x_3(t)\big)$ of system (1.2) with initial conditions (1.3) eventually enters and remains in the region D.*

The organization of this paper is as follows. In the next section, we present permanence result for system (1.2). Section 3 provides sufficient conditions for the positive equilibrium of system (1.2) to be globally attractive. Finally, a suitable example is given to illustrate the feasibility of our main results.

2 Uniform Persistence

System (1.2) has a unique positive equilibrium if and only if the following conditions are true:

(H1) $a_{32} > a_3$,

(H2) $a_{21} - \Big(a_2 + \dfrac{a_{23}}{a_{32}m_{23}}(a_{32} - a_3)\Big) > 0$,

(H3) $a_1 - \dfrac{a_{12}}{a_{21}m_{12}}\Big[a_{21} - \Big(a_2 + \dfrac{a_{23}}{a_{32}m_{23}}(a_{32} - a_3)\Big)\Big] > 0$.

In the following, we always assume that such a positive equilibrium exists and denote it by $E^*(x_1^*, x_2^*, x_3^*)$.

The following lemmas are elementary and are concerned with the qualitative nature of solutions of system (1.2).

Lemma 2.1. *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 proof of Lemma 2.1 is similar to that of Lemma 2.1 in [11], we therefore omit it here.

Lemma 2.2. *Let* $x(t) = \big(x_1(t), x_2(t), x_3(t)\big)$ *denote any positive solution of system (1.2) with initial conditions (1.3). Suppose that system (1.2) satisfies (H1)–(H2) and the following:*

(H4) $\displaystyle\int_0^\infty K_2(s)e^{(a_{21}-a_2)s}ds < \infty$,

(H5) $\displaystyle\int_0^\infty K_3(s)e^{(a_{32}-a_3)s}ds < \infty$.

Then there exists a $T > 0$ *such that*

$$x_i(t) \leq M_i, \qquad i = 1, 2, 3, \qquad \text{for } t \geq T, \tag{2.1}$$

where

$$\begin{aligned} &M_i > M_i^*, \qquad i = 1, 2, 3; \\ &M_1^* = \frac{a_1}{a_{11}\displaystyle\int_0^\infty K_1(s)e^{-a_1 s}ds}, \qquad M_2^* = \frac{M_1}{m_{12}a_2}\Big(a_{21}\int_0^\infty K_2(s)e^{(a_{21}-a_2)s}ds - a_2\Big), \\ &M_3^* = \frac{M_2}{m_{23}a_3}\Big(a_{32}\int_0^\infty K_3(s)e^{(a_{32}-a_3)s}ds - a_3\Big). \end{aligned} \tag{2.2}$$

Proof. From the first equation of (1.2), we obtain

$$\dot{x}_1(t) \leq x_1(t)\Big(a_1 - a_{11}\int_0^\infty K_1(s)x_1(t-s)ds\Big). \tag{2.3}$$

It follows from (2.3) that

$$\dot{x}_1(t) < a_1 x_1(t),$$

which implies

$$x_1(t) \leq x_1(t-s)e^{a_1 s} \qquad \text{for } t \geq s \geq 0. \tag{2.4}$$

From (2.3) and (2.4), we have

$$\dot{x}_1(t) \leq x_1(t)\Big(a_1 - a_{11}\int_0^t K_1(s)x_1(t-s)ds\Big) \leq x_1(t)\Big[a_1 - a_{11}\Big(\int_0^t K_1(s)e^{-a_1 s}ds\Big)x_1(t)\Big].$$

By comparison theorem, $x_1(t) \le N(t)$ for $t > 0$, where $N(t)$ satisfies

$$\frac{dN(t)}{dt} = N(t)\Big[a_1 - a_{11}\Big(\int_0^t K_1(s)e^{-a_1 s}ds\Big)N(t)\Big], \qquad N(0) = x_1(0). \tag{2.5}$$

Solving (2.5), we have

$$\frac{1}{N(t)} = \frac{1}{N(0)}e^{-a_1 t} + a_{11}\frac{\displaystyle\int_0^t\int_0^s K_1(u)e^{-a_1 u}e^{a_1 s}duds}{e^{a_1 t}}.$$

Noting that

$$\lim_{t\to\infty}\frac{\displaystyle\int_0^t\int_0^s K_1(u)e^{-a_1 u}e^{a_1 s}duds}{e^{a_1 t}} = \frac{\displaystyle\int_0^\infty K_1(s)e^{-a_1 s}ds}{a_1},$$

thus, we have

$$\lim_{t\to\infty}\frac{1}{N(t)} = \frac{a_{11}\displaystyle\int_0^\infty K_1(s)e^{-a_1 s}ds}{a_1}.$$

It follows that

$$\limsup_{t\to\infty} x_1(t) \le \limsup_{t\to\infty} N(t) = \frac{a_1}{a_{11}\displaystyle\int_0^\infty K_1(s)e^{-a_1 s}ds} \equiv M_1^*.$$

Therefore, there exists a $T_1 > 0$ and an $M_1 > M_1^*$ such that for $t \ge T_1$, $x_1(t) \le M_1$.

In addition, from the second equation of system (1.2), we see that

$$\dot{x}_2(t) \le (a_{21} - a_2)x_2(t),$$

which implies

$$\ln\frac{x_2(t)}{x_2(t-s)} \le (a_{21} - a_2)s \qquad \text{for} \;\; t \ge s \ge 0.$$

Thus, we have

$$x_2(t-s) \ge x_2(t)e^{-(a_{21}-a_2)s} \qquad \text{for} \;\; t \ge s \ge 0. \tag{2.6}$$

Noting that

$$\lim_{t\to\infty}\int_{t-T_1}^\infty K_2(s)\frac{x_1(t-s)}{m_{12}x_2(t-s) + x_1(t-s)}ds = 0,$$

therefore, for any $\varepsilon, 0 < \varepsilon < a_2$, there exists a $T_2 \ge T_1$ such that for $t \ge T_2$,

$$-\varepsilon < a_{21}\int_{t-T_1}^\infty K_2(s)\frac{x_1(t-s)}{m_{12}x_2(t-s) + x_1(t-s)}ds < \varepsilon. \tag{2.7}$$

By (2.6), (2.7) and the second equation of (1.2), for all $t \geq T_2$, we obtain

$$\begin{aligned}
\dot{x}_2(t) \leq & x_2(t)\Big[-a_2 + a_{21}\int_0^{t-T_1} K_2(s)\frac{x_1(t-s)}{m_{12}x_2(t-s)+x_1(t-s)}ds \\
& + a_{21}\int_{t-T_1}^{\infty} K_2(s)\frac{x_1(t-s)}{m_{12}x_2(t-s)+x_1(t-s)}ds\Big] \\
\leq & x_2(t)\Big[-a_2+\varepsilon+a_{21}\int_0^{t-T_1} K_2(s)\frac{M_1}{m_{12}e^{(a_2-a_{21})s}x_2(t)+M_1}ds\Big] \\
\leq & x_2(t)\Big[-a_2+\varepsilon+a_{21}\int_0^{\infty} K_2(s)\frac{M_1}{m_{12}e^{(a_2-a_{21})s}x_2(t)+M_1}ds\Big] \\
= & x_2(t)\Big[-a_2+\varepsilon+a_{21}\int_0^{\infty} K_2(s)\frac{M_1e^{(a_{21}-a_2)s}}{m_{12}x_2(t)+M_1e^{(a_{21}-a_2)s}}ds\Big] \\
\leq & x_2(t)\Big[-a_2+\varepsilon+a_{21}\int_0^{\infty} K_2(s)\frac{M_1e^{(a_{21}-a_2)s}}{m_{12}x_2(t)+M_1}ds\Big] \\
\leq & \frac{x_2(t)}{m_{12}x_2(t)+M_1}\Big[M_1\Big(a_{21}\int_0^{\infty}K_2(s)e^{(a_{21}-a_2)s}ds-a_2+\varepsilon\Big)-m_{12}(a_2-\varepsilon)x_2(t)\Big].
\end{aligned}$$

A standard comparison argument shows that

$$\limsup_{t\to+\infty} x_2(t) \leq \frac{M_1}{m_{12}(a_2-\varepsilon)}\Big(a_{21}\int_0^{\infty}K_2(s)e^{(a_{21}-a_2)s}ds-a_2+\varepsilon\Big).$$

Now let $\varepsilon \to 0$. Consequently, we have

$$\limsup_{t\to+\infty} x_2(t) \leq \frac{M_1}{m_{12}a_2}\Big(a_{21}\int_0^{\infty}K_2(s)e^{(a_{21}-a_2)s}ds-a_2\Big) \equiv M_2^*.$$

Therefore, there exists a $T_2^* \geq T_2$ and an $M_2 > M_2^*$ such that if $t \geq T_2^*$, we have $x_2(t) \leq M_2$.

Similarly, under assumptions (H1) and (H5), we can verify that

$$\limsup_{t\to+\infty} x_3(t) \leq \frac{M_2}{m_{23}a_3}\Big(a_{32}\int_0^{\infty}K_3(s)e^{(a_{32}-a_3)s}ds-a_3\Big) \equiv M_3^*.$$

Hence, there exists a $T \geq T_2^*$ such that if $t \geq T$, we have $x_3(t) \leq M_3$ for some $M_3 > M_3^*$. The proof is complete.

Theorem 2.1. *Suppose that system (1.2) satisfies (H4)–(H5) and the following:*

(H6) $a_1 > \dfrac{a_{12}}{m_{12}}$,

(H7) *there exists an* $\varepsilon_0 > 0$ *such that* $\displaystyle\int_0^{\infty} K_1(s)e^{-(a_1-\frac{a_{12}}{m_{12}}-a_{11}M_1-\varepsilon_0)s}ds < \infty$,

(H8) $\displaystyle a_{21}\int_0^{\infty}K_2(s)\exp\Big\{-\Big(a_2+\frac{a_{23}}{m_{23}}\Big)s\Big\}ds > a_2+\frac{a_{23}}{m_{23}}$,

(H9) $\displaystyle a_{32}\int_0^{\infty}K_3(s)\exp\{-a_3s\}ds > a_3$.

Then system (1.2) is uniformly persistent.

Proof. Suppose $x(t) = \big(x_1(t), x_2(t), x_3(t)\big)$ is a solution of system (1.2) which satisfies (1.3). According to the first equation of system (1.2), if (H6) holds, then

$$\begin{aligned}
\dot{x}_1(t) \geq & x_1(t)\Big[a_1-\frac{a_{12}}{m_{12}}-a_{11}\int_0^{\infty}K_1(s)x_1(t-s)ds\Big] \\
= & x_1(t)\Big[a_1-\frac{a_{12}}{m_{12}}-a_{11}\int_0^{t-T}K_1(s)x_1(t-s)ds-a_{11}\int_{t-T}^{\infty}K_1(s)x_1(t-s)ds\Big].
\end{aligned} \tag{2.8}$$

For each $\varepsilon_1, 0 < \varepsilon_1 < \varepsilon_0$, we define $M_{11} = M_1 + (\varepsilon_0 - \varepsilon_1)/a_{11}$, then (H7) holds with (M_1, ε_0) replaced by (M_{11}, ε_1) respectively. Using Lemma 2.2, there exists a $T > 0$ such that if $t \geq T$, we have $x_1(t) < M_{11}$.

Therefore, it follows from (2.8) that for $t \geq T$,

$$\begin{aligned}\dot{x}_1(t) \geq & x_1(t)\Big(a_1 - \frac{a_{12}}{m_{12}} - a_{11}M_{11}\int_0^{t-T} K_1(s)ds - a_{11}\int_{t-T}^{\infty} K_1(s)x_1(t-s)ds\Big) \\ \geq & x_1(t)\Big(a_1 - \frac{a_{12}}{m_{12}} - a_{11}M_{11}\int_0^{\infty} K_1(s)ds - a_{11}\int_{t-T}^{\infty} K_1(s)x_1(t-s)ds\Big) \\ = & x_1(t)\Big(a_1 - \frac{a_{12}}{m_{12}} - a_{11}M_{11} - a_{11}\int_{t-T}^{\infty} K_1(s)x_1(t-s)ds\Big). \end{aligned} \tag{2.9}$$

Let

$$C_1(t) = a_1 - \frac{a_{12}}{m_{12}} - a_{11}M_{11} - a_{11}\int_{t-T}^{\infty} K_1(s)x_1(t-s)ds.$$

Then (2.9) becomes

$$\dot{x}_1(t) \geq C_1(t)x_1(t), \tag{2.10}$$

which implies

$$x_1(t) \geq x_1(t-s)e^{\int_{t-s}^{t} C_1(u)du} \qquad \text{for } \ t-s \geq T, \ \ s \geq 0. \tag{2.11}$$

It follows from (2.8) and (2.11) that

$$\begin{aligned}\dot{x}_1(t) \geq x_1(t)\Big[a_1 - \frac{a_{12}}{m_{12}} - a_{11}\int_{t-T}^{\infty} K_1(s)x_1(t-s)ds \\ - a_{11}x_1(t)\int_0^{t-T} K_1(s)e^{-\int_{t-s}^{t} C_1(u)du}ds\Big].\end{aligned} \tag{2.12}$$

Noting that

$$\lim_{t\to\infty}\int_{t-T}^{\infty} K_1(s)x_1(t-s)ds = 0 \qquad \text{and} \qquad \lim_{t\to\infty} C_1(t) = a_1 - \frac{a_{12}}{m_{12}} - a_{11}M_{11},$$

therefore, for any $\varepsilon_2, \ 0 < \varepsilon_2 < \varepsilon_1$, there exists a $T_3 > T$ such that for $t \geq T_3$,

$$\int_{t-T}^{\infty} K_1(s)x_1(t-s)ds < \varepsilon_2, \tag{2.13}$$

$$\Big|C_1(t) - \Big(a_1 - \frac{a_{12}}{m_{12}} - a_{11}M_{11}\Big)\Big| < \varepsilon_2. \tag{2.14}$$

It follows from (2.12)–(2.14) that

$$\begin{aligned}\frac{dx_1(t)}{dt} \geq & x_1(t)\Big[a_1 - \frac{a_{12}}{m_{12}} - a_{11}\varepsilon_2 - a_{11}x_1(t)\int_0^{t-T} K_1(s)e^{-(a_1 - \frac{a_{12}}{m_{12}} - a_{11}M_{11} - \varepsilon_2)s}ds\Big] \\ \geq & x_1(t)\Big[a_1 - \frac{a_{12}}{m_{12}} - a_{11}\varepsilon_2 - \Big(a_{11}\int_0^{\infty} K_1(s)e^{-(a_1 - \frac{a_{12}}{m_{12}} - a_{11}M_{11} - \varepsilon_2)s}ds\Big)x_1(t)\Big],\end{aligned} \tag{2.15}$$

which implies

$$\liminf_{t\to+\infty} x_1(t) \geq \frac{a_1 - \dfrac{a_{12}}{m_{12}} - a_{11}\varepsilon_2}{a_{11}\displaystyle\int_0^{\infty} K_1(s)e^{-(a_1 - \frac{a_{12}}{m_{12}} - a_{11}M_{11} - \varepsilon_2)s}ds}.$$

Now let $\varepsilon_1 \to \varepsilon_0, \varepsilon_2 \to 0$ and $M_{11} \to M_1$. Consequently, we have

$$\liminf_{t\to\infty} x_1(t) \geq \frac{a_1 - \dfrac{a_{12}}{m_{12}}}{a_{11}\displaystyle\int_0^\infty K_1(s)e^{-(a_1-\frac{a_{12}}{m_{12}}-a_{11}M_1)s}ds} \equiv m_1.$$

Hence, there is a $T_1^* > 0$, such that for $t \geq T_1^*, x_1(t) > m_1/2$.

It follows from (H7) and (H8) that there exists an $A > 0$ such that

$$a_{21}\int_0^A K_2(s)e^{-(a_2+\frac{a_{23}}{m_{23}})s}ds > a_2 + \frac{a_{23}}{m_{23}}, \qquad a_{32}\int_0^A K_3(s)e^{-a_3 s}ds > a_3.$$

Therefore, from the second equation in system (1.2), we have that for $t \geq T_1^* + A$

$$\dot{x}_2(t) \geq x_2(t)\Big[-a_2 - \frac{a_{23}}{m_{23}} + a_{21}\int_0^A K_1(s)\frac{m_1/2}{m_{12}x_2(t-s)+m_1/2}ds\Big].$$

From this it follows (in a similar manner to the derivation of (2.3) above) that

$$x_2(t-s) \leq x_2(t)e^{(a_2+\frac{a_{23}}{m_{23}})s} \qquad \text{for} \ \ t \geq s \geq 0.$$

Hence, for t sufficiently large, we have

$$\begin{aligned}
\dot{x}_2(t) \geq& x_2(t)\Big[-a_2 - \frac{a_{23}}{m_{23}} + a_{21}\int_0^A K_2(s)\frac{m_1/2}{m_{12}x_2(t)\exp\{(a_2+\frac{a_{23}}{m_{23}})s\}+m_1/2}ds\Big] \\
=& x_2(t)\Big[-a_2 - \frac{a_{23}}{m_{23}} + a_{21}\int_0^A K_2(s)\frac{m_1\exp\{-(a_2+\frac{a_{23}}{m_{23}})s\}/2}{m_{12}x_2(t)+m_1\exp\big\{-\big(a_2+\frac{a_{23}}{m_{23}}\big)s\big\}/2}ds\Big] \\
\geq& x_2(t)\Big[-a_2 - \frac{a_{23}}{m_{23}} + a_{21}\int_0^A K_2(s)\frac{m_1\exp\big\{-\big(a_2+\frac{a_{23}}{m_{23}}\big)s\big\}/2}{m_{12}x_2(t)+m_1/2}ds\Big] \\
=& \frac{x_2(t)}{m_{12}x_2(t)+m_1/2}\Big[\frac{1}{2}m_1\Big(a_{21}\int_0^A K_2(s)\exp\Big\{-\Big(a_2+\frac{a_{23}}{m_{23}}\Big)s\Big\}ds - a_2 - \frac{a_{23}}{m_{23}}\Big) \\
&- m_{12}\Big(a_2+\frac{a_{23}}{m_{23}}\Big)x_2(t)\Big],
\end{aligned} \tag{2.16}$$

which yields

$$\liminf_{t\to+\infty} x_2(t) \geq \frac{m_1}{2m_{12}(a_2+\frac{a_{23}}{m_{23}})}\Big(a_{21}\int_0^A K_2(s)\exp\Big\{-\Big(a_2+\frac{a_{23}}{m_{23}}\Big)s\Big\}ds - a_2 - \frac{a_{23}}{m_{23}}\Big) \equiv m_2.$$

Therefore, for t sufficiently large, we have $x_2(t) > m_2/2$.

Similarly, under assumption (H9), we can derive

$$\liminf_{t\to+\infty} x_3(t) \geq \frac{m_2}{2m_{23}a_3}\Big(a_{32}\int_0^A K_3(s)e^{-a_3 s}ds - a_3\Big) \equiv m_3.$$

Hence, for t sufficiently large, we have $x_3(t) > m_3/2$.

Now, we let

$$D = \{(x_1,x_2,x_3)|\ m_i/2 \leq x_i \leq M_i,\ i=1,2,3\}. \tag{2.17}$$

Then D is a bounded compact region in R_+^3 which has positive distance from coordinate planes. From what has been discussed above, we obtain that there exists a $T^* > 0$ such that if $t \geq T^*$, then every positive solution of system (1.2) with initial conditions (1.3) eventually enters and remains in the region D. The proof is complete.

3 Global Attractivity

We now provide conditions under which the positive equilibrium E^* of system (1.2) is globally attractive. Our strategy in the proof of the global attractivity of the positive equilibrium E^* of (1.2) is to construct a suitable Lyapunov functional.

Let $P_i(u)$ be defined by

$$P_i(u) = \frac{u}{m_{i,i+1}+u}, \qquad i=1,2.$$

Then system (1.2) can be rewritten as

$$\begin{cases} \dot{x}_1 = x_1\Big\{ -a_{11}\displaystyle\int_0^\infty K_1(s)\big(x_1(t-s)-x_1^*\big)ds + a_{12}\Big[\frac{x_2^*}{x_1^*}P_1\Big(\frac{x_1^*}{x_2^*}\Big) - \frac{x_2}{x_1}P_1\Big(\frac{x_1}{x_2}\Big)\Big]\Big\}, \\ \dot{x}_2 = x_2(t)\Big\{a_{21}\displaystyle\int_0^\infty K_2(s)\Big[P_1\Big(\frac{x_1(t-s)}{x_2(t-s)}\Big) - P_1\Big(\frac{x_1^*}{x_2^*}\Big)\Big]ds \\ \qquad +a_{23}\Big[\frac{x_3^*}{x_2^*}P_2\Big(\frac{x_2^*}{x_3^*}\Big) - \frac{x_3}{x_2}P_2\Big(\frac{x_2}{x_3}\Big)\Big]\Big\}, \\ \dot{x}_3 = a_{32}x_3(t)\displaystyle\int_0^\infty K_3(s)\Big[P_2\Big(\frac{x_2(t-s)}{x_3(t-s)}\Big) - P_2\Big(\frac{x_2^*}{x_3^*}\Big)\Big]ds. \end{cases} \tag{3.1}$$

Define

$$x_1 = x_1, \qquad u_1 = \frac{x_1}{x_2}, \qquad u_2 = \frac{x_2}{x_3}, \qquad u_1^* = \frac{x_1^*}{x_2^*}, \qquad u_2^* = \frac{x_2^*}{x_3^*}.$$

Then system (3.1) becomes

$$\begin{cases} \dot{x}_1(t) = x_1(t)\Big\{ -a_{11}\displaystyle\int_0^\infty K_1(s)(x_1(t-s)-x_1^*)ds + a_{12}\Big[\frac{P_1(u_1^*)}{u_1^*} - \frac{P_1(u_1)}{u_1}\Big]\Big\}, \\ \dot{u}_1(t) = u_1(t)\Big\{ -a_{11}\displaystyle\int_0^\infty K_1(s)(x_1(t-s)-x_1^*)ds + a_{12}\Big[\frac{P_1(u_1^*)}{u_1^*} - \frac{P_1(u_1)}{u_1}\Big] \\ \qquad -a_{21}\displaystyle\int_0^\infty K_2(s)[P_1(u_1(t-s)) - P_1(u_1^*)]ds - a_{23}\Big[\frac{P_2(u_2^*)}{u_2^*} - \frac{P_2(u_2)}{u_2}\Big]\Big\}, \\ \dot{u}_2(t) = u_2(t)\Big\{a_{21}\displaystyle\int_0^\infty K_2(s)[P_1(u_1(t-s)) - P_1(u_1^*)]ds + a_{23}\Big[\frac{P_2(u_2^*)}{u_2^*} - \frac{P_2(u_2)}{u_2}\Big] \\ \qquad -a_{32}\displaystyle\int_0^\infty K_3(s)[P_2(u_2(t-s)) - P_2(u_2^*)]ds\Big\}. \end{cases} \tag{3.2}$$

Define $v(t) = \big(v_1(t), v_2(t), v_3(t)\big)$ by

$$\begin{aligned} & v_1(t) = x_1(t)-x_1^*, \qquad v_2(t) = u_1(t)-u_1^*, \qquad v_3(t) = u_2(t)-u_2^*; \\ & F_1(v_2) = P_1(u_1) - P_1(u_1^*) = \frac{m_{12}v_2}{(m_{12}+u_1^*)(m_{12}+u_1)}, \\ & F_2(v_3) = P_2(u_2) - P_2(u_2^*) = \frac{m_{23}v_3}{(m_{23}+u_2^*)(m_{23}+u_2)}. \end{aligned} \tag{3.3}$$

It is easy to examine that

$$\begin{aligned} & F_1'(v_2)u_1 = \frac{m_{12}u_1}{(m_{12}+u_1)^2} < 1, \qquad F_2'(v_3)u_2 = \frac{m_{23}u_2}{(m_{23}+u_2)^2} < 1, \\ & \frac{P_i(u_i^*)}{u_i^*} - \frac{P_i(u_i)}{u_i} = \frac{1}{m_{i,i+1}}F_i(v_{i+1}), \qquad i=1,2. \end{aligned} \tag{3.4}$$

Therefore, from (3.2) and (3.3), we finally obtain

$$\begin{cases} \dot{v}_1 = (v_1 + x_1^*)\Big[- a_{11} \displaystyle\int_0^\infty K_1(s)v_1(t-s)ds + \frac{a_{12}}{m_{12}} F_1\big(v_2(t)\big)\Big], \\ \dot{v}_2 = (v_2 + u_1^*)\Big[- a_{11} \displaystyle\int_0^\infty K_1(s)v_1(t-s)ds + \frac{a_{12}}{m_{12}} F_1\big(v_2(t)\big) \\ \qquad - \dfrac{a_{23}}{m_{23}} F_2\big(v_3(t)\big) - a_{21} \displaystyle\int_0^\infty K_2(s)F_1\big(v_2(t-s)\big)ds\Big], \\ \dot{v}_3 = (v_3 + u_2^*)\Big[a_{21} \displaystyle\int_0^\infty K_2(s)F_1\big(v_2(t-s)\big)ds + \frac{a_{23}}{m_{23}} F_2\big(v_3(t)\big) \\ \qquad - a_{32} \displaystyle\int_0^\infty K_3(s)F_2\big(v_3(t-s)\big)ds\Big], \end{cases} \tag{3.5}$$

We now formulate the result on the global attractivity of the equilibrium E^* of (1.2) as follows.

Theorem 3.1. *Suppose that system (1.2) satisfies (H1)–(H3) and the following:*
(H10) $A_i > 0, \quad i = 1, 2, 3,$
where

$$\begin{aligned} A_1 =& a_{11}\Big\{c_1 - \frac{1}{2}a_{21}\sigma_2(1+c_2) - \frac{1}{2}a_{11}M_1\sigma_1(c_1+c_2) - \frac{1}{2}c_1M_1\sigma_1\Big(a_{11} + \frac{a_{12}}{m_{12}}\Big)\Big\}, \\ A_2 =& c_2\Big\{a_{21} - \frac{a_{12}}{m_{12}} - \frac{1}{2}a_{21}\sigma_2\Big(a_{11} + 2\frac{a_{12}}{m_{12}} + \frac{a_{23}}{m_{23}} + 2a_{21}\Big) - \frac{1}{2}a_{11}M_1\sigma_1\Big(a_{11} + 2\frac{a_{12}}{m_{12}}\Big)\Big\} \\ & - \frac{1}{2m_{12}}c_1a_{11}a_{12}M_1\sigma_1 - \frac{1}{2}a_{21}\sigma_2\Big(a_{21} + \frac{a_{12}}{m_{12}}\Big) - \frac{1}{2}a_{32}a_{21}\sigma_3, \\ A_3 =& a_{32} - \frac{a_{23}}{m_{23}} - \frac{1}{2}a_{21}\sigma_2\Big(a_{11} + \frac{a_{12}}{m_{12}} + 2\frac{a_{23}}{m_{23}} + 2a_{21}\Big) - \frac{1}{2}a_{32}\sigma_3\Big(a_{21} + 2\frac{a_{23}}{m_{23}} + 2a_{32}\Big); \\ c_1 =& \frac{a_{11}a_{21}m_{12}m_{23}}{a_{12}a_{23}}, \qquad c_2 = \frac{a_{21}m_{23}}{a_{23}}. \end{aligned}$$

Then the positive equilibrium $E^*(x_1^*, x_2^*, x_3^*)$ of system (1.2) is globally attractive.

Proof. To prove that the global attractivity of the positive equilibrium E^* of system (1.2) is equivalent to that of the trivial solution of (3.5).

Let

$$V_1(t) = c_1\Big(v_1 - x_1^* \ln \frac{v_1 + x_1^*}{x_1^*}\Big) + c_2 \int_{u_1^*}^{u_1} \frac{P_1(v) - P_1(u_1^*)}{v} dv + \int_{u_2^*}^{u_2} \frac{P_2(v) - P_2(u_2^*)}{v} dv, \tag{3.6}$$

where c_1 and c_2 are defined in (H10).

Calculating the derivative of $V_1(t)$ along the solution of (3.5), we have

$$\begin{aligned} \frac{d}{dt}V_1(t) =& c_1 \frac{v_1}{v_1 + x_1^*}\dot{v}_1(t) + c_2 \frac{F_1(v_2)}{u_1}\dot{v}_2(t) + \frac{F_2(v_3)}{u_2}\dot{v}_3(t) \\ =& c_1v_1(t)\Big\{ - a_{11} \int_0^\infty K_1(s)v_1(t-s)ds + \frac{a_{12}}{m_{12}} F_1\big(v_2(t)\big)\Big\} \\ & + c_2F_1\big(v_2(t)\big)\Big\{ - a_{11} \int_0^\infty K_1(s)v_1(t-s)ds + \frac{a_{12}}{m_{12}}F_1\big(v_2(t)\big) - \frac{a_{23}}{m_{23}}F_2\big(v_3(t)\big) \\ & - a_{21} \int_0^\infty K_2(s)F_1\big(v_2(t-s)\big)ds\Big\} + F_2\big(v_3(t)\big)\Big\{a_{21} \int_0^\infty K_2(s)F_1\big(v_2(t-s)\big)ds \\ & + \frac{a_{23}}{m_{23}}F_2\big(v_3(t)\big) - a_{32} \int_0^\infty K_3(s)F_2\big(v_3(t-s)\big)ds\Big\} \end{aligned}$$

$$
\begin{aligned}
=&c_1v_1(t)\Big\{-a_{11}v_1(t)+\frac{a_{12}}{m_{12}}F_1\big(v_2(t)\big)+a_{11}\int_0^t\int_{t-s}^t K_1(s)v_1'(l)dlds\Big\}\\
&+c_2F_1\big(v_2(t)\big)\Big\{-a_{11}v_1(t)+\Big(\frac{a_{12}}{m_{12}}-a_{21}\Big)F_1\big(v_2(t)\big)-\frac{a_{23}}{m_{23}}F_2\big(v_3(t)\big)\\
&+a_{11}\int_0^t\int_{t-s}^t K_1(s)v_1'(l)dlds+a_{21}\int_0^t\int_{t-s}^t K_2(s)F_1'\big(v_2(l)\big)v_2'(l)dlds\Big\}\\
&+F_2\big(v_3(t)\big)\Big\{a_{21}F_1\big(v_2(t)\big)-a_{21}\int_0^t\int_{t-s}^t K_2(s)F_1'\big(v_2(l)\big)v_2'(l)dlds\\
&+\Big(\frac{a_{23}}{m_{23}}-a_{32}\Big)F_2\big(v_3(t)\big)+a_{32}\int_0^t\int_{t-s}^t K_3(s)F_2'(v_3(l))v_3'(l)dlds\Big\}+R(t)\\
=&-c_1a_{11}v_1^2(t)+c_2\Big(\frac{a_{12}}{m_{12}}-a_{21}\Big)F_1^2\big(v_2(t)\big)+\Big(\frac{a_{23}}{m_{23}}-a_{32}\Big)F_2^2\big(v_3(t)\big)\\
&+a_{11}\big(c_1v_1(t)+c_2F_1(v_2(t))\big)\int_0^t\int_{t-s}^t K_1(s)v_1'(l)dlds\\
&+a_{21}\big(c_2F_1(v_2(t))-F_2(v_3(t))\big)\int_0^t\int_{t-s}^t K_2(s)F_1'\big(v_2(l)\big)v_2'(l)dlds\\
&+a_{32}F_2\big(v_3(t)\big)\int_0^t\int_{t-s}^t K_3(s)F_2'\big(v_3(l)\big)v_3'(l)dlds+R(t),
\end{aligned}\tag{3.7}
$$

where

$$
\begin{aligned}
R(t)=&a_{11}\big(c_1v_1(t)+c_2F_1(v_2(t))\big)\int_t^\infty K_1(s)\big(v_1(t)-v_1(t-s)\big)ds\\
&+a_{21}\big(c_2F_1(v_2(t))-F_2(v_3(t))\big)\int_t^\infty K_2(s)\big(F_1(v_2(t))-F_1(v_2(t-s))\big)ds\\
&+a_{32}F_2\big(v_3(t)\big)\int_t^\infty K_3(s)\big(F_2(v_3(t))-F_2(v_3(t-s))\big)ds.
\end{aligned}
$$

On substituting (3.5) into (3.7), we have

$$
\begin{aligned}
\frac{d}{dt}V_1(t)=&-c_1a_{11}v_1^2(t)+c_2\Big(\frac{a_{12}}{m_{12}}-a_{21}\Big)F_1^2(v_2(t))+\Big(\frac{a_{23}}{m_{23}}-a_{32}\Big)F_2^2(v_3(t))\\
&+a_{11}\big(c_1v_1(t)+c_2F_1(v_2(t))\big)\int_0^t\int_{t-s}^t K_1(s)x_1(l)\Big[-a_{11}\int_0^\infty K_1(r)v_1(l-r)dr\\
&+\frac{a_{12}}{m_{12}}F_1(v_2(l))\Big]dlds+a_{21}\big(c_2F_1\big(v_2(t)\big)-F_2(v_3(t))\big)\\
&\times\int_0^t\int_{t-s}^t K_2(s)F_1'\big(v_2(l)\big)u_1(l)\Big[-a_{11}\int_0^\infty K_1(r)v_1(l-r)dr\\
&+\frac{a_{12}}{m_{12}}F_1\big(v_2(l)\big)-\frac{a_{23}}{m_{23}}F_2\big(v_3(l)\big)-a_{21}\int_0^\infty K_2(r)F_1\big(v_2(l-r)\big)dr\Big]dlds\\
&+a_{32}F_2\big(v_3(t)\big)\int_0^t\int_{t-s}^t K_3(s)F_2'\big(v_3(l)\big)u_2(l)\Big[a_{21}\int_0^\infty K_2(r)F_1\big(v_2(l-r)\big)dr\\
&+\frac{a_{23}}{m_{23}}F_2\big(v_3(l)\big)-a_{32}\int_0^\infty K_3(r)F_2\big(v_3(l-r)\big)dr\Big]dlds+R(t)\\
\le&-c_1a_{11}v_1^2(t)+c_2\big(\frac{a_{12}}{m_{12}}-a_{21}\big)F_1^2\big(v_2(t)\big)+\Big(\frac{a_{23}}{m_{23}}-a_{32}\Big)F_2^2\big(v_3(t)\big)\\
&+a_{11}\big(c_1v_1(t)+c_2F_1(v_2(t))\big)\int_0^\infty\int_{t-s}^t K_1(s)x_1(l)\Big[-a_{11}\int_0^\infty K_1(r)v_1(l-r)dr
\end{aligned}
$$

$$
\begin{aligned}
&+\frac{a_{12}}{m_{12}}F_1\big(v_2(l)\big)\Big]dlds+a_{21}\big(c_2F_1(v_2(t))-F_2(v_3(t))\big)\\
&\times\int_0^\infty\int_{t-s}^t K_2(s)F_1'\big(v_2(l)\big)u_1(l)\Big[-a_{11}\int_0^\infty K_1(r)v_1(l-r)dr\\
&+\frac{a_{12}}{m_{12}}F_1\big(v_2(l)\big)-\frac{a_{23}}{m_{23}}F_2\big(v_3(l)\big)-a_{21}\int_0^\infty K_2(r)F_1\big(v_2(l-r)\big)dr\Big]dlds\\
&+a_{32}F_2\big(v_3(t)\big)\int_0^\infty\int_{t-s}^t K_3(s)F_2'\big(v_3(l)\big)u_2(l)\Big[a_{21}\int_0^\infty K_2(r)F_1\big(v_2(l-r)\big)dr\\
&+\frac{a_{23}}{m_{23}}F_2\big(v_3(l)\big)-a_{32}\int_0^\infty K_3(r)F_2\big(v_3(l-r)\big)dr\Big]dlds+R(t). \qquad (3.8)
\end{aligned}
$$

It follows from (2.1) and (3.4) that for $t\ge T$,

$$
\begin{aligned}
\frac{d}{dt}V_1(t)\le&-c_1a_{11}v_1^2(t)+c_2\Big(\frac{a_{12}}{m_{12}}-a_{21}\Big)F_1^2\big(v_2(t)\big)+\Big(\frac{a_{23}}{m_{23}}-a_{32}\Big)F_2^2(v_3(t))\\
&+a_{11}\big(c_1|v_1(t)|+c_2|F_1(v_2(t))|\big)\int_0^\infty\int_{t-s}^t K_1(s)x_1(l)\Big[a_{11}\int_0^\infty K_1(r)|v_1(l-r)|dr\\
&+\frac{a_{12}}{m_{12}}\big|F_1(v_2(l))\big|\Big]dlds+a_{21}\big(c_2\big|F_1(v_2(t))\big|+\big|F_2(v_3(t))\big|\big)\\
&\times\int_0^\infty\int_{t-s}^t K_2(s)F_1'\big(v_2(l)\big)u_1(l)\Big[a_{11}\int_0^\infty K_1(r)|v_1(l-r)|dr\\
&+\frac{a_{12}}{m_{12}}\big|F_1(v_2(l))\big|+\frac{a_{23}}{m_{23}}\big|F_2(v_3(l))\big|+a_{21}\int_0^\infty K_2(r)\big|F_1(v_2(l-r))\big|dr\Big]dlds\\
&+a_{32}\big|F_2(v_3(t))\big|\int_0^\infty\int_{t-s}^t K_3(s)F_2'(v_3(l))u_2(l)\Big[a_{21}\int_0^\infty K_2(r)\big|F_1(v_2(l-r))\big|dr\\
&+\frac{a_{23}}{m_{23}}\big|F_2(v_3(l))\big|+a_{32}\int_0^\infty K_3(r)\big|F_2(v_3(l-r))\big|dr\Big]dlds+R(t)\\
\le&-c_1a_{11}v_1^2(t)+c_2\Big(\frac{a_{12}}{m_{12}}-a_{21}\Big)F_1^2\big(v_2(t)\big)+\Big(\frac{a_{23}}{m_{23}}-a_{32}\Big)F_2^2\big(v_3(t)\big)\\
&+a_{11}M_1\big(c_1|v_1(t)|+c_2\big|F_1(v_2(t))\big|\big)\int_0^\infty\int_{t-s}^t K_1(s)\Big[a_{11}\int_0^\infty K_1(r)|v_1(l-r)|dr\\
&+\frac{a_{12}}{m_{12}}\big|F_1(v_2(l))\big|\Big]dlds+a_{21}\big(c_2\big|F_1(v_2(t))\big|+\big|F_2(v_3(t))\big|\big)\\
&\times\int_0^\infty\int_{t-s}^t K_2(s)\Big[a_{11}\int_0^\infty K_1(r)|v_1(l-r)|dr+\frac{a_{12}}{m_{12}}\big|F_1(v_2(l))\big|\\
&+\frac{a_{23}}{m_{23}}\big|F_2(v_3(l))\big|+a_{21}\int_0^\infty K_2(r)\big|F_1(v_2(l-r))\big|dr\Big]dlds\\
&+a_{32}\big|F_2(v_3(t))\big|\int_0^\infty\int_{t-s}^t K_3(s)\Big[a_{21}\int_0^\infty K_2(r)\big|F_1(v_2(l-r))\big|dr\\
&+\frac{a_{23}}{m_{23}}\big|F_2(v_3(l))\big|+a_{32}\int_0^\infty K_3(r)\big|F_2(v_3(l-r))\big|dr\Big]dlds+R(t). \qquad (3.9)
\end{aligned}
$$

Using the inequality $a^2+b^2\ge 2ab$, we derive for $t\ge T$ that

$$
\begin{aligned}
\frac{d}{dt}V_1(t)\le&-c_1a_{11}v_1^2(t)+c_2\Big(\frac{a_{12}}{m_{12}}-a_{21}\Big)F_1^2(v_2(t))+\Big(\frac{a_{23}}{m_{23}}-a_{32}\Big)F_2^2(v_3(t))\\
&+\frac{1}{2}a_{11}M_1\sigma_1\Big(a_{11}+\frac{a_{12}}{m_{12}}\Big)\big(c_1v_1^2(t)+c_2F_1^2(v_2(t))\big)
\end{aligned}
$$

$$
\begin{aligned}
&+\frac{1}{2}\sigma_2 a_{21}\Big(a_{11}+\frac{a_{12}}{m_{12}}+\frac{a_{23}}{m_{23}}+a_{21}\Big)\big(c_2F_1^2(v_2(t))+F_2^2(v_3(t))\big)\\
&+\frac{1}{2}\sigma_3 a_{32}\Big(a_{21}+\frac{a_{23}}{m_{23}}+a_{32}\Big)F_2^2(v_3(t))+\frac{1}{2}a_{11}M_1(c_1+c_2)\\
&\times\int_0^\infty\int_{t-s}^t K_1(s)\Big[a_{11}\int_0^\infty K_1(r)v_1^2(l-r)dr+\frac{a_{12}}{m_{12}}F_1^2(v_2(l))\Big]dlds\\
&+\frac{1}{2}a_{21}(1+c_2)\int_0^\infty\int_{t-s}^t K_2(s)\Big[a_{11}\int_0^\infty K_1(r)v_1^2(l-r)dr\\
&+\frac{a_{12}}{m_{12}}F_1^2(v_2(l))+\frac{a_{23}}{m_{23}}F_2^2(v_3(l))+a_{21}\int_0^\infty K_2(r)F_1^2(v_2(l-r))dr\Big]dlds\\
&+\frac{1}{2}a_{32}\int_0^\infty\int_{t-s}^t K_3(s)\Big[a_{21}\int_0^\infty K_2(r)F_1^2(v_2(l-r))dr\\
&+\frac{a_{23}}{m_{23}}F_2^2(v_3(l))+a_{32}\int_0^\infty K_3(r)F_2^2(v_3(l-r))dr\Big]dlds+R(t). \qquad (3.10)
\end{aligned}
$$

Define

$$
\begin{aligned}
V_2(t)=&V_1(t)+\frac{1}{2}a_{11}M_1(c_1+c_2)\int_0^\infty\int_{t-s}^t\int_v^t K_1(s)\Big[a_{11}\int_0^\infty K_1(r)v_1^2(l-r)dr\\
&+\frac{a_{12}}{m_{12}}F_1^2(v_2(l))\Big]dldvds+\frac{1}{2}a_{21}(1+c_2)\\
&\times\int_0^\infty\int_{t-s}^t\int_v^t K_2(s)\Big[a_{11}\int_0^\infty K_1(r)v_1^2(l-r)dr+\frac{a_{12}}{m_{12}}F_1^2(v_2(l))\\
&+\frac{a_{23}}{m_{23}}F_2^2(v_3(l))+a_{21}\int_0^\infty K_2(r)F_1^2(v_2(l-r))|dr\Big]dldvds\\
&+\frac{1}{2}a_{32}\int_0^\infty\int_{t-s}^t\int_v^t K_3(s)\Big[a_{21}\int_0^\infty K_2(r)F_1^2(v_2(l-r))dr\\
&+\frac{a_{23}}{m_{23}}F_2^2(v_3(l))+a_{32}\int_0^\infty K_3(r)F_2^2(v_3(l-r))dr\Big]dldvds. \qquad (3.11)
\end{aligned}
$$

It follows from (3.10) and (3.11) that for $t\geq T$,

$$
\begin{aligned}
\frac{d}{dt}V_2(t)\leq&-c_1a_{11}v_1^2(t)+c_2\Big(\frac{a_{12}}{m_{12}}-a_{21}\Big)F_1^2(v_2(t))+\Big(\frac{a_{23}}{m_{23}}-a_{32}\Big)F_2^2(v_3(t))\\
&+\frac{1}{2}a_{11}M_1\sigma_1\Big(a_{11}+\frac{a_{12}}{m_{12}}\Big)\big(c_1v_1^2(t)+c_2F_1^2(v_2(t))\big)\\
&+\frac{1}{2}\sigma_2 a_{21}\Big(a_{11}+\frac{a_{12}}{m_{12}}+\frac{a_{23}}{m_{23}}+a_{21}\Big)\big(c_2F_1^2(v_2(t))+F_2^2(v_3(t))\big)\\
&+\frac{1}{2}\sigma_3 a_{32}\Big(a_{21}+\frac{a_{23}}{m_{23}}+a_{32}\Big)F_2^2(v_3(t))+\frac{1}{2}a_{11}M_1\sigma_1(c_1+c_2)\\
&\times\Big[a_{11}\int_0^\infty K_1(r)v_1^2(t-r)dr+\frac{a_{12}}{m_{12}}F_1^2(v_2(t))\Big]\\
&+\frac{1}{2}a_{21}\sigma_2(1+c_2)\Big[a_{11}\int_0^\infty K_1(r)v_1^2(t-r)dr+\frac{a_{12}}{m_{12}}F_1^2(v_2(t))\\
&+\frac{a_{23}}{m_{23}}F_2^2(v_3(t))+a_{21}\int_0^\infty K_2(r)F_1^2(v_2(t-r))dr\Big]\\
&+\frac{1}{2}a_{32}\sigma_3\Big[a_{21}\int_0^\infty K_2(r)F_1^2(v_2(t-r))dr+\frac{a_{23}}{m_{23}}F_2^2(v_3(t))
\end{aligned}
$$

$$+ a_{32}\int_0^{\infty} K_3(r)F_2^2(v_3(t-r))dr\Big] + R(t). \tag{3.12}$$

We now define a Lyapunov functional $V(t)$ as

$$\begin{aligned}V(t) =& V_2(t) + \frac{1}{2}a_{11}^2 M_1\sigma_1(c_1+c_2)\int_0^{\infty}\int_{t-r}^{t} K_1(r)v_1^2(l)dldr\\ &+ \frac{1}{2}a_{21}\sigma_2(1+c_2)\Big[a_{11}\int_0^{\infty}\int_{t-r}^{t} K_1(r)v_1^2(l)dldr + a_{21}\int_0^{\infty}\int_{t-r}^{t} K_2(r)F_1^2(v_2(l))dldr\Big]\\ &+ \frac{1}{2}a_{32}\sigma_3\Big[a_{21}\int_0^{\infty}\int_{t-r}^{t} K_2(r)F_1^2(v_2(l))dldr + a_{32}\int_0^{\infty}\int_{t-r}^{t} K_3(r)F_2^2(v_3(l))dldr\Big].\end{aligned} \tag{3.13}$$

Then it follows from (3.12) and (3.13) that for $t \ge T$,

$$\begin{aligned}\frac{d}{dt}V(t) \le& -c_1a_{11}v_1^2(t) + c_2\Big(\frac{a_{12}}{m_{12}} - a_{21}\Big)F_1^2(v_2(t)) + \Big(\frac{a_{23}}{m_{23}} - a_{32}\Big)F_2^2(v_3(t))\\ &+ \frac{1}{2}a_{11}M_1\sigma_1\Big(a_{11} + \frac{a_{12}}{m_{12}}\Big)\big(c_1v_1^2(t) + c_2F_1^2(v_2(t))\big)\\ &+ \frac{1}{2}\sigma_2 a_{21}\Big(a_{11} + \frac{a_{12}}{m_{12}} + \frac{a_{23}}{m_{23}} + a_{21}\Big)\big(c_2F_1^2(v_2(t)) + F_2^2(v_3(t))\big)\\ &+ \frac{1}{2}\sigma_3 a_{32}\Big(a_{21} + \frac{a_{23}}{m_{23}} + a_{32}\Big)F_2^2(v_3(t))\\ &+ \frac{1}{2}a_{11}M_1\sigma_1(c_1+c_2)\Big[a_{11}v_1^2(t) + \frac{a_{12}}{m_{12}}F_1^2(v_2(t))\Big]\\ &+ \frac{1}{2}a_{21}\sigma_2(1+c_2)\Big[a_{11}v_1^2(t) + \frac{a_{12}}{m_{12}}F_1^2(v_2(t)) + \frac{a_{23}}{m_{23}}F_2^2(v_3(t)) + a_{21}F_1^2(v_2(t))\Big]\\ &+ \frac{1}{2}a_{32}\sigma_3\Big[a_{21}F_1^2(v_2(t)) + \frac{a_{23}}{m_{23}}F_2^2(v_3(t)) + a_{32}F_2^2(v_3(t))\Big] + R(t)\\ \le& -A_1v_1^2(t) - A_2F_1^2(v_2(t)) - A_3F_2^2(v_3(t)) + a_{11}\Big(\frac{3}{2}c_1 + \frac{1}{2}c_2\Big)v_1^2(t)\int_t^{\infty} K_1(s)ds\\ &+ \frac{1}{2}a_{11}(c_1+c_2)\int_t^{\infty} K_1(s)v_1^2(t-s)ds + a_{11}c_2F_1^2(v_2(t))\int_t^{\infty} K_1(s)ds\\ &+ a_{21}\Big(\frac{3}{2}c_2 + \frac{1}{2}\Big)F_1^2(v_2(t))\int_t^{\infty} K_2(s)ds + \frac{1}{2}a_{21}(1+c_2)\int_t^{\infty} K_2(s)F_1^2(v_2(t-s))ds\\ &+ a_{21}F_2^2(v_3(t))\int_t^{\infty} K_2(s)ds + \frac{3}{2}a_{32}F_2^2(v_3(t))\int_t^{\infty} K_3(s)ds\\ &+ \frac{1}{2}a_{32}\int_t^{\infty} K_3(s)F_2^2(v_3(t-s))ds\\ \le& -A_1v_1^2(t) - A_2F_1^2(v_2(t)) - A_3F_2^2(v_3(t)) + a_{11}\Big(\frac{3}{2}c_1 + \frac{1}{2}c_2\Big)v_1^2(t)\int_t^{\infty} K_1(s)ds\\ &+ \frac{1}{2}a_{11}(c_1+c_2)\|\psi_1\|^2\int_t^{\infty} K_1(s)ds + a_{11}c_2F_1^2(v_2(t))\int_t^{\infty} K_1(s)ds\\ &+ a_{21}\Big(\frac{3}{2}c_2 + \frac{1}{2}\Big)F_1^2(v_2(t))\int_t^{\infty} K_2(s)ds + \frac{1}{2}a_{21}(1+c_2)F_1^2(\|\psi_2\|)\int_t^{\infty} K_2(s)ds\\ &+ a_{21}F_2^2(v_3(t))\int_t^{\infty} K_2(s)ds + \frac{3}{2}a_{32}F_2^2(v_3(t))\int_t^{\infty} K_3(s)ds\\ &+ \frac{1}{2}a_{32}F_2^2(\|\psi_3\|)\int_t^{\infty} K_3(s)ds,\end{aligned} \tag{3.14}$$

where $\psi_i \in BC(-\infty, 0]$ is the initial data of $v_i(t)$ $(i = 1, 2, 3)$ and A_i $(i = 1, 2, 3)$ are defined by (H10). Therefore, we can choose $\varepsilon_i > 0$ $(i = 1, 2, 3)$ such that

$$a_{11}\varepsilon_1\Big(\frac{3}{2}c_1 + \frac{1}{2}c_2\Big) < A_1, \qquad a_{11}c_2\varepsilon_1 + a_{21}\Big(\frac{3}{2}c_2 + \frac{1}{2}\Big)\varepsilon_2 < A_2, \qquad a_{21}\varepsilon_2 + \frac{3}{2}a_{32}\varepsilon_3 < A_3.$$

Let $T = T(\varepsilon_1, \varepsilon_2, \varepsilon_3) > 0$ be such that $\int_t^\infty K_i(s)ds < \min\{\varepsilon_1, \varepsilon_2, \varepsilon_3\}$ for all $t \geq T$, $i = 1, 2, 3$. It then follows from (3.14) that for all $t \geq T$,

$$\begin{aligned}\frac{d}{dt}V(t) \leq &- \Big[A_1 - a_{11}\varepsilon_1\Big(\frac{3}{2}c_1 + \frac{1}{2}c_2\Big)\Big]v_1^2(t) - \Big[A_2 - a_{11}c_2\varepsilon_1 - a_{21}\Big(\frac{3}{2}c_2 + \frac{1}{2}\Big)\varepsilon_2\Big]F_1^2(v_2(t)) \\ &- \Big(A_3 - \frac{3}{2}a_{32}\varepsilon_3 - a_{21}\varepsilon_2\Big)F_2^2(v_3(t)) + \frac{1}{2}a_{11}(c_1 + c_2)\|\psi_1\|^2\int_t^\infty K_1(s)ds \\ &+ \frac{1}{2}a_{21}(1 + c_2)F_1^2(\|\psi_2\|)\int_t^\infty K_2(s)ds + \frac{1}{2}a_{32}F_2^2(\|\psi_3\|)\int_t^\infty K_3(s)ds. \end{aligned} \tag{3.15}$$

Integrating both sides of (3.15) from T to $t \geq T$, we get

$$\begin{aligned} V_1(t) \leq &V(t) + \Big[A_1 - a_{11}\varepsilon_1\Big(\frac{3}{2}c_1 + \frac{1}{2}c_2\Big)\Big]\int_T^t v_1^2(s)ds \\ &+ \Big[A_2 - a_{11}c_2\varepsilon_1 - a_{21}\Big(\frac{3}{2}c_2 + \frac{1}{2}\Big)\varepsilon_2\Big]\int_T^t F_1^2(v_2(s))ds \\ &+ \Big(A_3 - \frac{3}{2}a_{32}\varepsilon_3 - a_{21}\varepsilon_2\Big)\int_T^t F_2^2(v_3(s))ds \\ \leq &V(T) + \frac{1}{2}a_{11}(c_1 + c_2)\|\psi_1\|^2\int_T^t\int_s^\infty K_1(u)duds \\ &+ \frac{1}{2}a_{21}(1 + c_2)F_1^2(\|\psi_2\|)\int_T^t\int_s^\infty K_2(u)duds + \frac{1}{2}a_{32}F_2^2(\|\psi_3\|)\int_T^t\int_s^\infty K_3(u)duds \\ \leq &V(T) + \frac{1}{2}a_{11}(c_1 + c_2)\|\psi_1\|^2\int_0^\infty sK_1(s)ds \\ &+ \frac{1}{2}a_{21}(1 + c_2)F_1^2(\|\psi_2\|)\int_0^\infty sK_2(s)ds + \frac{1}{2}a_{32}F_2^2(\|\psi_3\|)\int_0^\infty sK_3(s)ds < \infty. \end{aligned}$$

This implies that $v_i(t)$ $(i = 1, 2, 3)$ are bounded, and $v_1^2(t), F_i^2\big(v_{i+1}(t)\big) \in L_1[0, +\infty)$, $i = 1, 2$. It follows from the equations in system (3.5) and the boundedness of $v_i(t)$ that $\dot{v}_i(t)(i = 1, 2, 3)$ are also bounded. Therefore, $v_i(t)$ $(i = 1, 2, 3)$ are uniformly continuous on $[0, \infty)$. It follows that $F_i(v_{i+1}(t))$ $(i = 1, 2)$ are also uniformly continuous. Thus, by the Babalat's Lemma (see [11]), we have $v_1(t) \to 0, F_i(v_{i+1}(t)) \to 0$ as $t \to \infty$. This leads to $\lim_{t\to\infty} v_i(t) = 0$, $i = 1, 2, 3$. Therefore, we have $\lim_{t\to\infty} x_i(t) = x_i^*$ for every solution $\big(x_1(t), x_2(t), x_3(t)\big)$ of system (1.2), this completes the proof.

Remark. If $K_i(s) = \delta(s)$, the Kronecker delta function, then $\sigma_i = 0$ $(i = 1, 2, 3)$, and (1.2) reduces to an instantaneous system i.e. one without time delay. Substituting $\sigma_i = 0$ $(i = 1, 2, 3)$ into (H10), Theorem 3.1 yields that E^* is globally attractive provided that the following assumption holds:

(H11) $a_{21} > \dfrac{a_{12}}{m_{12}}, \qquad a_{32} > \dfrac{a_{23}}{m_{23}}.$

Alternatively, with $\sigma_i = 0$ $(i = 1, 2, 3)$ system (3.5) becomes

$$\begin{cases} \dot{v}_1 = (v_1 + x_1^*)\Big[- a_{11}v_1(t) + \dfrac{a_{12}}{m_{12}} F_1\big(v_2(t)\big)\Big], \\ \dot{v}_2 = (v_2 + u_1^*)\Big[- a_{11}v_1(t) + \Big(\dfrac{a_{12}}{m_{12}} - a_{21}\Big) F_1\big(v_2(t)\big) - \dfrac{a_{23}}{m_{23}} F_2\big(v_3(t)\big)\Big], \\ \dot{v}_3 = (v_3 + u_2^*)\Big[a_{21}F_1\big(v_2(t)\big) + \Big(\dfrac{a_{23}}{m_{23}} - a_{32}\Big) F_2\big(v_3(t)\big)\Big]. \end{cases} \tag{3.16}$$

In this case, we may employ the Lyapunov function $V_1(t)$ defined by (3.6) directly. Indeed, it is straight forward to show that

$$\frac{d}{dt}V_1(t) \le -c_1 a_{11} v_1^2(t) + c_2\Big(\frac{a_{12}}{m_{12}} - a_{21}\Big)F_1^2\big(v_2(t)\big) + \Big(\frac{a_{23}}{m_{23}} - a_{32}\Big)F_2^2\big(v_3(t)\big),$$

which is negative definite provided (H11) holds, where c_1 and c_2 are defined by (H10). We therefore have the following corollary to Theorem 3.1.

Corollary 3.1. *The positive equilibrium E^* of system (1.2) is globally attractive if the positive equilibrium of the corresponding instantaneous system (without time delay) is globally attractive and σ_i $(i = 1, 2, 3)$ are sufficiently small to satisfy the assumption (H10).*

Finally, we give a suitable example to illustrate the feasibility of the conditions of Theorem 2.1, 3.1.

Example. We consider the following system

$$\begin{cases} \dot{x}_1 = x_1(t)\Big(2 - 2\displaystyle\int_0^\infty \alpha_1 e^{-\alpha_1 s} x_1(t-s)ds - \dfrac{x_2(t)}{x_2(t) + x_1(t)}\Big), \\ \dot{x}_2 = x_2(t)\Big(- 1 + 3\displaystyle\int_0^\infty \alpha_2 e^{-\alpha_2 s} \dfrac{x_1(t-s)}{x_2(t-s) + x_1(t-s)}ds - \dfrac{x_3(t)}{x_3(t) + x_2(t)}\Big), \\ \dot{x}_3 = x_3(t)\Big(- 1 + 2\displaystyle\int_0^\infty \alpha_3 e^{-\alpha_3 s} \dfrac{x_2(t-s)}{x_3(t-s) + x_2(t-s)}ds\Big), \end{cases} \tag{3.17}$$

where $\alpha_i > 0,\ i = 1, 2, 3$. In this case, $K_i(s) = \alpha_i e^{-\alpha_i s}$ $(i = 1, 2, 3)$ and it follows directly that $K_i(s)$ satisfies (1.4) and that $\sigma_i = \frac{1}{\alpha_i}$ $(i = 1, 2, 3)$. System (3.17) has a unique positive equilibrium $E^*\big(\frac{3}{4}, \frac{3}{4}, \frac{3}{4}\big)$. We choose $M_1 = 1 + 4\sigma_1,\ \varepsilon_0 = 1$. It is easy to verify that system (3.17) satisfies all assumptions in (H1)–(H9) when $\alpha_1 > 4,\ \alpha_2 > 4$ and $\alpha_3 > 1$ $\big($i.e. $\sigma_1 < \frac{1}{4},\ \sigma_2 < \frac{1}{4},\ \sigma_3 < 1\big)$. Using Theorem 2.1, we know that system (3.17) is uniformly persistent. By Theorem 3.1, we see that the positive equilibrium $E^*\big(\frac{3}{4}, \frac{3}{4}, \frac{3}{4}\big)$ is globally attractive provided that $12M_1\sigma_1 + 37\sigma_2 + 2\sigma_3 < 4$ and $33\sigma_2 + 18\sigma_3 < 2$.

Acknowledgment. The authors would like to thank the referees for their careful reading of the original manuscript and their many valuable comments and suggestions on this work.

References

[1] Arditi, R., Ginzburg, L.R. Coupling in predator-prey dynamics: ratio-dependence. *J. Theoretical Biology*, 139: 311–326 (1989)

[2] Arditi, R., Ginzburg, L.R., Akcakaya, H.R. Variation in Plankton densities among lakes: a case for ratio-dependent models. *The American Naturalist*, 138: 1287–1296 (1991)

[3] Arditi, R., Perrin, N., Saiah, H. Functional response and heterogeneities: an experiment test with cladocerans. *OIKOS*, 60: 69–75 (1991)

[4] Arditi, R., Saiah, H. Empirical evidence of the role of heterogeneity in ratio-dependent consumption. *Ecology*, 73: 1544–1551 (1992)

[5] Beretta, E., Kuang, Y. Global analysis in some delayed ratio-dependent predator-prey systems. *Nonlinear Analysis, T.M.A.*, 32: 381–408 (1998)

[6] Caperon, J. Time lag in population growth response of isochrysis galbana to a variable nitrate environment. *Ecology*, 50: 188–192 (1969)

[7] Caswell, H.A. A simulation study of a time lag population model. *J. Theoret. Biol.,* 34: 419–439 (1972)

[8] Cushing, J.M. Integro-differential equations and delay models in population dynamics. In: "Lecture notes in biomathematics", Vol.20, Springer-Verlag, Berlin, Heidelberg, New York, 1977

[9] Freedman, H.I., Rao, V.S.H. The tradeoff between mutual interference and time lag in predator-prey models. *Bull. Math. Biol.*, 45: 991–1004 (1983)

[10] Freedman, H.I., So, J., Waltman, P. Coexistence in a model of competition in the chemostat incorporating discrete time delays. *SIAM J. Appl. Math.,* 49: 859–870 (1989)

[11] Gopalsamy, K. Stability and oscillations in delay differential equations of population dynamics. Kluwer Academic, Dordrecht/Norwell, MA., 1992

[12] Gutierrez, A.P. The physiological basis of ratio-dependent predator-prey theory: a methbolic pool model of Nicholson's blowflies as an example. *Ecology*, 73: 1552–1563 (1992)

[13] Hanski, I. The functional response of predator: worries about scale. *TREE*, 6: 141–142 (1991)

[14] Kuang, Y. Delay differential equations with applications in population dynamics. Academic Press, New York, 1993

[15] Wang, W., Ma, Z. Harmless delays for uniform persistence. *J. Math. Anal. Appl.*, 158: 256–268 (1991)