Persistence and global stability in a delayed predator–prey system with Michaelis–Menten type functional response

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Abstract

A delayed three-species predator–prey food-chain model with Michaelis–Menten type functional response is investigated. It is proved that the system is uniformly persistent under some appropriate conditions. By means of constructing suitable Lyapunov functional, sufficient conditions are derived for the global asymptotic stability of the positive equilibrium of the system. © 2002 Elsevier Science Inc. All rights reserved.

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1. Introduction

An important problem in predator–prey theory and related topics in mathematical ecology, concerns the global stability of ecological system. For Lotka–Volterra systems without time delays, it is well known that global stability of a positive steady state holds when the intraspecific competition dominates the interspecific interactions (i.e., the so-called community matrix is diagonally dominant) (see [1] for a comprehensive discussion of such kinds of results). This result was extended to the delayed Lotka–Volterra-type systems by Kuang and Smith [2], where it was shown that if, for every species, the
instantaneous intraspecific competition (i.e., instantanenous negative feedback) dominates the total competition due to delayed intraspecific competition and interspecific competition, then the positive steady state of the system remains globally asymptotically stable.

Most of the global stability or convergence results appearing so far for delayed ecological systems require that the instantaneous negative feedbacks dominate both delayed feedback and interspecific interactions. Such a requirement is rarely met in real systems since feedbacks are generally delayed. This leads to the standing question: under what conditions will the global stability of a nonnegative steady state of a delay differential system persist when time delays involved in some part of the negative feedbacks are small enough? Kuang [3] presented a partial answer to this open question for Lotka–Volterra-type systems.

The traditional Lotka–Volterra type predator–prey models with Michaelis–Menten type functional response have received great attention among theoretical and mathematical biologists. Motivated by the work of Kuang [3] and Freedman and Ruan [4] for retarded functional differential equations, in the present paper, we consider the following delayed predator–prey model with Michaelis–Menten type functional response

\[
\begin{align*}
\dot{x}_1 &= x_1(t) \left( a_1 - a_{11}x_1(t - \tau_{11}) - \frac{a_{12}x_2(t)}{m_1 + x_1(t)} \right), \\
\dot{x}_2 &= x_2(t) \left( -a_2 + \frac{a_{21}x_1(t - \tau_{21})}{m_1 + x_1(t - \tau_{21})} - a_{22}x_2(t - \tau_{22}) - \frac{a_{23}x_3(t)}{m_2 + x_2(t)} \right), \\
\dot{x}_3 &= x_3(t) \left( -a_3 + \frac{a_{32}x_2(t - \tau_{32})}{m_2 + x_2(t - \tau_{32})} - a_{33}x_3(t - \tau_{33}) \right),
\end{align*}
\tag{1.1}
\]

with initial conditions
\[
x_i(t) = \phi_i(t), \quad t \in [-\tau, 0], \quad \phi_i(0) > 0, \quad i = 1, 2, 3,
\tag{1.2}
\]

where \(x_1(t), x_2(t)\) and \(x_3(t)\) denote the densities of the prey, predator and top predator population, respectively. \(a_i, a_{ij} \ (i, j = 1, 2, 3)\) are positive constants. \(\tau_{11}, \tau_{21}, \tau_{22}, \tau_{32}\) and \(\tau_{33}\) are nonnegative constants, \(\tau = \max\{\tau_{11}, \tau_{21}, \tau_{22}, \tau_{32}, \tau_{33}\}\). \(\phi_i(t) \ (i = 1, 2, 3)\) are continuous bounded functions in the interval \([-\tau, 0]\). We have assumed in (1.1) that when the predator species are absent, the prey species \(x_1\) is governed by the well-known delay logistic equation

\[
\frac{dx_1(t)}{dt} = x_1(t)(a_1 - a_{11}x_1(t - \tau_{11}))
\]

where \(\tau_{11} > 0\) denotes the delay in the negative feedback of the prey species \(x_1\). \(\tau_{21}, \tau_{32}\) are constant delays due to gestation, that is, mature adult predators can only contribute to the production of predator biomass. In addition, we have included the term \(-a_{22}x_2(t - \tau_{22})\) and \(-a_{33}x_3(t - \tau_{33})\) in the dynamics of pre-
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 (1.1), only in \( \text{Int} \ R_+^3 \).

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

The organization of this paper is as follows. In the next section, we present permanence results for system (1.1). Section 3 provides sufficient conditions for the positive equilibrium of system (1.1) to be globally asymptotically stable. Finally, a suitable example is given to illustrate the feasibility of the conditions of our theorems.

### 2. Uniform persistence

The following lemmas are elementary and are concerned with the qualitative nature of solutions of system (1.1).

**Lemma 2.1.** Solutions of system (1.1) with initial conditions (1.2) are defined on \([0, +\infty)\) and remain positive for all \( t \geq 0 \).

**Lemma 2.2.** Let \( x(t) = (x_1(t), x_2(t), x_3(t)) \) denote any positive solution of system (1.1) with initial conditions (1.2). Suppose that system (1.1) satisfies the following:

\[(H1) \ a_1(a_{21} - a_2) > m_1a_2a_{11},\]

\[(H2) \ (a_{32} - a_3)[a_1(a_{21} - a_2) - m_1a_2] - m_2a_3a_{22}(a_1 + m_1a_{11}) > 0.\]

Then there exists a \( T > 0 \), such that

\[x_i(t) \leq M_i \quad (i = 1, 2, 3) \text{ for } t \geq T,\]

where

\[M_1 = \frac{a_1}{a_{11}} \exp[a_1\tau_{11}],\]

\[M_2 = \frac{(a_{21} - a_2)M_1 - m_1a_2}{a_{22}(m_1 + M_1)} \exp\left[\frac{(a_{21} - a_2)M_1 - m_1a_2}{m_1 + M_1} \tau_{22}\right],\]

\[M_3 = \frac{(a_{32} - a_3)M_2 - m_2a_3}{a_{22}(m_2 + M_2)} \exp\left[\frac{(a_{32} - a_3)M_2 - m_2a_3}{m_2 + M_2} \tau_{33}\right].\]
The proofs of Lemmas 2.1 and 2.2 are omitted because they are similar to those of Lemmas 2.1 and 2.2 of [5].

In order to analyse the long term coexistence of the three species of (1.1), we need to know the flow on the boundary. For that we first search the boundary invariant sets, that is equilibria or periodic orbits.

Firstly, we consider the following subsystem:

\[
\begin{align*}
\dot{x}_1 &= x_1(t) \left( a_1 - a_{11} x_1(t - \tau_{11}) - a_{12} \frac{x_2(t)}{m_1 + x_1(t)} \right), \\
\dot{x}_2 &= x_2(t) \left( -a_2 + a_{21} \frac{x_1(t - \tau_{21})}{m_1 + x_1(t - \tau_{21})} - a_{22} x_2(t - \tau_{22}) \right).
\end{align*}
\]  

(2.2)

The following result shows that subsystem (2.2) is uniformly persistent.

**Theorem 2.1.** Suppose that system (2.2) satisfies (H1) and the following:

(H3) \(a_1 \tau_1 \leq \frac{3}{2}\).

Then system (2.2) is uniformly persistent.

**Proof.** It is easy to verify that system (2.2) has two equilibria \(E_{00}(0, 0)\) and \(E_{10}(a_1/a_{11}, 0)\) on the boundary of \(R^2_+\). From the assumptions of the theorem we know that the omega limit set of boundary of \(R^2_+\) is the union of the boundary equilibria \(E_{00}\) and \(E_{10}\). We choose

\[
p_1(x_1(t), x_2(t)) = x_1^{x_{11}}(t) x_2^{x_{21}}(t),
\]

where \(x_{ai}\) (\(i = 1, 2\)) are undetermined positive constants. We have

\[
\psi_1(x) = \frac{\dot{p}_1(x)}{p_1(x)} = x_{11} \left( a_1 - a_{11} x_1(t - \tau_{11}) - a_{12} \frac{x_2(t)}{m_1 + x_1(t)} \right) + x_{21} \left( -a_2 + a_{21} \frac{x_1(t - \tau_{21})}{m_1 + x_1(t - \tau_{21})} - a_{22} x_2(t - \tau_{22}) \right).
\]

If we choose \(x_{11} = 1\), and \(x_{21}\) so small such that \(x_{11} a_1 - x_{21} a_2 > 0\), then \(\psi_1\) is positive at \(E_{00}\). Under Assumption (H1), it is easy to verify that \(\psi_1\) is positive at \(E_{10}\). Hence, there is a choice of \(x_{21}\) to ensure \(\psi_1 > 0\) at the boundary equilibria. If the condition (H3) holds, it follows from [6] that \(E_{10}\) is globally asymptotically stable with respect to solutions initiating in the \(x_1\)-axis. It is easy to verify that \(E_{00}\) is globally asymptotically stable in the \(x_2\)-axis. Thus system (2.2) is
uniformly persistent follows from Theorem 3.12 of Freedman and Ruan [4]. The proof is complete. □

**Remark 1.** If \( \tau_{11} = \tau_{21} = \tau_{22} = 0 \), then system (2.2) reduces to an instantaneous system i.e., one without time delay. From the proof of Theorem 2.1, we see that, if (H1) holds, then the corresponding instantaneous system of (2.2) is uniformly persistent, which implies that system (2.2) must have a positive equilibrium (see [7]), we denote it by \( E_{12}(x_{11}, x_{21}) \) (\( x_{11} \) and \( x_{21} \) can be evaluated explicitly).

**Theorem 2.2.** Suppose that system (2.2) satisfies (H1). Then the positive equilibrium \( E_{12} \) of (2.2) is globally asymptotically stable provided that

(H4) \( \omega_{ii} > 0, \quad i = 1, 2, \)

(H5) \( \omega_{11}\omega_{22} - \omega_{12}\omega_{21} > 0, \)

where

\[
\begin{align*}
\omega_{11} &= a_{11} - \frac{a_1}{m_1} - a_{11}M_1\tau_{11}\left(a_{11} + \frac{a_1}{m_1}\right), \\
\omega_{12} &= -\frac{a_{12}}{m_1}\left(1 + a_{11}M_1\tau_{11}\right), \quad \omega_{21} = -\frac{a_{21}}{m_1}\left(1 + a_{22}M_2\tau_{22}\right), \\
\omega_{22} &= a_{22}\left(1 - a_{22}M_2\tau_{22}\right)
\end{align*}
\]

in which \( M_i \) is defined by (2.1).

**Proof.** Let \( x(t) = (x_1(t), x_2(t)) \) be any solution of (2.2) with initial conditions (1.2). Define \( u(t) = (u_1(t), u_2(t)) \) by

\[
u_i(t) = \ln \frac{x_i(t)}{x_{i1}} \quad (i = 1, 2).
\]

It follows from (2.2) and (2.3) that

\[
\begin{align*}
\frac{du_1}{dt} &= -a_{11}x_{11}\left(e^{a_{11}(t-\tau_{11})} - 1\right) - \frac{a_{12}x_{21}}{m_1 + x_1}\left(e^{a_{21}(t)} - 1\right) \\
&\quad + \frac{a_{12}x_{11}x_{21}}{(m_1 + x_1)(m_1 + x_{11})}\left(e^{a_{11}(t)} - 1\right), \\
\frac{du_2}{dt} &= \frac{m_1a_{21}x_{11}}{(m_1 + x_1(t - \tau_{21}))(m_1 + x_{11})}\left(e^{a_{21}(t-\tau_{21})} - 1\right) - a_{22}x_{21}\left(e^{a_{22}(t-\tau_{22})} - 1\right).
\end{align*}
\]
System (2.4) can be rewritten as
\[
\frac{du_1}{dt} = -a_{11}x_1 \left( e^{u_1(t)} - 1 \right) - \frac{a_{12}x_{21}}{m_1 + x_1} \left( e^{u_2(t)} - 1 \right) + a_{12}x_{11}x_{21} \left( e^{u_1(t)} - 1 \right) \\
+ a_{11}x_1 \int_{t-t_{11}}^{t} e^{u_1(s)} \left\{ -a_{11}x_1 \left( e^{u_1(s-t_{11})} - 1 \right) \right\} ds
\]
\[
- \frac{a_{12}x_{21}}{m_1 + x_1} \left( e^{u_2(s)} - 1 \right) + \frac{a_{12}x_{11}x_{21}}{(m_1 + x_1)(m_1 + x_{11})} \left( e^{u_1(s)} - 1 \right) \right\} ds,
\]
\[
\frac{du_2}{dt} = \frac{m_1a_{21}x_{11}}{(m_1 + x_1(t - \tau_{21}))(m_1 + x_{11})} \left( e^{u_1(t-\tau_{21})} - 1 \right) - a_{22}x_{21} \left( e^{u_2(t-\tau_{21})} - 1 \right)
\]
\[
+ a_{22}x_{21} \int_{t-\tau_{22}}^{t} e^{u_2(s)} \left\{ \frac{m_1a_{21}x_{11}}{(m_1 + x_1(s - \tau_{21}))(m_1 + x_{11})} \left( e^{u_1(s-\tau_{21})} - 1 \right) - a_{22}x_{21} \left( e^{u_2(s-\tau_{22})} - 1 \right) \right\} ds.
\]

According to Assumptions (H4) and (H5), we know that $C_{12} = (\omega_{ij})_{2 \times 2}$ is an M-matrix, and hence there exist positive constants $b_i \ (i = 1, 2)$ such that
\[
\omega_{11}b_1 + \omega_{21}b_2 = d_1 > 0, \quad \omega_{12}b_1 + \omega_{22}b_2 = d_2 > 0.
\]

Let us define a Lyapunov functional $V_{10}(t)$ by
\[
V_{10}(t) = b_1 \left\{ |u_1(t)| + a_{11}M_1 \int_{t-t_{11}}^{t} \int_{s}^{t} \left\{ a_{11}x_1 \left| e^{u_1(s-t_{11})} - 1 \right| \right\} ds dv \\
+ \frac{a_{12}x_{21}}{m_1} \left| e^{u_2(s)} - 1 \right| + \frac{a_{12}x_{11}x_{21}}{m_1(m_1 + x_1)} \left| e^{u_1(s)} - 1 \right| \right\} ds dv
\]
\[
+ a_{11}x_1 \int_{t-t_{11}}^{t} |e^{u_1(s)} - 1| ds + b_2 \left\{ |u_2(t)| \right\} + a_{22}M_2 \left\{ \frac{a_{21}x_{11}}{m_1 + x_1} \int_{t-\tau_{21}}^{t} \int_{s}^{t} \left| e^{u_1(s-\tau_{21})} - 1 \right| ds dv \\
+ a_{22}x_{21} \int_{t-\tau_{22}}^{t} \int_{s}^{t} \left| e^{u_2(s-\tau_{22})} - 1 \right| ds dv \right\} \right\}
\]
\[
+ \frac{a_{21}x_{11}}{m_1 + x_{11}} \int_{t-\tau_{21}}^{t} \left| e^{u_1(s)} - 1 \right| ds + a_{22}M_2 \tau_{22}
\]
\[
\times \left\{ \frac{a_{21}x_{11}}{m_1 + x_{11}} \int_{t-\tau_{21}}^{t} \left| e^{u_1(s)} - 1 \right| ds \right\} + a_{22}x_{21} \int_{t-\tau_{22}}^{t} \left| e^{u_2(s)} - 1 \right| ds \right\} \right\}.
\]

By Lemma 2.2 we see that there exists a $T > 0$, such that
\[
x_{k1}e^{u_k(t)} = x_k(t) \leq M_k \quad \text{for} \quad t \geq T, \ k = 1, 2.
\]

Calculating the upper right derivative of $V_{10}(t)$ along the solution of (2.5), we have for $t \geq T + \tau$ that
Using the mean valued theorem one obtains

\[ D^+ V_{10}(t) \leq -d_1 x_{11} |e^{\alpha_1(t)} - 1| - d_2 x_{21} |e^{\alpha_2(t)} - 1| \]  \hfill (2.7)

Since system (2.2) is uniformly persistent, one can see that there exist positive constants \( n_{k_1} \) \((k = 1, 2)\) and a \( T^* \geq T + \tau \) such that

\[ x_{k_1} e^{\alpha_1(t)} = x_k(t) \geq n_{k_1} \quad (k = 1, 2) \text{ for } t \geq T^*. \]

Using the mean valued theorem one obtains

\[ x_{k_1} |e^{\alpha_1(t)} - 1| = x_{k_1} e^{\theta_k(t)} |u_k(t)| \geq n_{k_1} |u_k(t)| \quad (k = 1, 2), \]

where \( x_{k_1} e^{\theta_k(t)} \) lies between \( x_k(t) \) and \( x_{k_1} \). Let \( \alpha = \min\{n_{11} a_1, n_{21} a_2\} \). Then it follows from (2.7) that for \( t \geq T^* \)

\[ D^+ V_{10}(t) \leq - \alpha (|u_1(t)| + |u_2(t)|). \]  \hfill (2.8)

Noting that \( V_{10}(t) \geq \min\{b_1, b_2\} (|u_1(t)| + |u_2(t)|) \), we can conclude from the Lyapunov Theorem and (2.8) that the zero solution of (2.4) is globally asymptotically stable, and hence the positive equilibrium \( E(x_{11}, x_{21}) \) of (2.2) is globally asymptotically stable. This completes the proof. \( \square \)

The following result shows that system (1.1) is uniformly persistent.

**Theorem 2.3.** Suppose that system (1.1) satisfies (H1), (H2), (H4) and (H5) and the following:

(H6) \( x_{21}(a_{32} - a_3) - m_2 a_3 > 0 \).

Then system (1.1) is uniformly persistent.

**Proof.** System (1.1) has three equilibria \( E_0(0, 0, 0), E_1(a_1/a_{11}, 0, 0) \) and \( E_{12}(x_{11}, x_{21}, 0) \) on the boundary of \( R_+^3 \). From the assumptions of the theorem we know that the omega limit set of boundary of \( R_+^3 \) is the union of the boundary equilibria \( E_0, E_1 \) and \( E_{12} \). We choose

\[ p(x_1(t), x_2(t), x_3(t)) = x_1^{z_1}(t)x_2^{z_2}(t)x_3^{z_3}(t), \]

where \( z_i \) \((i = 1, 2, 3)\) are undetermined positive constants. We have

\[ \psi(x) = \frac{\dot{p}(x)}{p(x)} \]

\[ = z_1 \left( a_1 - a_{11} x_1(t - \tau_{11}) - a_{12} \frac{x_2(t)}{m_1 + x_1(t)} \right) \]

\[ + z_2 \left( -a_2 + a_{21} \frac{x_1(t - \tau_{21})}{m_1 + x_1(t - \tau_{21})} - a_{22} x_2(t - \tau_{22}) - \frac{a_{32} x_3(t)}{m_2 + x_2(t)} \right) \]

\[ + z_3 \left( -a_3 + a_{32} \frac{x_2(t - \tau_{32})}{m_2 + x_2(t - \tau_{32})} - a_{33} x_3(t - \tau_{33}) \right). \]
If we choose \(a_1 = \frac{1}{2} \), \(a_2\) and \(a_3\) so small such that \(a_1a_1 - a_2a_2 - a_3a_3 > 0\), then \(\psi\) is positive at \(E_0\). Under Assumption (H1), if we choose \(a_3\) small enough, then \(\psi\) is positive at \(E_1\). Under Assumption (H6), it is easy to verify that \(\psi\) is positive at \(E_{12}\). Hence, there are choices of \(a_2\) and \(a_3\) to ensure \(\psi > 0\) at the boundary equilibria. Because the boundary equilibrium \(E_{12}\) has been shown as the \(\omega\)-limit set of the corresponding boundary system by assumptions of the theorem. The conditions (H4) and (H5) imply \(a_1\tau_{11} < 3/2\), it follows from [6] that \(E_1\) is globally asymptotically stable with respect to solutions initiating in the \(x_1\)-axis. It is easy to verify that \(E_0\) is globally asymptotically stable in the \(x_2\)–\(x_3\) plane. Thus system (1.1) is uniformly persistent follows from Theorem 3.12 of Freedman and Ruan [4].

**Remark 2.** If \(\tau_{11} = \tau_{21} = \tau_{22} = \tau_{32} = \tau_{33} = 0\), then system (1.1) reduces to an instantaneous system, i.e., one without time delay. From the proof of Theorem 2.1, we see that, if (H1), (H2) and (H6) hold, then the corresponding instantaneous system of (1.1) is uniformly persistent provided that

\[
a_{22}(a_{11} - (a_1/m_1)) - (a_{12}a_{21}/m_1^2) > 0,
\]

which implies that system (1.1) must have a positive equilibrium (see [7]), we denote it by \(E^*(x_1^*, x_2^*, x_3^*)\).

3. Global asymptotic stability

In this section, we derive sufficient conditions which guarantee that the positive equilibrium \(E^*(x_1^*, x_2^*, x_3^*)\) of system (1.1) is globally asymptotically stable. Our strategy in the proof of the global asymptotic stability of the positive equilibrium \(E^*\) of (1.1) is to construct suitable Lyapunov functionals.

**Theorem 3.1.** Suppose that system (1.1) satisfies (H1), (H2) and (H6). Then the positive equilibrium \(E^*\) of (1.1) is globally asymptotically stable provided that

\[
\begin{align*}
(H8) \quad & r_{ii} > 0, \quad i = 1, 2, \\
(H9) \quad & r_{11}r_{22}r_{33} - r_{12}r_{21}r_{33} - r_{11}r_{23}r_{32} > 0,
\end{align*}
\]

where

\[
\begin{align*}
& r_{11} = a_{11} - \frac{a_1}{m_1} - a_{11}M_1\tau_{11} \left( a_{11} + \frac{a_1}{m_1} \right), \\
& r_{12} = -\frac{a_{12}}{m_1} \left( 1 + a_{11}M_1\tau_{11} \right), \quad r_{21} = -\frac{a_{21}}{m_1} \left( 1 + a_{22}M_2\tau_{22} \right), \\
& r_{22} = a_{22} - \frac{a_{21}}{m_2} - a_{22}M_2\tau_{22} \left( a_{22} + \frac{a_{21}}{m_2} \right), \\
& r_{23} = -\frac{a_{23}}{m_2} \left( 1 + a_{22}M_2\tau_{22} \right), \quad r_{32} = -\frac{a_{32}}{m_2} \left( 1 + a_{33}M_3\tau_{33} \right), \\
& r_{33} = a_{33} \left( 1 - a_{33}M_3\tau_{33} \right).
\end{align*}
\]
in which $M_i$ is defined by (2.1).

**Proof.** Let $x(t) = (x_1(t), x_2(t), x_3(t))$ be any solution of (1.1) with initial conditions (1.2). Define

$$u(t) = (u_1(t), u_2(t), u_3(t))$$

by

$$u_i(t) = \ln \frac{x_i(t)}{x_i^*} \quad (i = 1, 2, 3). \quad (3.1)$$

It follows from (1.1) and (3.1) that

$$\frac{du_1}{dt} = -a_{11}x_1^*(e^{u_1(t)} - 1) - \frac{a_{12}x_2^*}{m_1 + x_1}(e^{u_2(t)} - 1)$$

$$+ \frac{a_{12}x_1^*x_2^*}{(m_1 + x_1)(m_1 + x_1^*)}(e^{u_1(t)} - 1),$$

$$\frac{du_2}{dt} = \frac{m_1a_2x_1^*}{(m_1 + x_1(t - \tau_{11}))(m_1 + x_1^*)}(e^{u_1(t - \tau_{11})} - 1) - a_{22}x_2^*(e^{u_2(t - \tau_{22})} - 1)$$

$$+ \frac{a_{22}x_1^*x_2^*}{(m_2 + x_2)(m_2 + x_2^*)}(e^{u_2(t)} - 1) - \frac{a_{23}x_2^*}{m_2 + x_2}(e^{u_3(t)} - 1),$$

$$\frac{du_3}{dt} = -a_3m_2x_2^*(e^{u_2(t)} - 1) - a_{33}x_3^*(e^{u_3(t - \tau_{33})} - 1). \quad (3.2)$$

The first equation of (3.2) can be rewritten as

$$\frac{du_1}{dt} = -a_{11}x_1^*(e^{u_1(t)} - 1) - \frac{a_{12}x_2^*}{m_1 + x_1}(e^{u_2(t)} - 1) + \frac{a_{12}x_1^*x_2^*}{(m_1 + x_1)(m_1 + x_1^*)}(e^{u_1(t)} - 1)$$

$$+ a_{11}x_1^* \int_{t - \tau_{11}}^{t} e^{u_1(s)} \frac{du_1(s)}{ds} \, ds$$

$$= -a_{11}x_1^*(e^{u_1(t)} - 1) - \frac{a_{12}x_2^*}{m_1 + x_1}(e^{u_2(t)} - 1)$$

$$+ \frac{a_{12}x_1^*x_2^*}{(m_1 + x_1)(m_1 + x_1^*)}(e^{u_1(t)} - 1) + a_{11}x_1^* \int_{t - \tau_{11}}^{t} e^{u_1(s)} \left\{ -a_{11}x_1^*(e^{u_1(t - \tau_{11})} - 1) \right\} ds. \quad (3.3)$$

Let

$$V_{11}(t) = |u_1(t)|. \quad (3.4)$$

Calculating the upper right derivative of $V_{11}(t)$ along the solution of (3.2), it follows from (3.3) and (3.4) that
Define a Lyapunov functional

\[ V(t) = V_1(t) + V_12(t), \]

where

\[ V_12(t) = a_{11}M_1 \int_{t-	au_{11}}^{t} \int_{t}^{t'} \left\{ a_{11}x_1^s \left| e^{u_1(s)} - 1 \right| + \frac{a_{12}x_1^2}{m_1} \left| e^{u_2(s)} - 1 \right| \right\} \, ds \, dv + a_{11}^2x_1^s \int_{t-	au_{11}}^{t} \left| e^{u_1(s)} - 1 \right| \, ds. \]
Next, let

\[ V_2(t) = |u_2(t)| + a_{22}M_2 \int_{t-T_2}^t \int_{\gamma} \left\{ \frac{a_{21}x_1^s}{m_1 + x_1^s} |e^{a_1(s-t_2)} - 1| \ight. \\
\left. + \frac{a_{22}x_2^s}{m_2} |e^{a_2(s-t_2)} - 1| + \frac{a_{23}x_3^s}{m_2} |e^{a_3(s-t_2)} - 1| \right\} ds \, dv \\
\left. + a_{22}M_2 \int_{t-T_2}^t \int_{\gamma} |e^{a_1(s-t_2)} - 1| ds \\
\left. + a_{22}x_2^s \int_{t-T_2}^t |e^{a_2(s-t_2)} - 1| ds \right\}. \tag{3.10} \]

Then it follows from (3.2), (3.10) and (1.1) that for \( t \geq T + \tau \)

\[
D^+ V_2(t) \leq -x_2^s \left[ a_{22} - \frac{a_{23}x_3^s}{m_2(m_2 + x_2^s)} \right] \left| e^{a_2(t)} - 1 \right| \\
- a_{22}M_2 \tau_{22} \left( a_{22} + \frac{a_{23}x_3^s}{m_2(m_2 + x_3^s)} \right) \left| e^{a_2(t)} - 1 \right| \\
+ \frac{a_{21}x_1^s}{m_1 + x_1^s} (1 + a_{22}M_2 \tau_{22}) |e^{a_1(t)} - 1| \\
+ \frac{a_{23}x_3^s}{m_2} (1 + a_{22}M_2 \tau_{22}) |e^{a_3(t)} - 1| \\
\leq -x_2^s \left[ a_{22} - \frac{a_{21}x_1^s}{m_2(m_1 + x_1^s)} \right] \left| e^{a_2(t)} - 1 \right| \\
- a_{22}M_2 \tau_{22} \left( a_{22} + \frac{a_{21}x_1^s}{m_2(m_1 + x_1^s)} \right) \left| e^{a_2(t)} - 1 \right| \\
+ \frac{a_{21}x_1^s}{m_1} (1 + a_{22}M_2 \tau_{22}) |e^{a_1(t)} - 1| \\
+ \frac{a_{23}x_3^s}{m_2} (1 + a_{22}M_2 \tau_{22}) |e^{a_3(t)} - 1| \tag{3.11} \\
\leq -r_{21}x_1^s |e^{a_1(t)} - 1| - r_{22}x_2^s |e^{a_2(t)} - 1| - r_{23}x_3^s |e^{a_3(t)} - 1|. \]
Finally, let
\[
V_3(t) = |u_3(t)| + a_{33}M_3 \int_{t-\tau_{33}}^t \int_{t-\tau_{33}}^t \left\{ \frac{a_{32}x_2^s}{m_2 + x_2} |e^{a_2(s-\tau_{33})} - 1| + a_{33}x_3^s |e^{a_3(s-\tau_{33})} - 1| \right\} ds \, dv + a_{33}M_3 \int_{t-\tau_{33}}^t \int_{t-\tau_{33}}^t |e^{a_3(v)} - 1| ds
\]
\[+ a_{33}x_3^s \int_{t-\tau_{33}}^t |e^{a_3(s)} - 1| ds \]  
\[+ \frac{a_{32}x_2^s}{m_2 + x_2} \int_{t-\tau_{33}}^t |e^{a_2(v)} - 1| ds. \quad (3.12)
\]

Then it follows from (3.2) and (3.12) that for \( t \geq T + \tau \)
\[
D^+ V_3(t) \leq \frac{a_{32}x_2^s}{m_2 + x_2^s} (1 + a_{33}M_3 \tau_{33}) |e^{a_2(t)} - 1| - a_{33}x_3^s (1 - a_{33}M_3 \tau_{33}) |e^{a_3(t)} - 1|
\]
\[\leq \frac{a_{32}x_2^s}{m_2} (1 + a_{33}M_3 \tau_{33}) |e^{a_2(t)} - 1| - a_{33}x_3^s (1 - a_{33}M_3 \tau_{33}) |e^{a_3(t)} - 1|
\]
\[= - r_{32}x_2^s |e^{a_2(t)} - 1| - r_{33}x_3^s |e^{a_3(t)} - 1|. \quad (3.13)
\]

According to Assumptions (H8) and (H9), we know that \( C = (r_{ij})_{3 \times 3} \) is an M-matrix, hence there exist positive constants \( c_i \) (\( i = 1, 2, 3 \)) such that
\[r_{11}c_1 + r_{21}c_2 = h_1 > 0, \quad r_{12}c_1 + r_{22}c_2 + r_{32}c_3 = h_2 > 0,
\]
\[r_{23}c_2 + r_{33}c_3 = h_3 > 0.
\]

Now define a Lyapunov functional \( V(t) \) as
\[
V(t) = c_1 V_1(t) + c_2 V_2(t) + c_3 V_3(t). \quad (3.14)
\]

Then it follows from (3.9), (3.11) and (3.13) that for \( t \geq T + \tau \)
\[
D^+ V(t) \leq - h_1 x_1^s |e^{a_1(t)} - 1| - h_2 x_2^s |e^{a_2(t)} - 1| - h_3 x_3^s |e^{a_3(t)} - 1|. \quad (3.15)
\]

Since system (1.1) is uniformly persistent, one can see that there exist positive constants \( n_k \) (\( k = 1, 2, 3 \)) and a \( T^* > 0 \) such that
\[x_k^s e^{u_k(t)} = x_k(t) \geq n_k \quad (k = 1, 2, 3) \quad \text{for} \quad t \geq T^*.
\]

Using the mean valued theorem one obtains
\[x_k^s |e^{u_k(t)} - 1| = x_k^s e^{\delta_k} |u_k(t)| \geq n_k |u_k(t)| \quad (k = 1, 2, 3),
\]
where \( x_k^s e^{\delta_k} \) lies between \( x_k(t) \) and \( x_k^s \). Let \( \delta = \min\{n_1h_1, n_2h_2, n_3h_3\} \). Then it follows from (3.15) that for \( t \geq T^* \)
\[
D^+ V(t) \leq - \delta (|u_1(t)| + |u_2(t)| + |u_3(t)|). \quad (3.16)
\]

Noting that \( V(t) \geq \min\{c_1, c_2, c_3\} (|u_1(t)| + |u_2(t)| + |u_3(t)|) \), we can conclude from the Lyapunov Theorem and (3.16) that the zero solution of (3.2) is globally asymptotically stable, and hence the positive equilibrium \( E^*(x_1^*, x_2^*, x_3^*) \) of (1.1) is globally asymptotically stable. This completes the proof. □
**Remark 3.** It is interesting to discuss the effect of time delays on the stability of the positive equilibrium of (1.1). We assume that the positive equilibrium $E^*$ exists for system (1.1).

Linearizing system (1.1) at $E^*(x_1^*, x_2^*, x_3^*)$, we obtain

$$
\begin{align*}
\dot{x}_1(t) &= A_{11}x_1(t - \tau_{11}) + B_{11}x_1(t) + A_{12}x_2(t), \\
\dot{x}_2(t) &= A_{21}x_1(t - \tau_{21}) + A_{22}x_2(t - \tau_{22}) + B_{22}x_2(t) + A_{23}x_3(t), \\
\dot{x}_3(t) &= A_{32}x_2(t - \tau_{32}) + A_{33}x_3(t - \tau_{33}),
\end{align*}
$$

(3.17)

where

$$
\begin{align*}
A_{11} &= -a_{11}x_1^*, & A_{12} &= -\frac{a_{12}x_1^*}{m_1 + x_1^*}, & B_{11} &= -\frac{a_{12}x_1^*x_2^*}{(m_1 + x_1^*)^2}, \\
A_{21} &= \frac{m_1a_{21}x_1^*}{(m_1 + x_1^*)^2}, & A_{22} &= -a_{22}x_2^*, & B_{22} &= -\frac{a_{23}x_2^*x_3^*}{(m_2 + x_2^*)^2}, \\
A_{23} &= -\frac{a_{23}x_3^*}{m_2 + x_2^*}, & A_{32} &= \frac{m_2a_{32}x_3^*}{(m_2 + x_2^*)^2}, & A_{33} &= -a_{33}x_3^*.
\end{align*}
$$

For simplicity, firstly, we let $\tau_{21} = \tau$, $\tau_{11} = \tau_{22} = \tau_{32} = \tau_{33} = 0$.

The characteristic equation for (3.17) takes the form

$$
P_1(\lambda) + Q_1(\lambda)e^{-\delta t} = 0
$$

in which

$$
\begin{align*}
P_1(\lambda) &= (\lambda - A_{11} - B_{11})(\lambda - A_{22} - B_{22})(\lambda - A_{33}) - A_{23}A_{32}(\lambda - A_{11} - B_{11}), \\
Q_1(\lambda) &= -A_{12}A_{21}(\lambda - A_{33}).
\end{align*}
$$

It is easy to verify that the positive equilibrium $E^*$ of (1.1) is stable for $\tau = 0$ provided that

$$(H10) \ 2(A_{11} + B_{11}) - A_{12} + A_{21} < 0,$$

$$(H11) \ 2(A_{22} + B_{22}) - A_{12} + A_{21} - A_{23} + A_{32} < 0,$$

$$(H12) \ 2A_{33} - A_{23} + A_{32} < 0.$$

Let $F_1(y) = |P_1(iy)|^2 - |Q_1(iy)|^2$. If (H10)–(H12) hold, then it is easy to verify that $F_1(y) = 0$ has no positive roots. By applying Theorem 4.1 on p. 83 in [8], we see that as $\tau$ increases, no stability switch may occur. If we let $\tau_{32} = \tau$, $\tau_{11} = \tau_{21} = \tau_{22} = \tau_{33} = 0$, a similar result can be obtained. From Theorem 3.1, we see that time delay due to gestation is harmless for the global stability of the positive equilibrium of system (1.1).

Secondly, we let $\tau_{11} = \tau$, $\tau_{21} = \tau_{22} = \tau_{32} = \tau_{33} = 0$. Then the characteristic equation for (3.17) takes the form

$$
P_2(\lambda) + Q_2(\lambda)e^{-\delta t} = 0
$$
in which
\[ P_2(\lambda) = (\lambda - B_{11})(\lambda - A_{22} - B_{22})(\lambda - A_{33}) - A_{12}A_{21}(\lambda - A_{33}) - A_{23}A_{32}(\lambda - B_{11}), \]
\[ Q_2(\lambda) = -A_{11}(\lambda - A_{22} - B_{22})(\lambda - A_{33}) + A_{11}A_{23}A_{32}. \]

Let \( F_2(y) = |P_2(iy)|^2 - |Q_2(iy)|^2 \). If (H10)–(H12) hold, then it is easy to verify that \( F_2(y) = 0 \) has at least one positive root. By applying Theorem 4.1 on p. 83 in [8], we see that there is a positive constant \( \tau_0 \) (which can be evaluated explicitly), such that for \( \tau > \tau_0, E^r \) becomes unstable. Similarly, if we let \( \tau_2 = \tau, \tau_1 = 1, \tau_2 = 0, \) or let \( \tau_3 = \tau, \tau_1 = \tau_2 = \tau_3 = 0, \) a similar conclusion can be obtained. Therefore, the global asymptotic stability of \( E^r \) will impose restrictions on the length of time delays \( \tau_i \) \( (i = 1, 2, 3) \). In other words, time delay in the negative feedback of each species destabilizes \( E^r \) for system (1.1).

Finally, we give a suitable example to illustrate the feasibility of the conditions of Theorems 2.3 and 3.1.

**Example.** We consider the following system:
\[
\begin{align*}
\dot{x}_1(t) & = x_1(t) \left( 3 - \frac{53}{9} x_1(t - \tau_{11}) - \frac{x_2(t)}{1 + x_1(t)} \right), \\
\dot{x}_2(t) & = x_2(t) \left( -1 + \frac{81}{13} \frac{x_1(t - \tau_{21})}{1 + x_1(t - \tau_{21})} - 12 x_2(t - \tau_{22}) - \frac{x_3(t)}{1 + x_2(t)} \right), \\
\dot{x}_3(t) & = x_3(t) \left( -\frac{1}{13} + 12x_2(t - \tau_{32}) + \frac{14 x_2(t - \tau_{32})}{1 + x_3(t - \tau_{33})} - 12x_3(t - \tau_{33}) \right). 
\end{align*}
\]

System (3.18) has a unique positive equilibrium \( E^r(\frac{1}{2}, \frac{1}{2}, \frac{1}{2}) \). By a standard calculation, one can derive

\[
\begin{align*}
x_{11} & = \left( -\frac{q}{2} - \sqrt{R} \right)^{1/3} + \left( -\frac{q}{2} + \sqrt{R} \right)^{1/3} - \frac{79}{159} \approx 0.499288102412, \\
x_{21} & = (1 + x_{11}) \left( 3 - \frac{53}{9} x_{11} \right) \approx 0.08957922768325, \\
R & = \frac{p^3}{27} + \frac{q^2}{4}, \quad p = -\frac{75091}{109551}, \quad q = -\frac{63893209}{209023308}.
\end{align*}
\]

Thus, system (3.18) satisfies all Assumptions (H1), (H2) and (H6). Using Theorem 2.3 we know that system (3.18) is uniformly persistent provided that
\[
\omega_{11} > 0, \quad \omega_{22} > 0, \quad \omega_{11} \omega_{22} - \omega_{12} \omega_{21} > 0,
\]

(3.19)
where
\[ \omega_{11} = \frac{26}{9} - \frac{4240}{81} M_1 \tau_{11}, \quad \omega_{12} = -\left(1 + \frac{53}{9} M_1 \tau_{11}\right), \]
\[ \omega_{21} = -\frac{81}{13} \left(1 + 12 M_2 \tau_{22}\right), \quad \omega_{22} = 12(1 - 12 M_2 \tau_{22}), \]
\[ M_1 = \frac{27}{53} e^{\tau_{11}}, \quad M_2 = \frac{68 M_1 - 13}{156(1 + M_1)} \exp\left[\frac{68 M_1 - 13}{13(1 + M_1)} \tau_{22}\right]. \]

From Theorem 3.1 we see that the positive equilibrium \(E^*\) of (3.18) is globally asymptotically stable provided that
\[ r_{11} > 0, \quad r_{22} > 0, \quad r_{33} > 0, \quad r_{13} r_{22} r_{33} - r_{12} r_{21} r_{33} - r_{11} r_{23} r_{32} > 0, \quad (3.20) \]
where
\[ r_{11} = \frac{26}{9} - \frac{4240}{81} M_1 \tau_{11}, \quad r_{12} = -\left(1 + \frac{53}{9} M_1 \tau_{11}\right), \]
\[ r_{21} = -\frac{81}{13} \left(1 + 12 M_2 \tau_{22}\right), \quad r_{22} = \frac{75}{13} - \frac{2844}{13} M_2 \tau_{22}, \]
\[ r_{23} = -(1 + 12 M_2 \tau_{22}), \quad r_{32} = -14(1 + 12 M_3 \tau_{33}), \]
\[ r_{33} = 12(1 - 12 M_3 \tau_{33}), \quad M_3 = \frac{181 M_2 - 1}{156(1 + M_2)} \exp\left[\frac{181 M_2 - 1}{13(1 + M_2)} \tau_{33}\right]. \]

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