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Persistence and global stability in a delayed Leslie–Gower type three species food chain

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Abstract

Our investigation concerns the three-dimensional delayed continuous time dynamical system which models a predator–prey food chain. This model is based on the Holling-type II and a Leslie–Gower modified functional response. This model can be considered as a first step towards a tritrophic model (of Leslie–Gower and Holling–Tanner type) with inverse trophic relation and time delay. That is when a certain species that is usually eaten can consume immature predators. It is proved that the system is uniformly persistent under some appropriate conditions. By constructing a proper Lyapunov function, we obtain a sufficient condition for global stability of the positive equilibrium.

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1. Introduction

A major trend in theoretical work on predator–prey dynamics has been launched so as to derive more realistic models. These models had to be more consistent with real phenomena, trying to keep to maximum the unavoidable increase in complexity of their mathematics. This effort has been concentrated mainly on the functional form of per capita growth rates and on taking into account the effects of time delay. As far as the topic is concerned, we decided to focus on a three-dimensional system of autonomous delayed differential equations based on a modified version of the Leslie–Gower scheme, see [1,2,8,10] and also [13,14]. General problems of food chains have largely been studied. The papers about this issue concern three trophic-level food chains models composed of logistic prey x and Lotka–Volterra or Holling type specialist predator y and top-predator z . Our study deals with three-species food chain model. It describes a prey population x , which serves as only food for a predator y . This specialist predator y is also the prey of a top-predator z . The interaction between species y and its prey x has been modeled by the Volterra scheme (the predator population dies out exponentially in absence of its prey). The interaction between species z and its prey y has

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been modeled by a modified version of Leslie–Gower scheme given in [1,2]. It shows that the loss in the top predator population is proportional to the reciprocal of per capita availability of its most favorite food. The instantaneous model is the following:

$$\begin{cases} \dot{x}(t) = x(t) \left(a_1 - b_1 x(t) - \frac{v_0 y(t)}{x(t) + d_0} \right), \\ \dot{y}(t) = y(t) \left(-a_2 + \frac{v_1 x(t)}{x(t) + d_0} - \frac{v_2 z(t)}{y(t) + d_2} \right), \\ \dot{z}(t) = z(t) \left(a_3 - \frac{v_3 z(t)}{y(t) + d_3} \right), \end{cases} \quad (1)$$

with the initial conditions, $x(0) = x_0$, $y(0) = y_0$, $z(0) = z_0$. In Eq. (1), $x(t)$, $y(t)$ and $z(t)$ denote the densities of the prey, predator and top-predator population at time t , respectively; a_1 , b_1 , v_0 , d_0 , a_2 , v_1 , v_2 , d_2 , a_3 , v_3 and d_3 are model parameters assuming only positive values. The parameters are defined as follows: a_1 is the growth rate of prey x , b measures the strength of competition among individuals of species x , v_0 is the maximum value which per capita reduction rate of prey x can attain, d_0 measures the extent to which environment provides protection to prey and intermediate predator y , a_2 represents the rate which y will die out when there is no x ; v_1, v_2 and v_3 have a similar biological connotation as that of v_0 , d_2 is the value of y at which the per capita removal rate of y becomes $v_2/2$, a_3 describes the growth rate of z , assuming that the number of males and females is equal; d_3 represents the residual loss in species z due to severe scarcity of its favorite food y ; the second term on the right-hand side in the third equation of (1) depicts the loss in predator population.

In this model the third equation is not classical. It contains a modified Leslie–Gower term. Leslie [9] introduced a predator–prey model where the carrying capacity of the predator’s environment is proportional to the number of prey. He noted the fact that there are upper limits to the rates of increase of both prey and predator, which are not recognized in Lotka–Volterra model. In case of continuous time, the above considerations lead to the following:

$$\frac{dz}{dt} = a_3 z \left(1 - \frac{z}{\alpha y} \right),$$

in which the growth of the top predator population is in logistic form (i.e. $dz/dt = a_3 z(1 - z/C)$). Here, ‘ C ’ measures the carrying capacity set by the environmental resources and proportional to prey abundance, $C = \alpha y$, where α is the conversion factor of prey into predator. The term $z/\alpha y$ is called the Leslie–Gower term. It measures the loss in predator population due to the rarity (per capita z/y) of its favorite food. In the case of severe scarcity, z can switch over to other population, but its growth will be limited by the fact that its most favorite food, the ‘prey’ y , is not available in abundance. The situation can be taken care of by adding a positive constant to the denominator, hence the equation becomes $\frac{dz}{dt} = a_3 z \left(1 - \frac{z}{\alpha y + d} \right)$. Thus $\frac{dz}{dt} = a_3 z - \frac{a_3}{\alpha} \left(\frac{z^2}{\alpha + y} \right)$, that is, the third equation of system (1): $\frac{dz}{dt} = a_3 z - \frac{v_3 z^2}{d_3 + y}$.

This model was motivated more by the mathematics analysis interest than by its ecological meaning. However, there may be situations in which the interaction between species is modeled by systems with such a functional response. It may, for example, be considered as a representation of some aquatic ecosystems. In this case, a toxin producing phytoplankton (TPP) population (prey) of size x is predated by individuals of specialist predator zooplankton population y . This zooplankton population, in turn, serves as a favorite food for the predator molluscs population of size z . A more detailed description of such a situation is given in [14], see also [11,12].

Furthermore, it is a first step towards a tritrophic model (of Leslie–Gower and Holling–Tanner type) with inverse trophic relation and time delay, that is where the prey eaten by the mature predator can consume the immature predators.

A rather characteristic behavior of predator–prey dynamics is the oscillatory phenomenon of population densities that is often observed. A common mechanism to model such a behavior is to introduce time delays in the models, which are, indeed, a more realistic and interesting approach to the understanding of food-chain dynamics. Therefore, it is of paramount importance to study the following autonomous delayed predator–prey model with a modified Leslie–Gower functional response:

$$\begin{cases} \dot{x}(t) = x(t) \left(a_1 - b_1 x(t - r_1) - \frac{v_0 y(t)}{x(t) + d_0} \right), \\ \dot{y}(t) = y(t) \left(-a_2 + \frac{v_1 x(t - r_{12})}{x(t - r_{12}) + d_0} - b_2 y(t - r_2) - \frac{v_2 z(t)}{y(t) + d_2} \right), \\ \dot{z}(t) = z(t) \left(a_3 - \frac{v_3 z(t - r_3)}{y(t - r_{23}) + d_3} \right). \end{cases} \quad (2)$$

The initial conditions for this system are as follows:

$$\begin{aligned} x_0(\theta) = \phi_1(\theta) \geq 0, \quad y_0(\theta) = \phi_2(\theta) \geq 0, \quad z_0(\theta) = \phi_3(\theta), \\ x(0) > 0, \quad y(0) > 0, \quad z(0) > 0, \quad \theta \in [-r, 0], \end{aligned} \quad (3)$$

where $r = \max\{r_1, r_2, r_3, r_{12}, r_{23}\}$, $\phi = (\phi_1, \phi_2, \phi_3) \in C([-r, 0], \mathbb{R}_+^3)$, $\mathbb{R}_+^3 = \{(x, y, z), x \geq 0, y \geq 0, z \geq 0\}$.

We use the conventional notation $x_t(\theta) = x(\theta + t)$, for $\theta \in [-r, 0]$.

In system (2), r_1, r_2, r_3, r_{12} and r_{23} are nonnegative constant; r_1 denotes the delay in the negative feedback, we assume that the prey growth rate response to resources limitations involves delay, r_{12} is due to gestation of intermediate predator y , that is, the delay in time for prey biomass to increase predator numbers. We are assuming in (2) that the growth of top predator is influenced by the amount of the prey y , in the past. r_{23} can be regarded as a gestation period. We further assume that the top predator growth rate response to resources limitations involves also a delay, so, r_3 has the same meaning as r_1 . In addition, we have included the term $-b_2 y(t - r_2)$ in the dynamics of predator y , to incorporate the negative feedback of intermediate predator crowding.

In this paper, we discuss the global stability of equilibria and the persistence of the system. Global stability results on delayed differential systems are numerous. However, in the instantaneous case, most of them require the considered system to satisfy the so-called diagonal instantaneous negative feedback dominance condition. In the delayed Lotka–Volterra-type system, Kuang and Smith [7] show that if, for every species, the instantaneous intraspecific competition (instantaneous negative feedback) dominates the total competition due to delayed intraspecific competition and interspecific competition. Then the positive steady state of 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.

The aim in this paper is to derive natural and verifiable conditions, under which the global stability of a nonnegative steady state of system (2) will persist when time delays involved here are small enough.

The organization of the paper is as follows. In Section 2 we present conditions for the permanence of system (2). Section 3 provides sufficient conditions for positive equilibrium of system (2) to be globally asymptotically stable. The paper ends with a brief discussion which includes local stability results for positive equilibrium of this system.

2. Uniform persistence of the system

In this section, we present conditions for the uniform persistence of system (2). We denote by $\mathbb{R}_+^3 = \{(x, y, z) \in \mathbb{R}^3 / x \geq 0, y \geq 0, z \geq 0\}$ the nonnegative cone and by $\text{int}(\mathbb{R}_+^3) = \{(x, y, z) \in \mathbb{R}^3 / x > 0, y > 0, z > 0\}$ the positive cone.

Definition 1. System (2) is said to be uniformly persistent if a compact region $D \subset \text{Int}(\mathbb{R}_+^3)$ exists such that every solution $\Psi(t) = (x(t), y(t), z(t))$ of system (2) with initial conditions (3) eventually enters and remains in the region D .

2.1. Boundedness of the solutions

We start by two lemmas which present some qualitative nature of solutions of system (2).

Lemma 2. *The positive cone is invariant for the system (2).*

Proof. It is true since,

$$\begin{aligned}
 x(t) &= x(0) \exp \left\{ \int_0^t \left[a_1 - b_1 x(s - r_1) - \frac{v_0 y(s)}{x(s) + d_0} \right] ds \right\}, \\
 y(t) &= y(0) \exp \left\{ \int_0^t \left[-a_2 + \frac{v_1 x(s - r_{12})}{x(s - r_{12}) + d_0} - b_1 y(s - r_2) - \frac{v_2 z(s)}{y(s) + d_2} \right] ds \right\}, \\
 z(t) &= z(0) \exp \left\{ \int_0^t \left[a_3 - \frac{v_3 z(s - r_3)}{y(s - r_{23}) + d_3} \right] ds \right\}
 \end{aligned}$$

and $x(0) > 0, y(0) > 0, z(0) > 0$. \square

Lemma 3. Let $\Psi(t) = (x(t), y(t), z(t))$, with initial conditions (3), denote any positive solution of system (2). Suppose that system (2) satisfies the following hypothesis:

$$(H_1) \quad a_1(v_1 - a_2) > b_1 a_2 d_0,$$

then there exist $M_1, M_2, M_3 > 0$ and $T > 0$, such that $x(t) \leq M_1, y(t) \leq M_2, z(t) \leq M_3$, for $t > T$, where

$$\begin{aligned}
 M_1 &= \frac{a_1 e^{a_1 r_1}}{b_1}, \\
 M_2 &= \frac{(v_1 - a_2)M_1 - d_0 a_2}{b_2(d_0 + M_1)} \exp \left\{ \left(\frac{(v_1 - a_2)M_1 - d_0 a_2}{(d_0 + M_1)} \right) r_2 \right\}, \\
 M_3 &= \frac{a_3(d_3 + M_2)}{v_3} e^{a_3 r_3}.
 \end{aligned}$$

Proof. We have, from the prey equation,

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

thus, for $t > r_1$,

$$x(t) \leq x(t - r_1) e^{a_1 r},$$

which is equivalent, for $t > r_1$, to

$$x(t - r_1) \geq x(t) e^{-a_1 r_1}.$$

Therefore, for $t > r_1$, we have

$$\dot{x}(t) < x(t) (a_1 - b_1 e^{-a_1 r_1} x(t)).$$

A standard comparison argument shows that

$$\limsup_{t \rightarrow +\infty} x(t) \leq \frac{a_1 e^{a_1 r_1}}{b_1}. \tag{4}$$

By similar arguments to those in the proof of Lemma 2.2 of paper [15] we see that there exists $T_1 > 0$, such that, for $t > T_1$,

$$x(t) \leq M_1.$$

Hence, from the second equation of the system, we have, for $t > T_1 + r_2$,

$$\dot{y}(t) < y(t) \left(\frac{v_1 M_1}{d_0 + M_1} - a_2 - b_2 y(t - r_2) \right).$$

Thus, for $t > T_1 + r_2$,

$$\dot{y}(t) < \left(\frac{v_1 M_1}{d_0 + M_1} - a_2 \right) y(t),$$

which yields, for $t > T_1 + r_2$,

$$y(t - r_2) > y(t) \exp \left\{ \left(a_2 - \frac{v_1 M_1}{d_0 + M_1} \right) r_2 \right\}.$$

Therefore, for $t > T_1 + r_2$, we have

$$\dot{y}(t) < y(t) \left[\frac{v_1 M_1}{d_0 + M_1} - a_2 - b_2 y(t) \exp \left\{ \left(a_2 - \frac{v_1 M_1}{d_0 + M_1} \right) r_2 \right\} \right].$$

If assumption (H₁) is satisfied, then again by standard comparison arguments, we get

$$\limsup_{t \rightarrow +\infty} y(t) \leq \frac{(v_1 - a_2) M_1 - d_0 a_2}{b_2 (d_0 + M_1)} \exp \left\{ \left(\frac{(v_1 - a_2) M_1 - d_0 a_2}{(d_0 + M_1)} \right) r_2 \right\}. \tag{5}$$

From the third equation of system (2), we have

$$\dot{z}(t) < a_3 z(t),$$

thus, for $t > r_3$,

$$z(t - r_3) \geq z(t) e^{-a_3 r_3}.$$

Again, we observe that there exists T_2 such that, for $t \geq T_2$, $y(t) \leq M_2$. Therefore, for $t \geq T_2 + r_3$, we have

$$\dot{z}(t) < \left(a_3 - \frac{v_3 e^{-a_3 r_3}}{d_3 + M_2} z(t) \right) z(t).$$

Therefore, it follows that every nonnegative solution $\Psi(t) = (x(t), y(t), z(t))$, satisfies

$$\limsup_{t \rightarrow +\infty} z(t) \leq \frac{a_3 (d_3 + M_2)}{v_3} e^{a_3 r_3}. \tag{6}$$

Finally, if (H₁) holds, then there exist $M_1 > 0$, $M_2 > 0$, $M_3 > 0$ and $T > 0$ such that $x(t) \leq M_1$, $y(t) \leq M_2$ and $z(t) \leq M_3$, for $t > T$. □

2.2. Boundary dynamics

In order to analyze the long term coexistence of three species of system (2), we need to know the flow on the boundaries of \mathbb{R}_+^3 . System (2) has four trivial boundary equilibria

$$E_0(0, 0, 0), \quad E_1(a_1/b_1, 0, 0), \quad E_3(0, 0, a_3 d_3/v_3) \quad \text{and} \quad E_4(a_1/b_1, 0, a_3 d_3/v_3).$$

We consider the following subsystem in xy -plane:

$$\begin{aligned} \dot{x}(t) &= x(t) \left(a_1 - b_1 x(t - r_1) - \frac{v_0 y(t)}{x(t) + d_0} \right), \\ \dot{y}(t) &= y(t) \left(-a_2 + \frac{v_1 x(t - r_{12})}{d_0 + x(t - r_{12})} - b_2 y(t - r_2) \right). \end{aligned} \tag{7}$$

It is easy to verify that system (7) has two equilibria on the boundaries of \mathbb{R}_+^2 , $E_{00}(0, 0)$, $E_{11}(\frac{a_1}{b_1}, 0)$. Obviously, these points are restriction of E_0, E_1 , in the xy -plane. The following result shows that subsystem (7) is uniformly persistent.

Theorem 4. *Suppose that system (7) satisfies (H₁) and the following hypothesis:*

$$(H_2) \quad a_1 r_1 \leq 3/2,$$

then system (7) is uniformly persistent.

Proof. The aim is to use Theorem 3.12 of [3] by constructing a suitable function which is positive at each boundary equilibrium of system (7).

For $(x(t), y(t))$ in the ω -limit set of the boundary of \mathbb{R}_+^2 , first, if $y = 0$, from the first equation of system (7), and if the condition (H_2) holds (see for example [5]), then it follows that $x(t) \rightarrow \frac{a_1}{b_1}$ (a constant function) as $t \rightarrow +\infty$ for all solution with $x(0) > 0$. Second, if $x(0) = 0$, then $x(t) \equiv 0$. It is easy to verify that E_{00} is globally asymptotically stable in the y -axis. Thus, the ω -limit set of \mathbb{R}_+^2 is the union of the boundary equilibria E_{00} and E_{11} . We choose now

$$p(x(t), y(t)) = x^{\alpha_0} y^{\alpha_1},$$

where α_0 and α_1 are undetermined positive constants. We define

$$\Phi(x(t), y(t)) = \frac{\dot{p}(x(t), y(t))}{p(x(t), y(t))}.$$

We have

$$\Phi(x(t), y(t)) = \alpha_0 \left(a_1 - b_1 x(t - r_1) - \frac{v_0 y}{d_0 + x} \right) + \alpha_1 \left(-a_2 + \frac{v_1 x(t - r_{12})}{d_0 + x(t - r_{12})} - b_2 y(t - r_2) \right)$$

and $\Phi(0, 0) = \alpha_0 a_1 - a_2 \alpha_1$, $\Phi(\frac{a_1}{b_1}, 0) = \alpha_1 (-a_2 + \frac{v_1 a_1}{b_1 d_0 + a_1})$.

If we choose $\alpha_0 = 1$, and α_1 enough small such that $\alpha_0 a_1 - a_2 \alpha_1 > 0$, then Φ is positive at E_{00} . Under assumption (H_1) , it is easy to verify that Φ is positive at E_{11} . Hence, there is a choice of α_0 and α_1 to ensure $\Phi > 0$ at the boundary equilibria. Thus, system (7) is uniformly persistent from Theorem 3.12 of [3]. The proof is complete. \square

Remark. If $r_1 = r_{12} = r_2 = 0$, then system (2) is reduced to the instantaneous system, i.e. one without time delay. From the proof of Theorem 4, we see that if (H_1) holds, then the corresponding instantaneous system of (2) is uniformly persistent, which implies that system (2) must have a positive equilibrium (see [4]), we denote it by $E_{22}(x_2^*, y_2^*)$. We can also compute x_2^*, y_2^* explicitly. $E_{22}(x_2^*, y_2^*)$ is the restriction of the boundary equilibrium $E_2(x_2^*, y_2^*, 0)$ of system (2) in the xy -plan.

The next lemma establishes the global stability of E_{22} .

Lemma 5. Suppose that system (2) satisfies (H_1) . Then the positive equilibrium E_{22} of the subsystem (2.4) is globally asymptotically stable provided that:

$$(H_3) \quad \beta_{ii} > 0, \quad i = 1, 2,$$

$$(H_4) \quad \beta_{11} \beta_{22} - \beta_{12} \beta_{21} > 0,$$

where $\beta_{11} = b_1 - \frac{a_1}{d_0} - b_1 M_1 r_1 (b_1 + \frac{a_1}{d_0})$, $\beta_{12} = -\frac{v_1}{d_0} (b_2 M_2 r_2 + 1)$, $\beta_{22} = b_2 (1 - b_2 M_2 r_2)$ and $\beta_{21} = -\frac{v_0}{d_0} (1 + b_1 M_1 r_1)$.

Proof. The proof is based on constructing a suitable Lyapunov function. We define $X(t) = \ln(\frac{x(t)}{x_2^*})$, $Y(t) = \ln(\frac{y(t)}{y_2^*})$.

These coordinate changes transform the positive equilibrium (x_2^*, y_2^*) to the trivial equilibrium $X(t) = 0$ and $Y(t) = 0$. Thus, system (7) can be written by centering it on the positive equilibrium, as follows:

$$\begin{cases} \dot{X}(t) = -b_1 x_2^* (e^{X(t-r_1)} - 1) + \frac{v_0 x_2^* y_2^*}{(x_2^* + d_0)(x + d_0)} (e^{X(t)} - 1) - \frac{v_0 y_2^*}{x + d_0} (e^{Y(t)} - 1), \\ \dot{Y}(t) = \frac{v_1 d_0 x_2^*}{(x(t - r_{12}) + d_0)(x_2^* + d_0)} (e^{X(t-r_{12})} - 1) - b_2 y_2^* (e^{Y(t-r_2)} - 1). \end{cases} \quad (8)$$

The first equation of (8) can be rewritten as

$$\dot{X}(t) = -b_1 x_2^* (e^{X(t)} - 1) + \frac{v_0 x_2^* y_2^*}{(x_2^* + d_0)(x + d_0)} (e^{X(t)} - 1) - \frac{v_0 y_2^*}{x + d_0} (e^{Y(t)} - 1)$$

$$+ b_1 x_2^* \int_{t-r_1}^t e^{X(t)} \left\{ -b_1 x_2^* (e^{X(s-r_1)} - 1) + \frac{v_0 x_2^* y_2^*}{(x_2^* + d_0)(x + d_0)} (e^{X(s)} - 1) - \frac{v_0 y_2^*}{x + d_0} (e^{Y(s)} - 1) \right\} ds, \tag{9}$$

where we used the fact that

$$e^{X(t-r_1)} = e^{X(t)} - \int_{t-r_1}^t e^{X(s)} \frac{dX(s)}{ds} ds.$$

Now define

$$V_1(t) = |X(t)|.$$

Computing the upper right derivative of $V_1(t)$ along the solution of system (8), it follows from Eq. (9) that

$$D^+ V_1(t) \leq -b_1 x_2^* |e^{X(t)} - 1| + \frac{v_0 x_2^* y_2^*}{(x_2^* + d_0)(x + d_0)} |e^{X(t)} - 1| + \frac{v_0 y_2^*}{x + d_0} |e^{Y(t)} - 1| + b_1 x_2^* \int_{t-r_1}^t e^{X(t)} \left\{ b_1 x_2^* |e^{X(s-r_1)} - 1| + \frac{v_0 x_2^* y_2^*}{(x_2^* + d_0)(x + d_0)} |e^{X(s)} - 1| + \frac{v_0 y_2^*}{x + d_0} |e^{Y(s)} - 1| \right\} ds.$$

By Lemma 3, we see that there exists $T > 0$ such that $x_2^* e^{X(t)} \leq M_1$ for $t > T$. Hence, for $t \geq T + r$, we have

$$D^+ V_1(t) \leq -b_1 x_2^* |e^{X(t)} - 1| + \frac{v_0 x_2^* y_2^*}{(x_2^* + d_0)d_0} |e^{X(t)} - 1| + \frac{v_0 y_2^*}{d_0} |e^{Y(t)} - 1| + b_1 M_1 \int_{t-r_1}^t \left\{ b_1 x_2^* |e^{X(s-r_1)} - 1| + \frac{v_0 x_2^* y_2^*}{(x_2^* + d_0)d_0} |e^{X(s)} - 1| + \frac{v_0 y_2^*}{d_0} |e^{Y(s)} - 1| \right\} ds. \tag{10}$$

Owing to the structure of (10), let us now consider the functional

$$V_{12}(t) = V_1(t) + b_1 M_1 \int_{t-r_1}^t \int_v^t \left\{ b_1 x_2^* |e^{X(s-r_1)} - 1| + \frac{v_0 x_2^* y_2^*}{(x_2^* + d_0)d_0} |e^{X(s)} - 1| + \frac{v_0 y_2^*}{d_0} |e^{Y(s)} - 1| \right\} ds dv + b_1^2 M_1 r_1 x_2^* \int_{t-r_1}^t |e^{X(s)} - 1| ds,$$

whose upper right derivative along solution of (8) gives

$$D^+ V_{12} = D^+ V_1 + b_1 M_1 r_1 \left\{ b_1 x_2^* |e^{X(t-r_1)} - 1| + \frac{v_0 x_2^* y_2^*}{(x_2^* + d_0)d_0} |e^{X(t)} - 1| + \frac{v_0 y_2^*}{d_0} |e^{Y(t)} - 1| \right\} - b_1 M_1 \int_{t-r_1}^t \left\{ b_1 x_2^* |e^{X(s-r_1)} - 1| + \frac{v_0 x_2^* y_2^*}{(x_2^* + d_0)d_0} |e^{X(s)} - 1| + \frac{v_0 y_2^*}{d_0} |e^{Y(s)} - 1| \right\} ds + b_1^2 M_1 r_1 x_2^* \{ |e^{X(t)} - 1| - |e^{X(t-r_1)} - 1| \}. \tag{11}$$

Therefore, from (10) and (11) we get, for $t \geq T + r$,

$$D^+ V_{12} \leq -x_2^* \left[b_1 - \frac{a_1}{d_0} - b_1 M_1 r_1 \left(b_1 + \frac{a_1}{d_0} \right) \right] |e^{X(t)} - 1| + \frac{v_0}{d_0} (1 + b_1 M_1 r_1) y_2^* |e^{Y(t)} - 1|, \tag{12}$$

where in (12) the inequality $\frac{v_0 y_2^*}{x_2^* + d_0} \leq a_1$ has been used. From the second equation of (8), we have

$$\begin{aligned} \dot{Y}(t) = & -b_2 y_2^* (e^{Y(t)} - 1) + \frac{v_1 d_0 x_2^*}{(x(t-r_{12}) + d_0)(x_2^* + d_0)} (e^{X(t-r_{12})} - 1) \\ & + b_2 y_2^* \int_{t-r_1}^t e^{Y(s)} \left\{ \frac{v_1 d_0 x_2^*}{(x(s-r_{12}) + d_0)(x_2^* + d_0)} (e^{X(s-r_{12})} - 1) - b_2 y_2^* (e^{Y(s-r_2)} - 1) \right\} ds, \end{aligned} \tag{13}$$

again, we use the fact that

$$e^{Y(t-r_1)} = e^{Y(t)} - \int_{t-r_1}^t e^{Y(s)} \frac{dY(s)}{ds} ds.$$

Let

$$V_2(t) = |Y(t)|.$$

Computing the upper right derivative of $V_2(t)$ along the solution of (8), it follows from (13) that

$$\begin{aligned} D^+ V_2(t) \leq & -b_2 y_2^* |e^{Y(t)} - 1| + \frac{v_1 x_2^*}{(x_2^* + d_0)} |e^{X(t-r_{12})} - 1| \\ & + b_2 y_2^* \int_{t-r_2}^t e^{Y(s)} \left\{ \frac{v_1 d_0 x_2^*}{d_0(x_2^* + d_0)} |e^{X(s-r_{12})} - 1| + b_2 y_2^* |e^{Y(s-r_2)} - 1| \right\} ds. \end{aligned}$$

By Lemma 3, we see that there exists $T > 0$ such that $y_2^* e^{Y(t)} \leq M_2$, for $t > T$. Hence, for $t > T + r$, we have

$$\begin{aligned} D^+ V_2(t) \leq & -b_2 y_2^* |e^{Y(t)} - 1| + \frac{v_1 x_2^*}{(x_2^* + d_0)} |e^{X(t-r_{12})} - 1| \\ & + b_2 M_2 \int_{t-r_2}^t \left\{ \frac{v_1 d_0 x_2^*}{d_0(x_2^* + d_0)} |e^{X(s-r_{12})} - 1| + b_2 y_2^* |e^{Y(s-r_2)} - 1| \right\} ds. \end{aligned} \tag{14}$$

Again, due to the structure of (14), we consider the functional

$$\begin{aligned} V_{22}(t) = & V_2(t) + b_2 M_2 \int_{t-r_2}^t \int_v^t \left\{ \frac{v_1 x_2^*}{(x_2^* + d_0)} |e^{X(s-r_{12})} - 1| + b_2 y_2^* |e^{Y(s-r_2)} - 1| \right\} ds dv \\ & + b_2 M_2 r_2 \left\{ \frac{v_1 x_2^*}{(x_2^* + d_0)} \int_{t-r_{12}}^t |e^{X(s)} - 1| ds + b_2 y_2^* \int_{t-r_2}^t |e^{Y(s)} - 1| ds \right\} + \frac{v_1 x_2^*}{(x_2^* + d_0)} \int_{t-r_{12}}^t |e^{X(s)} - 1| ds, \end{aligned}$$

whose upper right derivative along solution of (8) gives

$$\begin{aligned} D^+ V_{22}(t) = & D^+ V_2(t) + b_2 M_2 r_2 \left\{ \frac{v_1 x_2^*}{(x_2^* + d_0)} |e^{X(t-r_{12})} - 1| + b_2 y_2^* |e^{Y(t-r_2)} - 1| \right\} \\ & - b_2 M_2 \int_{t-r_2}^t \left\{ \frac{v_1 x_2^*}{(x_2^* + d_0)} |e^{X(s-r_{12})} - 1| + b_2 y_2^* |e^{Y(s-r_2)} - 1| \right\} ds \\ & + b_2 M_2 r_2 \left\{ \frac{v_1 x_2^*}{(x_2^* + d_0)} |e^{X(t)} - 1| + b_2 y_2^* |e^{Y(t)} - 1| \right\} \\ & - b_2 M_2 r_2 \left\{ \frac{v_1 x_2^*}{(x_2^* + d_0)} |e^{X(t-r_{12})} - 1| + b_2 y_2^* |e^{Y(t-r_2)} - 1| \right\} \\ & + \frac{v_1 x_2^*}{(x_2^* + d_0)} \{ |e^{X(t)} - 1| - |e^{X(t-r_{12})} - 1| \}. \end{aligned} \tag{15}$$

Hence, from (14) and (15), we get

$$D^+ V_{22}(t) \leq -y_2^* b_2 (1 - b_2 M_2 r_2) |e^{Y(t)} - 1| + x_2^* \frac{v_1}{d_0} (1 + b_2 M_2 r_2) |e^{X(t)} - 1|. \tag{16}$$

According to assumptions (H₃) and (H₄), $\beta = (\beta_{ij})_{i,j=1,2}$ is an M-matrix, and hence there exist positive constants h_i ($i = 1, 2$) such that

$$\beta_{11} h_1 + \beta_{12} h_2 = l_1 > 0, \quad \beta_{21} h_1 + \beta_{22} h_2 = l_2 > 0. \tag{17}$$

Let us define the following Lyapunov functional V by

$$V(t) = h_1 V_{12}(t) + h_2 V_{22}(t).$$

From (12), (16), (17) we have

$$D^+ V \leq -l_1 x_2^* |e^{X(t)} - 1| - l_2 y_2^* |e^{Y(t)} - 1|.$$

Since system (7) is uniformly persistent, one can see that there exist positive constants N_1, N_2 and $T^* > T + r$ such that $x_2^* e^{X(t)} = x(t) \geq N_1$ and $y_2^* e^{Y(t)} = y(t) \geq N_2$ for $t \geq T^*$.

Using the mean valued theorem, one obtains

$$x_2^* |e^{X(t)} - 1| = x_2^* e^{\theta_1(t)} |X(t)|, \quad y_2^* |e^{Y(t)} - 1| = y_2^* e^{\theta_2(t)} |Y(t)|,$$

where $x_2^* e^{\theta_1(t)}$ lies between $x(t)$ and x_2^* and $y_2^* e^{\theta_2(t)}$ lies between $y(t)$ and y_2^* .

Let $\alpha = \min\{N_1 l_1, N_2 l_2\}$. Then one can easily conclude that, for $t \geq T^*$,

$$D^+ V \leq -\alpha (|X(t)| + |Y(t)|). \tag{18}$$

Noting that this Lyapunov functional is such that

$$V(t) \geq h_1 |X(t)| + h_2 |Y(t)| \geq \min\{h_1, h_2\} (|X(t)| + |Y(t)|).$$

Hence, by applying the global stability theorem on the method of Lyapunov function and (18), we can conclude that the zero solution of system (8) is globally asymptotically stable, therefore, the positive equilibrium of system (7) is globally asymptotically stable. The proof is complete. \square

We now discuss the dynamics on xz -plane ($y = 0$), system (2) gives the following subsystem:

$$\begin{cases} \dot{x}(t) = x(t)(a_1 - b_1 x(t - r_1)), \\ \dot{z}(t) = z(t) \left(a_3 - \frac{v_3 z(t - r_3)}{d_3} \right). \end{cases} \tag{19}$$

The two equations of this subsystem (19) are logistic and independent, hence all the boundary equilibria are unstable. The subsystem has an interior equilibrium $E_{31}(\frac{a_1}{b_1}, \frac{a_3 d_3}{v_3})$.

Lemma 6. *Suppose that system (19) satisfies (H₂) and the following hypothesis:*

$$(H_5) \quad a_3 r_3 \leq 3/2,$$

then the interior equilibrium $E_{31}(\frac{a_1}{b_1}, \frac{a_3 d_3}{v_3})$ is globally asymptotically stable.

2.3. Uniform persistence result

Theorem 7. *Suppose that system (2) satisfies assumptions (H₂), (H₄), (H₅) and the following condition:*

$$(H_6) \quad a_1 v_1 d_2 v_3 - (a_1 + b_1 d_0)(a_2 d_2 v_3 + a_3 d_3 v_2) > 0,$$

then system (2) is uniformly persistent.

Proof. Again, we want to use Theorem 3.12 in [3] by constructing a suitable function which is, for system (2), positive at the ω -limit set of the boundary of \mathbb{R}_+^3 .

If $(x(t), y(t), z(t))$ is a solution to system (2) initiating in y -axis, with $y(0) > 0$, then it is easy to see that $y(t) \rightarrow 0$ as $t \rightarrow +\infty$. Hence E_0 is globally asymptotically stable in the y -axis. If $(x(t), y(t), z(t))$ is the solution to system (2) initiating in x -axis with $x(0) > 0$, and if assumption (H₂) holds, then $x(t) \rightarrow \frac{a_1}{b_1}$ as $t \rightarrow +\infty$. Then E_1 is globally asymptotically stable with respect to solutions initiating in the x -axis. If $(x(t), y(t), z(t))$ is the solution to system (2) initiating in z -axis with $z(0) > 0$, and if assumption (H₅) holds, then $z(t) \rightarrow \frac{a_3 d_3}{v_3}$ as $t \rightarrow +\infty$.

By Lemma 5 we see that if assumptions (H₃) and (H₄) hold, then the boundary equilibrium E_{22} is in the ω -limit set of the corresponding boundary system. So E_2 is in the ω -limit set of the boundary \mathbb{R}_+^3 . By Lemma 5, we see that if (H₂) and (H₅) hold, then all solutions $(x(t), y(t), z(t))$ initiating in the xz -plan ($x(0) > 0, z(0) > 0$), it follows that $x(t) \rightarrow \frac{a_1}{b_1}$ and $z(t) \rightarrow \frac{a_3 d_3}{v_3}$. Thus the ω -limit set of the boundary of \mathbb{R}_+^3 is the union of E_0, E_1, E_2, E_3 and E_4 .

We choose,

$$p(x(t), y(t), z(t)) = x^{\alpha_1} y^{\alpha_2} z^{\alpha_3},$$

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

$$\begin{aligned} \Phi(x(t), y(t), z(t)) &= \frac{\dot{p}(x(t), y(t), z(t))}{p(x(t), y(t), z(t))} \\ &= \alpha_1 \left(a_1 - b_1 x(t - r_1) - \frac{v_0 y}{d_0 + x} \right) + \alpha_2 \left(-a_2 + \frac{v_1 x(t - r_{12})}{x(t - r_{12}) + d_0} - b_2 y(t - r_2) - \frac{v_2 z}{d_2 + y} \right) \\ &\quad + \alpha_3 \left(a_3 - \frac{v_3 z(t - r_3)}{d_3 + y(t - r_{23})} \right). \end{aligned}$$

By computing Φ at the boundary equilibria, we have

$$\begin{aligned} \Phi(0, 0, 0) &= \alpha_1 a_1 - \alpha_2 a_2 + \alpha_3 a_3, \\ \Phi\left(\frac{a_1}{b_1}, 0, 0\right) &= \alpha_2 \left(-a_2 + \frac{v_1 a_1}{a_1 + b_1 d_0} \right), \\ \Phi(x_2^*, y_2^*, 0) &= \alpha_3 a_3, \\ \Phi\left(0, 0, \frac{a_3 d_3}{v_3}\right) &= \alpha_1 a_1 - \alpha_2 \left(a_2 + \frac{a_3 d_3 v_2}{d_2 v_3} \right), \\ \Phi\left(\frac{a_1}{b_1}, 0, \frac{a_3 d_3}{v_3}\right) &= \alpha_2 \left(-a_2 + \frac{v_1 a_1}{a_1 + b_1 d_0} - \frac{a_3 d_3 v_2}{d_2 v_3} \right). \end{aligned}$$

If we choose $\alpha_1 = 1, \alpha_2$ and α_3 small enough so that $\alpha_1 a_0 - \alpha_2 a_1 + \alpha_3 a_2 > 0$, hence Φ is positive at E_0 . If (H₆) holds, then (H₁) holds to, so, under assumption (H₆), Φ is positive at E_1 and E_4 . Φ is always positive at E_2 . If we choose α_2 enough small such that, $\alpha_2 < \frac{a_1 d_2 v_3}{a_2 d_2 v_3 + a_3 d_3 v_2}$, then Φ is positive at E_3 .

Finally, there are choices of α_2 and α_3 to ensure $\Phi > 0$ at the boundary equilibria.

Therefore, system (2) is uniformly persistent, which follows from Theorem 3.12 of [3]. The proof is complete. \square

Remark. If $r_1 = r_2 = r_3 = r_{12} = r_{23} = 0$, then system (2) is reduced to an instantaneous system, i.e., one without time delay. From the proof of Theorem 7 we see that if (H₆) holds, then the corresponding nondelayed system of (2) is uniformly persistent, provided that,

$$(H_7) \quad b_2(b_1 - \frac{a_1}{d_0}) - \frac{v_0 v_1}{d_0^2} > 0.$$

Therefore, system (2) must have a positive equilibrium, see [4], we denote it by $E^*(x^*, y^*, z^*)$.

3. Global stability of the system

We derive sufficient conditions which guarantee that the positive equilibrium $E^*(x^*, y^*, z^*)$ of system (2) is globally asymptotically stable. The strategy used in this proof is to construct a suitable Lyapunov functional. To study the global stability of $E^*(x^*, y^*, z^*)$, similar to system (7), we define

$$X(t) = \ln\left(\frac{x(t)}{x^*}\right), \quad Y(t) = \ln\left(\frac{y(t)}{y^*}\right), \quad Z(t) = \ln\left(\frac{z(t)}{z^*}\right). \tag{20}$$

These coordinate changes transform the positive equilibrium into the trivial solution $X(t) = Y(t) = Z(t) = 0$ for all $t > 0$. Due to the variable change (20), system (2) can be written as follows,

$$\begin{cases} \dot{X}(t) = -b_1x_2^*(e^{X(t-r_1)} - 1) + \frac{v_0x_2^*y_2^*}{(x_2^* + d_0)(x + d_0)}(e^{X(t)} - 1) - \frac{v_0y_2^*}{x + d_0}(e^{Y(t)} - 1), \\ \dot{Y}(t) = \frac{v_1d_0x_2^*}{(x(t-r_{12}) + d_0)(x_2^* + d_0)}(e^{X(t-r_{12})} - 1) - b_2y_2^*(e^{Y(t-r_2)} - 1) \\ \quad + \frac{v_2y^*z^*}{(y + d_2)(y^* + d_2)}(e^{Y(t)} - 1) + \frac{v_2z^*}{y + d_2}(e^{Z(t)} - 1), \\ \dot{Z}(t) = -\frac{v_3z^*}{d_3 + y(t-r_{23})}(e^{Z(t-r_3)} - 1) + \frac{a_3y^*}{d_3 + y(t-r_{23})}(e^{Y(t-r_{23})} - 1). \end{cases} \tag{21}$$

Theorem 8. *Suppose that system (2) satisfies (H₆). Then, the positive equilibrium E^* of system (2) is globally asymptotically stable provided that:*

(H₈) $\beta_{ii} > 0, i = 1, 2, 3,$

(H₉) $\beta_{11}\beta_{22}\beta_{33} - \beta_{12}\beta_{21}\beta_{33} - \beta_{11}\beta_{23}\beta_{32} > 0,$

where

$$\begin{aligned} \beta_{11} &= b_1 - \frac{a_1}{d_0} - b_1M_1r_1\left(b_1 + \frac{a_1}{d_0}\right), & \beta_{12} &= -\frac{v_1}{d_0}(1 + b_2M_2r_2), \\ \beta_{22} &= b_2 - \frac{v_1}{d_2} - b_2M_2r_2\left(b_2 + \frac{v_1}{d_2}\right), & \beta_{21} &= -\frac{v_0}{d_0}(1 + b_1M_1r_1), \\ \beta_{33} &= \frac{v_3}{d_3 + M_2} - \left(\frac{v_3}{d_3}\right)^2 M_3r_3, & \beta_{23} &= -\frac{a_3}{d_3}\left(1 + \frac{v_3}{d_3}M_3r_3\right), & \beta_{32} &= -\frac{v_2}{d_2}(1 + b_2M_2r_2). \end{aligned}$$

Proof. We observe that assumption (H₆) implies (H₁). The first equation of (21) can be rewritten as

$$\begin{aligned} \dot{X}(t) &= -b_1x_2^*(e^{X(t)} - 1) + \frac{v_0x_2^*y_2^*}{(x_2^* + d_0)(x + d_0)}(e^{X(t)} - 1) - \frac{v_0y_2^*}{x + d_0}(e^{Y(t)} - 1) \\ &\quad + b_1x_2^* \int_{t-r_1}^t e^{X(t)} \left\{ -b_1x_2^*(e^{X(s-r_1)} - 1) + \frac{v_0x_2^*y_2^*}{(x_2^* + d_0)(x + d_0)}(e^{X(s)} - 1) - \frac{v_0y_2^*}{x + d_0}(e^{Y(s)} - 1) \right\} ds. \end{aligned} \tag{22}$$

Now define

$$V_1(t) = |X(t)|.$$

Computing the upper right derivative of $V_1(t)$ along the solution of (21), it follows from (22) that

$$D^+V_1(t) \leq -b_1x^*|e^{X(t)} - 1| + \frac{v_0x_2^*y_2^*}{(x_2^* + d_0)(x + d_0)}|e^{X(t)} - 1| + \frac{v_0y_2^*}{x + d_0}|e^{Y(t)} - 1|$$

$$+ b_1 x^* \int_{t-r_1}^t e^{X(t)} \left\{ b_1 x^* |e^{X(s-r_1)} - 1| + \frac{v_0 x^* y^*}{(x^* + d_0)(x + d_0)} |e^{X(s)} - 1| + \frac{v_0 y^*}{x + d_0} |e^{Y(s)} - 1| \right\} ds.$$

By Lemma 3 we see that there exists $T > 0$ such that $x^* e^{X(t)} \leq M_1$, for $t > T$. Hence for $t \geq T + r$, we have

$$D^+ V_1(t) \leq -b_1 x^* |e^{X(t)} - 1| + \frac{v_0 x^* y^*}{(x^* + d_0)d_0} |e^{X(t)} - 1| + \frac{v_0 y^*}{d_0} |e^{Y(t)} - 1| + b_1 M_1 \int_{t-r_1}^t \left\{ b_1 x^* |e^{X(s-r_1)} - 1| + \frac{v_0 x^* y^*}{(x^* + d_0)d_0} |e^{X(s)} - 1| + \frac{v_0 y^*}{d_0} |e^{Y(s)} - 1| \right\} ds. \tag{23}$$

Owing to the structure of (23), let us now consider the functional

$$V_{12}(t) = V_1(t) + b_1 M_1 \int_{t-r_1}^t \int_v^t \left\{ b_1 x^* |e^{X(s-r_1)} - 1| + \frac{v_0 x^* y^*}{(x^* + d_0)d_0} |e^{X(s)} - 1| + \frac{v_0 y^*}{d_0} |e^{Y(s)} - 1| \right\} ds dv + b_1^2 M_1 r_1 x^* \int_{t-r_1}^t |e^{X(s)} - 1| ds,$$

whose upper right derivative along solution of (21) gives

$$D^+ V_{12} = D^+ V_1 + b_1 M_1 r_1 \left\{ b_1 x^* |e^{X(t-r_1)} - 1| + \frac{v_0 x^* y^*}{(x^* + d_0)d_0} |e^{X(t)} - 1| + \frac{v_0 y^*}{d_0} |e^{Y(t)} - 1| \right\} - b_1 M_1 \int_{t-r_1}^t \left\{ b_1 x^* |e^{X(s-r_1)} - 1| + \frac{v_0 x^* y^*}{(x_2^* + d_0)d_0} |e^{X(s)} - 1| + \frac{v_0 y_2^*}{d_0} |e^{Y(s)} - 1| \right\} ds + b_1^2 M_1 r_1 x^* \{ |e^{X(t)} - 1| - |e^{X(t-r_1)} - 1| \}. \tag{24}$$

Therefore, from (23) and (24) we get, for $t \geq T + r$,

$$D^+ V_{12} = -x^* \left(b_1 - \frac{a_1}{d_0} - b_1 M_1 r_1 \left(b_1 + \frac{a_1}{d_0} \right) \right) |e^{X(t)} - 1| + \frac{v_0}{d_0} (1 + b_1 M_1 r_1) y^* |e^{Y(t)} - 1|, D^+ V_{12} \leq -x^* \beta_{11} |e^{X(t)} - 1| - y^* \beta_{21} |e^{Y(t)} - 1|. \tag{25}$$

The second equation of system (21) can be rewritten as

$$\dot{Y}(t) = -b_2 y^* (e^{Y(t)} - 1) + \frac{v_1 d_0 x_2^*}{(x(t-r_{12}) + d_0)(x_2^* + d_0)} (e^{X(t-r_{12})} - 1) + \frac{v_2 y^* z^*}{(y + d_2)(y^* + d_2)} (e^{Y(t)} - 1) + b_2 y^* \int_{t-r_2}^t e^{Y(s)} \left\{ \frac{v_1 d_0 x_2^*}{(x(s-r_{12}) + d_0)(x_2^* + d_0)} (e^{X(s-r_{12})} - 1) - b_2 y_2^* (e^{Y(s-r_2)} - 1) \right\} + \frac{v_2 y^* z^*}{(y + d_2)(y^* + d_2)} (e^{Y(t)} - 1) + \frac{v_2 z^*}{y + d_2} (e^{Z(s)} - 1) ds + \frac{v_2 z^*}{y + d_2} (e^{Z(t)} - 1). \tag{26}$$

Let

$$V_2(t) = |Y(t)|.$$

Computing the upper right derivative of $V_2(t)$ along the solution of (21), it follows from (26) that

$$\begin{aligned}
 D^+V_2(t) \leq & -b_2y^*|e^{Y(t)} - 1| + \frac{v_1x_2^*}{(x_2^* + d_0)}|e^{X(t-r_{12})} - 1| + \frac{v_2y^*z^*}{d_2(y^* + d_2)}|e^{Y(t)} - 1| + \frac{v_2z^*}{d_2}|e^{Z(t)} - 1| \\
 & + b_2y^* \int_{t-r_2}^t e^{Y(s)} \left\{ b_2y_2^*|e^{Y(s-r_2)} - 1| + \frac{v_1x_2^*}{(x_2^* + d_0)}|e^{X(s-r_{12})} - 1| \right. \\
 & \left. + \frac{v_2y^*z^*}{d_2(y^* + d_2)}|e^{Y(s)} - 1| + \frac{v_2z^*}{d_2}|e^{Z(s)} - 1| \right\} ds.
 \end{aligned}$$

By Lemma 3, we see that there exists $T > 0$ such that $y^*e^{Y(t)} \leq M_2$ for $t > T$. Hence for $t \geq T + r$, we have

$$\begin{aligned}
 D^+V_2(t) \leq & -b_2y^*|e^{Y(t)} - 1| + \frac{v_1x_2^*}{(x_2^* + d_0)}|e^{X(t-r_{12})} - 1| + \frac{v_2y^*z^*}{d_2(y^* + d_2)}|e^{Y(t)} - 1| + \frac{v_2z^*}{d_2}|e^{Z(t)} - 1| \\
 & + b_2M_2 \int_{t-r_2}^t \left\{ b_2y_2^*|e^{Y(s-r_2)} - 1| + \frac{v_1x_2^*}{(x_2^* + d_0)}|e^{X(s-r_{12})} - 1| \right. \\
 & \left. + \frac{v_2y^*z^*}{d_2(y^* + d_2)}|e^{Y(s)} - 1| + \frac{v_2z^*}{d_2}|e^{Z(s)} - 1| \right\} ds. \tag{27}
 \end{aligned}$$

Again, due to the structure of (27), we consider the functional

$$\begin{aligned}
 V_{22}(t) = & V_2(t) + \frac{v_1x_2^*}{(x_2^* + d_0)} \int_{t-r_{12}}^t |e^{X(s-r_{12})} - 1| ds \\
 & + b_2M_2 \int_{t-r_2}^t \int_v^t \left\{ b_2y_2^*|e^{Y(s-r_2)} - 1| + \frac{v_1x_2^*}{(x_2^* + d_0)}|e^{X(s-r_{12})} - 1| \right. \\
 & \left. + \frac{v_2y^*z^*}{d_2(y^* + d_2)}|e^{Y(s)} - 1| + \frac{v_2z^*}{d_2}|e^{Z(s)} - 1| \right\} ds dv \\
 & + b_2M_2r_2 \int_{t-r_2}^t \left\{ b_2y_2^*|e^{Y(s)} - 1| + \frac{v_1x_2^*}{(x_2^* + d_0)}|e^{X(s)} - 1| \right\} ds,
 \end{aligned}$$

whose time derivative along solution of (21) gives

$$\begin{aligned}
 D^+V_{22}(t) = & D^+V_2(t) + \frac{v_1x_2^*}{(x_2^* + d_0)} \{ |e^{X(t)} - 1| - |e^{X(t-r_{12})} - 1| \} \\
 & + b_2M_2r_2 \left\{ b_2y_2^*|e^{Y(t-r_2)} - 1| + \frac{v_1x_2^*}{(x_2^* + d_0)}|e^{X(t-r_{12})} - 1| \right. \\
 & \left. + \frac{v_2y^*z^*}{d_2(y^* + d_2)}|e^{Y(t)} - 1| + \frac{v_2z^*}{d_2}|e^{Z(s)} - 1| \right\} \\
 & - b_2M_2 \int_{t-r_2}^t \left\{ b_2y_2^*|e^{Y(s-r_2)} - 1| + \frac{v_1x_2^*}{(x_2^* + d_0)}|e^{X(s-r_{12})} - 1| \right. \\
 & \left. + \frac{v_2y^*z^*}{d_2(y^* + d_2)}|e^{Y(s)} - 1| + \frac{v_2z^*}{d_2}|e^{Z(s)} - 1| \right\} ds \\
 & + b_2M_2r_2 \left\{ b_2y_2^*|e^{Y(t)} - 1| + \frac{v_1x_2^*}{(x_2^* + d_0)}|e^{X(t)} - 1| \right. \\
 & \left. - b_2y_2^*|e^{Y(t-r_2)} - 1| - \frac{v_1x_2^*}{(x_2^* + d_0)}|e^{X(t-r_{12})} - 1| \right\}. \tag{28}
 \end{aligned}$$

Hence, from Eqs. (27) and (28) we get

$$D^+ V_{22}(t) \leq -y^* \left(b_2 - \frac{v_1}{d_2} - b_2 M_2 r_2 \left(b_2 + \frac{v_1}{d_2} \right) \right) |e^{Y(t)} - 1| + \frac{v_1}{d_0} (1 + b_2 M_2 r_2) x^* |e^{X(t)} - 1| + \frac{v_2}{d_2} (1 + b_2 M_2 r_2) z^* |e^{Z(t)} - 1|, \tag{29}$$

where the inequality $\frac{v_2 z^*}{(y^* + d_2)} \leq v_1$ has been used. Thus,

$$D^+ V_{22}(t) \leq -\beta_{22} y^* |e^{Y(t)} - 1| - \beta_{12} x^* |e^{X(t)} - 1| - \beta_{32} z^* |e^{Z(t)} - 1|. \tag{30}$$

The third equation of (21) can be rewritten as

$$\begin{aligned} \dot{Z}(t) = & -\frac{v_3 z^*}{d_3 + y(t - r_{23})} (e^{Z(t)} - 1) + \frac{a_3 y^*}{d_3 + y(t - r_{23})} (e^{Y(t - r_{23})} - 1) \\ & + \frac{v_3 z^*}{d_3 + y(t - r_{23})} \int_{t-r_3}^t e^{Z(s)} \left\{ -\frac{v_3 z^*}{d_3 + y(s - r_{23})} (e^{Z(s - r_3)} - 1) + \frac{a_3 y^*}{d_3 + y(s - r_{23})} (e^{Y(s - r_{23})} - 1) \right\} ds. \end{aligned} \tag{31}$$

Let

$$V_3(t) = |Z(t)|.$$

From Lemma 3, we see that there exists $T > 0$, such that $x^* e^{X(t)} \leq M_1$, $y^* e^{Y(t)} \leq M_2$, $z^* e^{Z(t)} \leq M_3$ for $t > T$. Computing the upper right derivative of $V_3(t)$ along the solution of (21), it follows from (31) that, for $t > T + r$, we have

$$D^+ V_3 \leq -\frac{v_3 z^*}{d_3 + M_2} |e^{Z(t)} - 1| + \frac{a_3 y^*}{d_3} |e^{Y(t - r_{23})} - 1| + \frac{v_3}{d_3} M_3 \int_{t-r_3}^t \left\{ \frac{v_3 z^*}{d_3} |e^{Z(s - r_3)} - 1| + \frac{a_3 y^*}{d_3} |e^{Y(s - r_{23})} - 1| \right\} ds. \tag{32}$$

Owing to the structure of (32), let us consider the functional

$$\begin{aligned} V_{33}(t) = & V_3(t) + \frac{v_3}{d_3} M_3 \int_{t-r_3}^t \int_v^t \left\{ \frac{v_3 z^*}{d_3} |e^{Z(s - r_3)} - 1| + \frac{a_3 y^*}{d_3} |e^{Y(s - r_{23})} - 1| \right\} ds dv \\ & + \frac{v_3}{d_3} M_3 r_3 \left\{ \frac{v_3 z^*}{d_3} \int_{t-r_3}^t |e^{Z(s)} - 1| ds + \frac{a_3 y^*}{d_3} \int_{t-r_{23}}^t |e^{Y(s)} - 1| ds \right\} + \frac{a_3 y^*}{d_3} \int_{t-r_{23}}^t |e^{Y(s)} - 1| ds, \end{aligned}$$

whose upper right derivative along solution of system, (21) is

$$\begin{aligned} D^+ V_{33}(t) = & D^+ V_3(t) + \frac{v_3}{d_3} M_3 r_3 \left\{ \frac{v_3 z^*}{d_3} |e^{Z(t - r_3)} - 1| + \frac{a_3 y^*}{d_3} |e^{Y(t - r_{23})} - 1| \right\} \\ & - \frac{v_3}{d_3} M_3 \int_{t-r_3}^t \left\{ \frac{v_3 z^*}{d_3} |e^{Z(s - r_3)} - 1| + \frac{a_3 y^*}{d_3} |e^{Y(s - r_{23})} - 1| \right\} ds \\ & + \frac{a_3 y^*}{d_3} \left\{ |e^{Y(t)} - 1| - |e^{Y(t - r_{23})} - 1| \right\} + \frac{v_3}{d_3} M_3 r_3 \left\{ \frac{v_3 z^*}{d_3} |e^{Z(t)} - 1| + \frac{a_3 y^*}{d_3} |e^{Y(t)} - 1| \right. \\ & \left. - \frac{v_3 z^*}{d_3} |e^{Z(t - r_3)} - 1| - \frac{a_3 y^*}{d_3} |e^{Y(t - r_{23})} - 1| \right\}. \end{aligned} \tag{33}$$

Therefore, from Eqs. (32), (33), we have

$$D^+ V_{33}(t) \leq -z^* \left(\frac{v_3}{d_3 + M_2} - \left(\frac{v_3}{d_3} \right)^2 M_3 r_3 \right) |e^{Z(t)} - 1| + \frac{a_3}{d_3} \left(1 + \frac{v_3}{d_3} M_3 r_3 \right) y^* |e^{Y(t)} - 1|,$$

thus

$$D^+ V_{33}(t) \leq -\beta_{33} z^* |e^{Z(t)} - 1| - \beta_{23} y^* |e^{Y(t)} - 1|. \tag{34}$$

According to assumptions (H₈) and (H₉), we know that $\beta = (\beta_{ij})_{3 \times 3}$ is an M-matrix, hence there exist positive constants h_i ($i = 1, 2, 3$) such that,

$$\begin{aligned} \beta_{11} h_1 + \beta_{12} h_2 &= l_1 > 0, & \beta_{21} h_1 + \beta_{22} h_2 + \beta_{23} h_3 &= l_2 > 0, \\ \beta_{32} h_2 + \beta_{33} h_3 &= l_3 > 0. \end{aligned} \tag{35}$$

Let us consider the Lyapunov function V defined by

$$V(t) = h_1 V_{11}(t) + h_2 V_{22}(t) + h_3 V_{33}(t) \tag{36}$$

then from Eqs. (25), (30) and (34), we obtain

$$\begin{aligned} \frac{dV}{dt} &\leq -\beta_{11} h_1 x^* |e^{X(t)} - 1| - \beta_{21} h_1 y^* |e^{Y(t)} - 1| - \beta_{22} h_2 y^* |e^{Y(t)} - 1| - \beta_{12} h_2 x^* |e^{X(t)} - 1| \\ &\quad - \beta_{32} h_2 z^* |e^{Z(t)} - 1| - \beta_{33} h_3 z^* |e^{Z(t)} - 1| - \beta_{23} h_3 y^* |e^{Y(t)} - 1|. \end{aligned} \tag{37}$$

It follows from (35) that, for all $t \geq T + r$, we have

$$\frac{dV}{dt} \leq -l_1 x^* |e^{X(t)} - 1| - l_2 y^* |e^{Y(t)} - 1| - l_3 z^* |e^{Z(t)} - 1|.$$

Since system (2) is uniformly persistent, one can see that there exist positive constants N_1, N_2, N_3 and $T^* > T + r$, such that, $x^* e^{X(t)} = x(t) \geq N_1, y^* e^{Y(t)} = y(t) \geq N_2$ and $z^* e^{Z(t)} \geq N_3$ for $t \geq T^*$.

Using the mean valued theorem one obtains,

$$\begin{aligned} x^* |e^{X(t)} - 1| &= x^* e^{\theta_1(t)} |X(t)|, & y^* |e^{Y(t)} - 1| &= y^* e^{\theta_2(t)} |Y(t)|, \\ z^* |e^{Z(t)} - 1| &= z^* e^{\theta_3(t)} |Z(t)|, \end{aligned}$$

where $x^* e^{\theta_1(t)}$ lies between $x(t)$ and x^* , $y^* e^{\theta_2(t)}$ lies between $y(t)$ and y^* and $z^* e^{\theta_3(t)}$ lies between $z(t)$ and z^* .

Let $\alpha = \min\{N_1 l_1, N_2 l_2, N_3 l_3\}$, then it follows that, for $t \geq T^*$,

$$D^+ V \leq -\alpha (|X(t)| + |Y(t)| + |Z(t)|). \tag{38}$$

Noting that the Lyapunov functional is such that

$$V(t) \geq \min\{h_1, h_2, h_3\} (|X(t)| + |Y(t)| + |Z(t)|).$$

Hence, by applying the global stability theorem of the method of Lyapunov function and (38), we can conclude that the zero solution of system (21) is globally asymptotically stable, therefore, the positive equilibrium of system (2) is globally asymptotically stable. The proof is complete. \square

4. Discussion

Conditions in Theorem 8 can be satisfied provided that b_1, b_2, d_0, d_2 are large enough and time delays lengths r_1, r_2, r_3 are appropriately small.

Theorem 8 shows that delay due to gestation is harmless for uniform persistence and for the global asymptotically stability of the positive equilibrium of system (2), by contrast, time delay in the negative feedback of each species destabilizes E^* for system (2), since the global asymptotic stability of E^* imposes restrictions on the length of time delays.

Linear analysis of system (2) will illustrate the effect of time delays on stability of the positive equilibrium of system (2). We assume that equilibrium $E^*(x^*, y^*, z^*)$ exists for system (2).

By putting $r_1 = r_2 = r_3 = r_{12} = r_{23} = 0$ the linearized system obtained from system (2) is reduced to the following system without delay

$$\begin{aligned} \dot{X}(t) &= (A_{11} + \bar{A}_{11})X(t) + A_{12}Y(t), \\ \dot{Y}(t) &= A_{21}X(t) + (A_{22} + \bar{A}_{22})Y(t) + A_{23}Z(t), \\ \dot{Z}(t) &= A_{32}Y(t) + A_{33}Z(t), \end{aligned} \tag{39}$$

where

$$\begin{aligned} A_{11} &= \frac{v_0 x^* y^*}{(d_0 + x^*)^2}, & \bar{A}_{11} &= -b_1 x^*, & A_{12} &= -\frac{v_0 x^*}{x^* + d_0}, & A_{21} &= \frac{d_0 v_1 y^*}{(x^* + d_0)^2}, \\ A_{22} &= \frac{v_2 y^* z^*}{(y^* + d_2)^2}, & \bar{A}_{22} &= -b_2 y^*, & A_{23} &= -\frac{v_2 y^*}{y^* + d_2}, & A_{32} &= \frac{a_3^2}{v_3}, & A_{33} &= -a_3. \end{aligned}$$

It is easy to see, by applying a classical Lyapunov function to the linear system (39), that the positive equilibrium $E^*(x^*, y^*, z^*)$ is stable, provided that

- (H₁₁) $2(A_{11} + \bar{A}_{11}) - A_{12} + A_{21} < 0$,
- (H₁₂) $2(A_{22} + \bar{A}_{22}) - A_{12} + A_{21} - A_{23} + A_{32} < 0$,
- (H₁₃) $2A_{33} + A_{32} - A_{23} < 0$.

By linearizing the delayed system (2) at $E^*(x^*, y^*, z^*)$, we obtain

$$\begin{aligned} \dot{X}(t) &= A_{11}X(t) + \bar{A}_{11}X(t - r_1) + A_{12}Y(t), \\ \dot{Y}(t) &= A_{21}X(t - r_{12}) + A_{22}Y(t) + \bar{A}_{22}Y(t - r_2) + A_{23}Z(t), \\ \dot{Z}(t) &= A_{32}Y(t - r_{23}) + A_{33}Z(t - r_3). \end{aligned} \tag{40}$$

Firstly, for simplicity, we let $r = r_{12}$ and $r_1 = r_2 = r_3 = r_{23} = 0$ and discuss the effect of r on system (40), the characteristic of which takes the form

$$p_1(\lambda) + q_1(\lambda)e^{-\lambda r} = 0, \tag{41}$$

where

$$p_1(\lambda) = \lambda^3 + A\lambda^2 + B\lambda + C, \quad q_1(\lambda) = D\lambda + E$$

and

$$\begin{aligned} A &= -(A_{11} + \bar{A}_{11}) + (A_{22} + \bar{A}_{22}) + A_{33}, \\ B &= (A_{11} + \bar{A}_{11})(A_{22} + \bar{A}_{22}) + (A_{11} + \bar{A}_{11})A_{33} + (A_{22} + \bar{A}_{22})A_{33} - A_{23}A_{32}, \\ C &= -(A_{11} + \bar{A}_{11})(A_{22} + \bar{A}_{22})A_{33} + (A_{11} + \bar{A}_{11})A_{23}A_{32}, \\ D &= -A_{12}A_{21}, \\ E &= A_{33}A_{12}A_{21}. \end{aligned}$$

Let

$$F_1(y) = |p_1(iy)|^2 - |q_1(iy)|^2, \quad y > 0,$$

then

$$F_1(y) = y^6 + (A^2 - 2B)y^4 + (B^2 - 2AC - D^2)y^2 + C^2 - E^2.$$

If (H₁₁), (H₁₂) and (H₁₃) hold, then it is easy to verify that $F_1(y) = 0$ has no positive roots. By applying Theorem 4.1 in [6, p. 83], we see that as r increases, no stability switch may occur.

Secondly, we let $r = r_{23}$ and $r_1 = r_2 = r_3 = r_{12} = 0$ and discuss the effect of r on system (40). The characteristic equation of the last takes the form

$$p_2(\lambda) + q_2(\lambda)e^{-\lambda r} = 0, \tag{42}$$

where

$$p_2(\lambda) = \lambda^3 + A\lambda^2 + B\lambda + C, \quad q_2(\lambda) = D\lambda + E$$

and

$$\begin{aligned} A &= -((A_{11} + \bar{A}_{11}) + (A_{22} + \bar{A}_{22}) + A_{33}), \\ B &= (A_{11} + \bar{A}_{11})(A_{22} + \bar{A}_{22}) + (A_{11} + \bar{A}_{11})A_{33} + (A_{22} + \bar{A}_{22})A_{33} - A_{12}A_{12}, \\ C &= -(A_{11} + \bar{A}_{11})(A_{22} + \bar{A}_{22})A_{33} + A_{33}A_{12}A_{21}, \\ D &= -A_{23}A_{32}, \\ E &= (A_{11} + \bar{A}_{11})A_{23}A_{32}. \end{aligned}$$

Let

$$F_2(y) = |p_1(iy)|^2 - |q_2(iy)|^2, \quad y > 0,$$

then

$$F_2(y) = y^6 + (A^2 - 2B)y^4 + (B^2 - 2AC - D^2)y^2 + C^2 - E^2.$$

Again, if (H_{11}) , (H_{12}) and (H_{13}) hold, then it is easy to verify that $F_2(y) = 0$ has no positive roots. By applying Theorem 4.1 in [6, p. 83], we see that as r increases, no stability switch may occur. This confirms that time delay due to gestation is harmless for the global stability of the positive equilibrium of system (2).

Thirdly, we let $r = r_1$ and $r_{12} = r_{23} = r_2 = r_3 = 0$. Then the characteristic equation for (40) takes the form

$$p_3(\lambda) + q_3(\lambda)e^{-\lambda r} = 0, \tag{43}$$

where

$$p_3(\lambda) = \lambda^3 + A\lambda^2 + B\lambda + C, \quad q_3(\lambda) = D\lambda^2 + E\lambda + G$$

and

$$\begin{aligned} A &= -(A_{11} + (A_{22} + \bar{A}_{22}) + A_{33}), \\ B &= A_{11}(A_{22} + \bar{A}_{22}) + A_{11}A_{33} + (A_{22} + \bar{A}_{22})A_{33} - A_{12}A_{21} - A_{23}A_{32}, \\ C &= -A_{11}(A_{22} + \bar{A}_{22})A_{33} + A_{11}A_{23}A_{32} + A_{33}A_{12}A_{21}, \\ D &= -\bar{A}_{11}, \\ E &= \bar{A}_{11}((A_{22} + \bar{A}_{22}) + A_{33}), \\ G &= \bar{A}_{11}(A_{23}A_{32} - A_{22}A_{33}). \end{aligned}$$

Let

$$F_3(y) = |p_3(iy)|^2 - |q_3(iy)|^2, \quad y > 0,$$

then

$$F_3(y) = y^6 + (A^2 - 2B - D^2)y^4 + (B^2 - E^2 + 2(DG - AC))y^2 + C^2 - G^2.$$

If (H_{11}) , (H_{12}) and (H_{13}) hold, then it is easy to verify that $C^2 - G^2 < 0$. Therefore, $F_3(y) = 0$ has at least one positive root. By applying Theorem 4.1 in [6, p. 83], we see that there exists a positive constant r_0 , such that for $r > r_0$, E^* becomes unstable. This shows that the global stability of E^* will impose restrictions on the length of time delay r .

Finally, we let $r_3 = r$ and $r_1 = r_2 = r_{12} = r_{23} = 0$, then the characteristic equation for (40) takes the form

$$p_4(\lambda) + q_4(\lambda)e^{-\lambda r} = 0, \tag{44}$$

where

$$p_4(\lambda) = \lambda^3 + A\lambda^2 + B\lambda + C, \quad q_4(\lambda) = D\lambda^2 + E\lambda + G$$

and

$$\begin{aligned} A &= -[(A_{11} + \bar{A}_{11}) + (A_{22} + \bar{A}_{22})], \\ B &= (A_{11} + \bar{A}_{11})(A_{22} + \bar{A}_{22}) - A_{12}A_{21} - A_{23}A_{32}, \\ C &= (A_{11} + \bar{A}_{11})A_{23}A_{32}, \\ D &= -A_{33}, \\ E &= A_{33}[(A_{11} + \bar{A}_{11}) + (A_{22} + \bar{A}_{22})], \\ G &= A_{33}[-(A_{11} + \bar{A}_{11})(A_{22} + \bar{A}_{22}) + A_{12}A_{21}]. \end{aligned}$$

Let

$$F_3(y) = |p_4(iy)|^2 - |q_4(iy)|^2, \quad y > 0,$$

then

$$F_4(y) = y^6 + (A^2 - 2B - D^2)y^4 + (B^2 - E^2 + 2(DG - AC))y^2 + C^2 - G^2.$$

Again, if (H_{11}) , (H_{12}) and (H_{13}) hold, then it is easy to verify that $C^2 - G^2 < 0$. Therefore, $F_4(y) = 0$ has at least one positive root. By applying Theorem 4.1 in [6, p. 83], we see that there is a positive constant r_0 , such that for $r > r_0$, E^* becomes unstable.

Similar conclusions can be obtained when $r_2 = r$ and $r_1 = r_3 = r_{12} = r_{23} = 0$.

This shows that the global stability of E^* will impose restrictions on the length of time delay r .

Therefore, time delay in negative feedback of each species destabilizes the positive equilibrium $E^*(x^*, y^*, z^*)$ for system (2), even if this negative feedback depends only on the concerned species or both prey and predator numbers.

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