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Persistence and Global Stability in a Delayed Gause-Type Predator–Prey System without Dominating Instantaneous Negative Feedbacks

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A delayed Gause-type predator–prey system without dominating instantaneous negative feedbacks is investigated. It is proved that the system is uniformly persistent under some appropriate conditions. By means of constructing a suitable Lyapunov functional, sufficient conditions are derived for the local and global asymptotic stability of the positive equilibrium of the system. © 2002 Elsevier Science

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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. For Lotka–Volterra systems without time delays, it is well known that the 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 Hofbauer and Sigmund [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

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species, the instantaneous intraspecific competition (i.e., instantaneous 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–Voterra-type systems.

In the present paper, motivated by the work of Kuang [3] and Freedman and Ruan [4] for retarded functional differential equations, we consider a delayed Gause-type predator–prey system without dominating instantaneous negative feedbacks,

$$\begin{aligned} \dot{x}_1 &= x_1(t)\left(a_1 - a_{11}x_1(t-\tau_1) - a_{12}\frac{x_2(t)}{m + x_1(t)}\right) \\ \dot{x}_2 &= x_2(t)\left(-a_2 + a_{21}\frac{x_1(t-\tau_2)}{m + x_1(t-\tau_2)} - a_{22}x_2(t-\tau_3)\right), \end{aligned} \tag{1.1}$$

with initial conditions

$$x_i(t) = \phi_i(t), \qquad t \in [-\tau, 0], \qquad \phi_i(0) > 0, i = 1, 2, \tag{1.2}$$

where a_i, a_{ij} $(i, j = 1, 2)$ are positive constants. τ_i $(i = 1, 2, 3)$ are nonnegative constants, $\tau = \max\{\tau_1, \tau_2, \tau_3\}$. $\phi_i(t)$ $(i = 1, 2)$ are continuous bounded functions on the interval $[-\tau, 0]$. $x_1(t), x_2(t)$ denote the densities of prey and predator populations, respectively. We have assumed in (1.1) that when the predator species is absent, the prey species x_1 is governed by the well-known delay logistic equation

$$\frac{dx_1(t)}{dt} = x_1(t)(a_1 - a_{11}x_1(t-\tau_1)), \tag{1.3}$$

where $\tau_1 \geq 0$ denotes the delay in the negative feedback of the prey species x_1; here τ_1 may represent the duration of pregnancy. Thus (1.3) states that the average rate of increase of species at time t is dependent on $x_1(t - \tau_1)$ (the density of species at time $t - \tau_1$), because the increased individuals at time t have existed in the mothers' body at time $t - \tau_1$. On the other hand, the number of pregnancies depends on the surplus amount of the resources provided by the environment at that time. If the resources supplied by the environment are certain, then the number of pregnancies will depend on the density of species at time $t - \tau_1$. τ_2 is a constant delay due to gestation; that is, mature adult predators can only contribute to the production of predator biomass. In addition, we have included the term $-a_{22}x_2(t - \tau_3)$ in the dynamics of predator x_2 to incorporate the negative feedback of predator crowding.

We adopt the following notations and concepts throughout this paper.

Let $R_+^2 = \{x \in R^2 : x_i \geq 0,\ i = 1, 2\}$. For ecological reasons, we consider system (1.1), only in Int R_+^2.

DEFINITION 1.1. System (1.1) is said to be uniformly persistent if there exists a compact region $D \subset \operatorname{Int} R_+^2$ such that every solution $x(t) = (x_1(t), x_2(t))$ 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). In the third section we derive conditions for the local stability of the positive equilibrium of (1.1), and the conditions depend on τ_1 and τ_3. Section 4 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

System (1.1) has a unique positive equilibrium if the following condition is true:

(H1) $2ma_{11} > a_1$.

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

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* $x(t) = (x_1(t), x_2(t))$ *denote any positive solution of system* (1.1) *with initial conditions* (1.2). *Suppose that system* (1.1) *satisfies* (H1) *and the following*:

(H2) $a_1(a_{21} - a_2) > ma_2a_{11}$.

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

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

where

$$M_1 = \frac{a_1}{a_{11}} e^{a_1 \tau_1}, \qquad M_2 = \frac{(a_{21} - a_2) M_1 - m a_2}{a_{22}(m + M_1)} e^{\{[(a_{21} - a_2)M_1 - m a_2]/(m + M_1)\}\tau_3}.$$

The proofs of Lemmas 2.1 and 2.2 are similar to those of Lemmas 2.1 and 2.2 of [5]; we therefore omit them here.

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

THEOREM 2.1. *Suppose that system* (1.1) *satisfies* (H1)–(H2) *and the following*:

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

Then system (1.1) *is uniformly persistent*.

Proof. It is easy to verify that system (1.1) has two equilibria, $E_0(0,0)$ and $E_1(a_1/a_{11}, 0)$, 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_0, E_1. We choose

$$p(x_1(t), x_2(t)) = x_1^{\alpha_1}(t) x_2^{\alpha_2}(t),$$

where α_i $(i = 1,2)$ are undetermined positive constants. We have

$$\begin{aligned} \psi(x) = \frac{\dot{p}(x)}{p(x)} &= \alpha\left(a_1 - a_{11} x_1(t - \tau_1) - a_{12} \frac{x_2(t)}{m + x_1(t)} \right) \\ &\quad + \alpha_2 \left(-a_2 + a_{21} \frac{x_1(t - \tau_2)}{m + x_1(t - \tau_2)} - a_{22} x_2(t - \tau_3) \right). \end{aligned}$$

If we choose $\alpha_1 = 1$ and α_2 so small such that $\alpha_1 a_1 - \alpha_2 a_2 > 0$, then ψ is positive at E_0. Under assumption (H2), it is easy to verify that ψ is positive at E_1. Hence, there is a choice of α_2 to ensure $\psi > 0$ at the boundary equilibria. If the condition (H3) holds, it follows from paper [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 axis. Thus, by Theorem 3.12 of Freedman and Ruan [4], we see that system (1.1) is uniformly persistent.

3. LOCAL ASYMPTOTIC STABILITY

In this section, we discuss the local asymptotic stability of the positive equilibrium E^* of (1.1).

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

$$\begin{aligned} \dot{N}_1(t) &= A_{11}N_1(t-\tau_1) + B_{11}N_1(t) + A_{12}N_2(t) \\ \dot{N}_2(t) &= A_{21}N_1(t-\tau_2) + A_{22}N_2(t-\tau_3), \end{aligned} \tag{3.1}$$

where

$$A_{11} = -a_{11}x_1^*, \qquad A_{12} = -\frac{a_{12}x_1^*}{m+x_1^*}, \qquad B_{11} = \frac{a_{12}x_1^*x_2^*}{(m+x_1^*)^2},$$
$$A_{21} = \frac{ma_{21}x_2^*}{(m+x_1^*)^2}, \qquad A_{22} = -a_{22}x_2^*.$$

It is known that the local uniform asymptotic stability of the positive equilibrium $E^*(x_1^*, x_2^*)$ of system (1.1) follows from that of the zero solution of system (3.1) (see [8, Theorem 4.2, p. 26]).

THEOREM 3.1. *Suppose that system* (1.1) *satisfies* (H1) *and the following*:

(H4) $2(A_{11}+B_{11}) - A_{12} + A_{21} + A_{11}\tau_1(2A_{11} - 2B_{11} + A_{12}) - A_{21}A_{22}\tau_3 < 0$,

(H5) $2A_{22} - A_{12} + A_{21} - A_{22}\tau_3(A_{21} - 2A_{22}) + A_{11}A_{12}\tau_1 < 0$.

Then the positive equilibrium E^* of (1.1) *is uniformly asymptotically stable.*

Proof. The first equation of (3.1) can be rewritten as

$$\begin{aligned} \dot{N}_1(t) &= (A_{11}+B_{11})N_1(t) + A_{12}N_2(t) - A_{11}\int_{t-\tau_1}^{t}\dot{N}_1(u)\,du \\ &= (A_{11}+B_{11})N_1(t) + A_{12}N_2(t) \\ &\qquad - A_{11}\int_{t-\tau_1}^{t}(A_{11}N_1(u-\tau_1) + B_{11}N_1(u) + A_{12}N_2(u))\,du. \end{aligned} \tag{3.2}$$

Define

$$W_{11}(t) = N_1^2(t). \tag{3.3}$$

Then along the solution of (3.1), we have

$$\frac{d}{dt}W_{11}(t) = 2N_1(t)\Big\{(A_{11}+B_{11})N_1(t) + A_{12}N_2(t) - A_{11}\int_{t-\tau_1}^{t}(A_{11}N_1(u-\tau_1) + B_{11}N_1(u) + A_{12}N_2(u))\,du\Big\}$$

$$= 2(A_{11}+B_{11})N_1^2(t) + 2A_{12}N_1(t)N_2(t) - 2A_{11}N_1(t) \times \int_{t-\tau_1}^{t}(A_{11}N_1(u-\tau_1) + B_{11}N_1(u) + A_{12}N_2(u))\,du.$$

Using the inequality $a^2+b^2 \geq 2ab$, we get

$$\frac{d}{dt}W_{11}(t) \leq 2(A_{11}+B_{11})N_1^2(t) - A_{12}N_1^2(t) - A_{12}N_2^2(t) + A_{11}\tau_1(A_{11}-B_{11}+A_{12})N_1^2(t) + A_{11}\int_{t-\tau_1}^{t}\left[A_{11}N_1^2(u-\tau_1) - B_{11}N_1^2(u) + A_{12}N_2^2(u)\right]du. \tag{3.4}$$

Define $W_{12}(t)$ as

$$W_{12}(t) = A_{11}\int_{t-\tau_1}^{t}\int_{v}^{t}\left[A_{11}N_1^2(u-\tau_1) - B_{11}N_1^2(u) + A_{12}N_2^2(u)\right]du\,dv. \tag{3.5}$$

It follows from (3.4) and (3.5) that

$$\frac{d}{dt}(W_{11}(t)+W_{12}(t)) \leq \left[2(A_{11}+B_{11}) - A_{12} + \tau_1 A_{11}(A_{11}-B_{11}+A_{12})\right]N_1^2(t) - A_{12}N_2^2(t) + A_{11}\tau_1\left[A_{11}N_1^2(t-\tau_1) - B_{11}N_1^2(t) + A_{12}N_2^2(t)\right]. \tag{3.6}$$

Let $W_1(t)$ be defined by

$$W_1(t) = W_{11}(t) + W_{12}(t) + W_{13}(t), \tag{3.7}$$

in which

$$W_{13}(t) = A_{11}^2 \tau_1 \int_{t-\tau_1}^{t} N_1^2(u)\, du. \tag{3.8}$$

Then we derive from (3.6)–(3.8) that

$$\begin{aligned}\frac{d}{dt} W_1(t) &\leq \left[2(A_{11} + B_{11}) - A_{12} + \tau_1 A_{11}(A_{11} - B_{11} + A_{12})\right] N_1^2(t) \\ &\quad - A_{12} N_2^2(t) + A_{11}\tau_1\left[A_{11} N_1^2(t) - B_{11} N_1^2(t) + A_{12} N_2^2(t)\right] \\ &= \left[2(A_{11} + B_{11}) - A_{12} + \tau_1 A_{11}(2A_{11} - 2B_{11} + A_{12})\right] N_1^2(t) \\ &\quad - A_{12}(1 - A_{11}\tau_1) N_2^2(t).\end{aligned} \tag{3.9}$$

Similarly, the second equation of (3.1) can be rewritten as

$$\begin{aligned}\dot{N}_2(t) &= A_{22} N_2(t) + A_{21} N_1(t - \tau_2) - A_{22} \int_{t-\tau_3}^{t} \dot{N}_2(u)\, du \\ &= A_{22} N_2(t) + A_{21} N_1(t - \tau_2) \\ &\quad - A_{22} \int_{t-\tau_3}^{t} \left[A_{21} N_1(u - \tau_2) + A_{22} N_2(u - \tau_3)\right] du.\end{aligned} \tag{3.10}$$

We define

$$W_{21}(t) = N_2^2(t). \tag{3.11}$$

Then along the solution of (3.1), we derive

$$\begin{aligned}\frac{d}{dt} W_{21}(t) &= 2N_2(t)\Big\{A_{22} N_2(t) + A_{21} N_1(t - \tau_2) \\ &\qquad - A_{22} \int_{t-\tau_3}^{t} \left[A_{21} N_1(u - \tau_2) + A_{22} N_2(u - \tau_3)\right] du\Big\} \\ &= 2A_{22} N_2^2(t) + 2A_{21} N_1(t - \tau_2) N_2(t) \\ &\quad - 2A_{22} N_2(t) \int_{t-\tau_3}^{t} \left[A_{21} N_1(u - \tau_2) + A_{22} N_2(u - \tau_3)\right] du.\end{aligned} \tag{3.12}$$

Using the inequality $a^2 + b^2 \geq 2ab$, we get

$$\begin{aligned}\frac{d}{dt}W_{21}(t) \leq{}& 2A_{22}N_2^2(t) + A_{21}N_1^2(t-\tau_2) + A_{21}N_2^2(t)\\ &- \tau_3 A_{22}(A_{21} - A_{22})N_2^2(t)\\ &- A_{22}\int_{t-\tau_3}^{t}\left[A_{21}N_1^2(u-\tau_2) - A_{22}N_2^2(u-\tau_3)\right]du. \quad (3.13)\end{aligned}$$

Define $W_{22}(t)$ as

$$\begin{aligned}W_{22}(t) ={}& -A_{22}\int_{t-\tau_3}^{t}\int_{v}^{t}\left[A_{21}N_1^2(u-\tau_2) - A_{22}N_2^2(u-\tau_3)\right]du\,dv\\ &+ A_{21}\int_{t-\tau_2}^{t}N_1^2(u)\,du. \quad (3.14)\end{aligned}$$

It follows from (3.13) and (3.14) that

$$\begin{aligned}&\frac{d}{dt}(W_{21}(t) + W_{22}(t))\\ &\quad\leq \left[2A_{22} + A_{21} - \tau_3 A_{22}(A_{21} - A_{22})\right]N_2^2(t)\\ &\qquad + A_{21}N_1^2(t) - A_{22}\tau_3\left[A_{21}N_1^2(t-\tau_2) - A_{22}N_2^2(t-\tau_3)\right]. \quad (3.15)\end{aligned}$$

Let $W_2(t)$ be defined by

$$W_2(t) = W_{21}(t) + W_{22}(t) + W_{23}(t), \quad (3.16)$$

in which

$$W_{23}(t) = -A_{22}\tau_3\left(A_{21}\int_{t-\tau_2}^{t}N_1^2(u)\,du - A_{22}\int_{t-\tau_3}^{t}N_2^2(u)\,du\right). \quad (3.17)$$

Then we derive from (3.15)–(3.17) that

$$\begin{aligned}\frac{d}{dt}W_2(t) \leq{}& \left[2A_{22} + A_{21} - \tau_3 A_{22}(A_{21} - A_{22})\right]N_2^2(t) + A_{21}N_1^2(t)\\ &- A_{22}\tau_3\left[A_{21}N_1^2(t) - A_{22}N_2^3(t)\right]\\ ={}& \left[2A_{22} + A_{21} - \tau_3 A_{22}(A_{21} - 2A_{22})\right]N_2^2(t)\\ &+ A_{21}(1 - A_{22}\tau_3)N_1^2(t). \quad (3.18)\end{aligned}$$

Let

$$W(t) = W_1(t) + W_2(t).$$

Then along the solution of (3.1), we have

$$\begin{aligned}\frac{d}{dt}W(t) \leq{}& \left[2(A_{11}+B_{11}) - A_{12} + \tau_1 A_{11}(2A_{11} - 2B_{11} + A_{12})\right] N_1^2(t) \\ &- A_{12}(1 - A_{11}\tau_1) N_2^2(t) + A_{21}(1 - A_{22}\tau_3) N_1^2(t) \\ &+ \left[2A_{22} + A_{21} - \tau_3 A_{22}(A_{21} - 2A_{22})\right] N_2^2(t) \\ ={}& -\alpha_1 N_1^2(t) - \alpha_2 N_2^2(t), \end{aligned} \tag{3.19}$$

in which

$$\begin{aligned}\alpha_1 &= -\left[2(A_{11}+B_{11}) - A_{12} + A_{21} + A_{11}\tau_1(2A_{11} - 2B_{11} + A_{12}) \right. \\ &\qquad \left. - A_{21}A_{22}\tau_3\right], \\ \alpha_2 &= -\left[2A_{22} - A_{12} + A_{21} + A_{11}A_{12}\tau_1 - A_{22}\tau_3(A_{21} - 2A_{22})\right].\end{aligned}$$

Clearly, assumptions (H4)–(H5) imply that $\alpha_1 > 0$, $\alpha_2 > 0$. According to the Lyapunov theorem (see [7, Theorem 5.1, p. 27]), we see that the zero solution of (3.1) is uniformly asymptotically stable, and this completes the proof.

Remark 1. From the proof of Theorem 3.1, it is easy to see that, under assumption (H1), if $2(A_{11} + B_{11}) - A_{12} + A_{21} < 0$ and $2A_{22} - A_{12} + A_{21} < 0$, then the positive equilibrium of the "instantaneous" (when $\tau_i = 0$, $i = 1,2,3$) model (1.1) is locally uniformly asymptotically stable. If $2(A_{11} + B_{11}) - A_{12} + A_{21} < 0$ and $2A_{22} - A_{12} + A_{21} < 0$, then the local uniform asymptotic stability of E^* of delayed model (1.1) is preserved for sufficiently small τ_1 and τ_3 satisfying (H4)–(H5).

4. GLOBAL ASYMPTOTIC STABILITY

In this section, we derive sufficient conditions which guarantee that the positive equilibrium $E^*(x_1^*, x_2^*)$ 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 4.1. *Suppose that system* (1.1) *satisfies* (H1)–(H3). *Then the positive equilibrium* E^* *of* (1.1) *is globally asymptotically stable provided that*

(H6) $r_{ii} > 0$, $i = 1, 2$,

(H7) $r_{11} r_{22} - r_{12} r_{21} > 0$,

where

$$r_{11} = a_{11} - \frac{a_{12} x_2^*}{m(m + x_1^*)} - a_{11} M_1 \tau_1 \left(a_{11} + \frac{a_{12} x_2^*}{m(m + x_1^*)} \right),$$

$$r_{22} = a_{22}(1 - a_{22} M_2 \tau_3), \qquad r_{12} = -\frac{a_{12}}{m}(1 + a_{11} M_1 \tau_1),$$

$$r_{21} = -\frac{a_{21}}{m + x_1^*}(1 + a_{22} M_2 \tau_3),$$

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

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

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

by

$$u_i(t) = \ln \frac{x_i(t)}{x_i^*} \qquad (i = 1, 2). \tag{4.1}$$

It follows from (1.1) and (4.1) that

$$\begin{aligned} \frac{du_1}{dt} &= -a_{11} x_1^* (e^{u_1(t-\tau_1)} - 1) - \frac{a_{12} x_2^*}{m + x_1} (e^{u_2(t)} - 1) \\ &\quad + \frac{a_{12} x_1^* x_2^*}{(m + x_1)(m + x_1^*)} (e^{u_1(t)} - 1) \\ \frac{du_2}{dt} &= \frac{m a_{21} x_1^*}{(m + x_1(t - \tau_2))(m + x_1^*)} (e^{u_1(t-\tau_2)} - 1) \\ &\quad - a_{22} x_2^* (e^{u_2(t-\tau_3)} - 1). \end{aligned} \tag{4.2}$$

The first equation of (4.2) can be rewritten as

$$
\begin{aligned}
\frac{du_1}{dt} &= -a_{11}x_1^*(e^{u_1(t)}-1) - \frac{a_{12}x_2^*}{m+x_1}(e^{u_2(t)}-1) \\
&\quad + \frac{a_{12}x_1^*x_2^*}{(m+x_1)(m+x_1^*)}(e^{u_1(t)}-1) + a_{11}x_1^*\int_{t-\tau_1}^{t} e^{u_1(s)}\frac{du_1(s)}{ds}\,ds \\
&= -a_{11}x_1^*(e^{u_1(t)}-1) - \frac{a_{12}x_2^*}{m+x_1}(e^{u_2(t)}-1) \\
&\quad + \frac{a_{12}x_1^*x_2^*}{(m+x_1)(m+x_1^*)}(e^{u_1(t)}-1) \\
&\quad + a_{11}x_1^*\int_{t-\tau_1}^{t} e^{u_1(s)}\Bigg\{-a_{11}x_1^*(e^{u_1(s-\tau_1)}-1) - \frac{a_{12}x_2^*}{m+x_1}(e^{u_2(s)}-1) \\
&\qquad + \frac{a_{12}x_1^*x_2^*}{(m+x_1)(m+x_1^*)}(e^{u_1(s)}-1)\Bigg\}\,ds. \qquad (4.3)
\end{aligned}
$$

Let

$$
V_{11}(t) = |u_1(t)|. \qquad (4.4)
$$

Calculating the upper right derivative of $V_{11}(t)$ along the solution of (4.2), we have from (4.3) and (4.4) that

$$
\begin{aligned}
D^+V_{11}(t) &\le -a_{11}x_1^*|e^{u_1(t)}-1| + \frac{a_{12}x_2^*}{m}|e^{u_2(t)}-1| \\
&\quad + \frac{a_{12}x_1^*x_2^*}{m(m+x_1^*)}|e^{u_1(t)}-1| \\
&\quad + a_{11}x_1^*\int_{t-\tau_1}^{t} e^{u_1(s)}\Bigg\{a_{11}x_1^*|e^{u_1(s-\tau_1)}-1| + \frac{a_{12}x_2^*}{m}|e^{u_2(s)}-1| \\
&\qquad + \frac{a_{12}x_1^*x_2^*}{m(m+x_1^*)}|e^{u_1(s)}-1|\Bigg\}\,ds. \qquad (4.5)
\end{aligned}
$$

By Lemma 2.2, we know that there exists a $T > 0$, such that $x_1^*e^{u_1(t)} = x_1(t) \le M_1$ for $t \ge T$. Hence for $t \ge T + \tau$, we have

$$
\begin{aligned}
D^+V_{11}(t) &\le -x_1^*\left(a_{11} - \frac{a_{12}x_2^*}{m(m+x_1^*)}\right)|e^{u_1(t)}-1| + \frac{a_{12}x_2^*}{m}|e^{u_2(t)}-1| \\
&\quad + a_{11}M_1\int_{t-\tau_1}^{t}\Bigg\{a_{11}x_1^*|e^{u_1(s-\tau_1)}-1| + \frac{a_{12}x_2^*}{m}|e^{u_2(s)}-1| \\
&\qquad + \frac{a_{12}x_1^*x_2^*}{m(m+x_1^*)}|e^{u_1(s)}-1|\Bigg\}\,ds. \qquad (4.6)
\end{aligned}
$$

Define a Lyapunov functional $V_1(t)$ as

$$V_1(t) = V_{11}(t) + V_{12}(t), \tag{4.7}$$

where

$$\begin{aligned} V_{12}(t) = a_{11}M_1\int_{t-\tau_1}^{t}\int_{v}^{t}\bigg\{ & a_{11}x_1^*|e^{u_1(s-\tau_1)} - 1| + \frac{a_{12}x_2^*}{m}|e^{u_2(s)} - 1| \\ & + \frac{a_{12}x_1^*x_2^*}{m(m + x_1^*)}|e^{u_1(s)} - 1|\bigg\}\, ds\, dv \\ & + a_{11}^2x_1^*M_1\tau_1\int_{t-\tau_1}^{t}|e^{u_1(s)} - 1|\, ds. \end{aligned} \tag{4.8}$$

Then we have from (4.6)–(4.8) that for $t \geq T + \tau$

$$\begin{aligned} D^+V_1(t) &\leq -x_1^*\left[a_{11} - \frac{a_{12}x_2^*}{m(m + x_1^*)} + a_{11}M_{11}\tau_1\left(a_{11} + \frac{a_{12}x_2^*}{m(m + x_1^*)}\right)\right] \\ &\quad \times |e^{u_1(t)} - 1| + \frac{a_{12}x_2^*}{m}(1 + a_{11}M_1\tau_1)|e^{u_2(t)} - 1| \\ &= -r_{11}x_1^*|e^{u_1(t)} - 1| - r_{12}x_2^*|e^{u_2(t)} - 1|. \end{aligned} \tag{4.9}$$

Next, let

$$\begin{aligned} V_2(t) = |u_2(t)| + a_{22}M_2\bigg\{ & \frac{a_{21}x_1^*}{m + x_1^*}\int_{t-\tau_3}^{t}\int_{v}^{t}|e^{u_1(s-\tau_2)} - 1|\, ds\, dv \\ & + a_{22}x_2^*\int_{t-\tau_3}^{t}\int_{v}^{t}|e^{u_2(s-\tau_3)} - 1|\, ds\, dv\bigg\} \\ & + \frac{a_{21}x_1^*}{m + x_1^*}\int_{t-\tau_2}^{t}|e^{u_1(s)} - 1|\, ds \\ & + a_{22}M_2\tau_3\bigg\{\frac{a_{21}x_1^*}{m + x_1^*}\int_{t-\tau_2}^{t}|e^{u_1(s)} - 1|\, ds \\ & + a_{22}x_2^*\int_{t-\tau_3}^{t}|e^{u_2(s)} - 1|\, ds\bigg\}. \end{aligned} \tag{4.10}$$

Then it follows from (4.2) and (4.10) that for $t \geq T + \tau$

$$\begin{aligned} D^+V_2(t) \leq & -a_{22}x_2^*(1 - a_{22}M_2\tau_3)|e^{u_2(t)} - 1| \\ & + \frac{a_{21}x_1^*}{m + x_1^*}(1 + a_{22}M_2\tau_3)|e^{u_1(t)} - 1| \\ = & -r_{21}x_1^*|e^{u_1(t)} - 1| - r_{22}x_2^*|e^{u_2(t)} - 1|. \end{aligned} \tag{4.11}$$

According to assumptions (H6)–(H7), we know that $C = (r_{ij})_{2\times 2}$ is an M-matrix; hence there exist positive constants c_i $(i = 1, 2)$ such that

$$r_{11}c_1 + r_{21}c_2 = h_1 > 0, \qquad r_{12}c_1 + r_{22}c_2 = h_2 > 0.$$

Now define a Lyapunov functional $V(t)$ as

$$V(t) = c_1V_1(t) + c_2V_2(t). \tag{4.12}$$

Then we have from (4.9), (4.11), and (4.12) that for $t \geq T + \tau$

$$D^+V(t) \leq -h_1x_1^*|e^{u_1(t)} - 1| - h_2x_2^*|e^{u_2(t)} - 1|. \tag{4.13}$$

Since system (1.1) is uniformly persistent, one can see that there exist positive constants m_k $(k = 1, 2)$ and a $T^* > T + \tau$ such that $x_k^*e^{u_k(t)} = x_k(t) \geq m_k$ $(k = 1, 2)$ for $t \geq T^*$. Using the mean value theorem, one obtains $x_k^*|e^{u_k(t)} - 1| = x_k^*e^{\theta_k(t)}|u_k(t)| \geq m_k|u_k(t)|$ $(k = 1, 2)$, where $x_k^*e^{\theta_k(t)}$ lies between $x_k(t)$ and x_k^*. Let $\delta = \min\{m_1h_1, m_2h_2\}$. Then it follows from (4.13) that for $t \geq T^*$

$$D^+V(t) \leq -\delta(|u_1(t)| + |u_2(t)|). \tag{4.14}$$

Noting that $V(t) \geq \min\{c_1, c_2\}(|u_1(t)| + |u_2(t)|)$, we can conclude from the Lyapunov Theorem and (4.14) that the zero solution of (4.2) is globally asymptotically stable, and hence the positive equilibrium $E^*(x_1^*, x_2^*)$ of (1.1) is globally asymptotically stable. This completes the proof.

Remark 2. 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). By Theorems 3.1 and 4.1, we see that time delay due to gestation is harmless for the local and global stability of the positive equilibrium of system (1.1). Therefore, in the following, we need only discuss the effect of time delays in the negative feedback of each species on the stability of E^*. For simplicity, we let $\tau_1 = \tau_2 = 0$, $\tau_3 = \tau$.

The characteristic equation for (3.1) takes the form

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

in which

$$\begin{aligned} P(\lambda) &= \lambda(\lambda - A_{11} - B_{11}) - A_{12}A_{21}, \\ Q(\lambda) &= -A_{22}(\lambda - A_{11} - B_{11}). \end{aligned}$$

It is easy to determine that

$$\begin{aligned} F(y) &= |P(iy)|^2 - |Q(iy)|^2 \\ &= y^4 + \left[(A_{11} + B_{11})^2 - A_{22}^2 + 2A_{12}A_{21}\right]y^2 \\ &\quad + A_{12}^2A_{21}^2 - A_{22}^2(A_{11} + B_{11})^2. \end{aligned}$$

If $2(A_{11} + B_{11}) - A_{12} + A_{21} < 0$ and $2A_{22} - A_{12} + A_{21} < 0$, then it is easy to verify that $F(y) = 0$ has at least one positive root and each of them is simple. By applying [7, Theorem 4.1, p. 83] of Kuang, we see that there is a positive constant τ_0 (which can be evaluated explicitly), such that for $\tau > \tau_0$, E^* becomes unstable. Similarly, if we let $\tau_2 = \tau_3 = 0$, $\tau_1 = \tau$, the same conclusion can be obtained. Therefore, the local and global asymptotic stability of E^* will impose restrictions on the length of time delays τ_1 and τ_3. In other words, time delay in the negative feedback of each species destabilizes E^* for system (1.1).

Finally, we give a suitable example to illustrate the feasibility of the conditions of Theorems 2.1, 3.1, and 4.1.

EXAMPLE. We consider the following system:

$$\begin{aligned} \dot{x}_1(t) &= x_1(t)\left(3 - \frac{53}{9}x_1(t - \tau_1) - \frac{x_2(t)}{1 + x_1(t)}\right) \\ \dot{x}_2(t) &= x_2(t)\left(-1 + \frac{4x_1(t - \tau_2)}{1 + x_1(t - \tau_2)} - 4x_2(t - \tau_3)\right). \end{aligned} \tag{4.15}$$

System (4.15) has a unique positive equilibrium $E^*(\frac{1}{2}, \frac{1}{12})$. Using Theorem 2.1, we know that system (4.15) is uniformly persistent provided that $\tau_1 \le \frac{1}{2}$. From Theorem 3.1, we see that the positive equilibrium $E^*(\frac{1}{2}, \frac{1}{12})$ is locally asymptotically stable provided that $8957\tau_1 + 24\tau_3 < 2610$ and $159\tau_1 + 44\tau_3 < 30$. From Theorem 4.1, we know that the positive equilibrium $E^*(\frac{1}{2}, \frac{1}{12})$ of (4.15) is globally asymptotically stable provided that $\tau_1 \le \frac{1}{2}$,

$r_{11} > 0$, $r_{22} > 0$, and $r_{11}r_{22} - r_{12}r_{21} > 0$, where

$$r_{11} = \frac{1}{162}(945 - 5671 M_1\tau_1), \qquad r_{12} = -\left(1 + \tfrac{53}{9}M_1\tau_1\right),$$

$$r_{21} = -\tfrac{8}{3}(1 + 4M_2\tau_3), \qquad r_{22} = 4(1 - 4M_2\tau_3),$$

$$M_1 = \frac{27}{53}e^{3\tau_1}, \qquad M_2 = \frac{3M_1 - 1}{4(1 + M_1)}e^{[(3M_1 - 1)/(1+M_1)]\tau_3}.$$

To conclude this paper, we state that it appears to be very difficult to derive a relationship between (H4)–(H5) and (H6)–(H7), which may indicate that our results leave room for improvement. We leave this for future work.

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