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PERMANENCE FOR TWO-SPECIES LOTKA-VOLTERRA SYSTEMS WITH DELAYS

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Abstract. The permanence of the following Lotka-Volterra system with time delays

$$\dot{x}_1(t) = x_1(t)[r_1 - a_1x_1(t) + a_{11}x_1(t-\tau_{11}) + a_{12}x_2(t-\tau_{12})],$$

$$\dot{x}_2(t) = x_2(t)[r_2 - a_2x_2(t) + a_{21}x_1(t-\tau_{21}) + a_{22}x_2(t-\tau_{22})],$$

is considered.With intraspecific competition, it is proved that in competitive case, the system is permanent if and only if the interaction matrix of the system satisfies condition (C1) and in cooperative case it is proved that condition (C2) is sufficient for the permanence of the system.

1. **Introduction.** We consider the following Lotka-Volterra system with discrete delays,

$$\begin{aligned}\dot{x}_1(t) &= x_1(t)[r_1 - a_1x_1(t) + a_{11}x_1(t-\tau_{11}) + a_{12}x_2(t-\tau_{12})],\\ \dot{x}_2(t) &= x_2(t)[r_2 - a_2x_2(t) + a_{21}x_1(t-\tau_{21}) + a_{22}x_2(t-\tau_{22})].\end{aligned} \tag{1.1}$$

The initial condition of (1.1) is given as

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

where $r_i,\ a_i,\ a_{ij}$ and τ_{ij} are constants with $a_i > 0, \tau_{ij} \geq 0$ $(i = 1,\ 2)$ and $\tau = \max\{\tau_{ij} :\ i,\ j = 1,\ 2\}$. $\phi_i(t)$ $(i = 1,\ 2)$ is continuous on $[-\tau,\ 0]$.

We assume that system (1.1) has a unique positive equilibrium $x^* = (x_1^*,\ x_2^*)$. That is,

$$x_1^* = \frac{r_1(a_2 - a_{22}) + r_2a_{12}}{(a_1 - a_{11})(a_2 - a_{22}) - a_{12}a_{21}},\ x_2^* = \frac{r_2(a_1 - a_{11}) + r_1a_{21}}{(a_1 - a_{11})(a_2 - a_{22}) - a_{12}a_{21}}. \tag{1.3}$$

If $a_1 = a_2 = 0$, system (1.1) simplifies to the form

$$\begin{aligned}\dot{x}_1(t) &= x_1(t)[r_1 + a_{11}x_1(t-\tau_{11}) + a_{12}x_2(t-\tau_{12})],\\ \dot{x}_2(t) &= x_2(t)[r_2 + a_{21}x_1(t-\tau_{21}) + a_{22}x_2(t-\tau_{22})].\end{aligned} \tag{1.4}$$

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DEFINITION 1.1. System (1.1) is said to be permanent if there is a compact set D in the interior of R_+^2 such that for each positive initial position, the orbit of system (1.1) through this initial position eventually enters and remains in D.

That is, there exist $M_i > 0,\ N_i > 0\ (i = 1,\ 2)$ such that

$$\limsup_{t\to+\infty} x_i(t) \le M_i, \quad \liminf_{t\to+\infty} x_i(t) \ge N_i.$$

The permanence of system (1.4) with $a_{ii} < 0\ \ (i = 1,\ 2)$ and $\tau_{11} + \tau_{22} \ne 0$ has been discussed under the following

$$\textbf{Condition (C)}:\ a_{11}a_{22} - a_{12}a_{21} > 0.$$

With the assumption that system (1.4) has a unique positive equilibrium, the following results are known.

THEOREM 1.1 [4, 6, 13]. In the competitive case ($a_{12} < 0$ and $a_{21} < 0$), system (1.4) is permanent if and only if condition (C) holds.

THEOREM 1.2 [14]. In the prey-predator case ($a_{12}a_{21} < 0$), system (1.4) is permanent.

REMARK 1.1. Since for a prey-predator system, $a_{12}a_{21} < 0$ implies that condition (C) holds, Theorem 1.2 means that the existence of a unique positive equilibrium guarantees the permanence of the system. In fact, if system (1.4) is permanent, it can be shown that it must have a unique positive equilibrium [2]. Thus, we can conclude that system (1.4) in the prey-predator case is permanent if and only if the system has a unique positive equilibrium.

REMARK 1.2. In both cases above, the delays are harmless for the permanence of system (1.4). However, in cooperative case ($a_{12} > 0$ and $a_{21} > 0$), two counterexamples given in [1] show that condition (C) can not ensure the permanence of system (1.4).

If $a_{11} = a_{22} = 0$, Lu and Wang [7] obtained necessary and sufficient conditions for the global stability of system (1.1) for all delays. This result was extended to general n by Hofbauer and So [3] and Lu and Lu [5].

Recently, Saito et al. [11, 12] derived necessary and sufficient conditions for the permanence and global stability of system (1.1) in some specific cases. Muroya [8, 9] also established sufficient conditions for the permanence of system (1.1).

In the prey-predator case, Saito [10] obtained the following theorem.

THEOREM 1.3 [10]. Suppose that system (1.1) has a unique positive equilibrium; then it is permanent for all $\tau_{ij} \ge 0$ if $a_i - a_{ii} > 0\ \ (i, j = 1, 2)$.

In a competitive case, with the assumption of $a_i - a_{ii} > 0$, we will show that system (1.1) is permanent if and only if the following condition (C1) holds.

$$\textbf{Condition(C1)}:\ \ (a_1 - a_{11})(a_2 - a_{22}) > a_{12}a_{21}.$$

In a cooperative case, Muroya [8] proved that system (1.1) is uniformly bounded above if the following condition (C2) holds.

$$\textbf{Condition(C2)}:\ \ a_1 - a_{11} > 0,\ \ a_2 - a_{22} > 0\ \text{ and }\ (a_1 - a_{11}^+)(a_2 - a_{22}^+) > a_{12}a_{21},$$

where $a_{11}^+ = \max(a_{11}, 0),\ a_{22}^+ = \max(a_{22}, 0)$.

In fact, we find that condition (C2) can ensure the permanence of system (1.1). Obviously, condition (C2) implies condition (C1). And it is known that condition (C1) is enough to guarantee the global attrativity of system (1.1) when $\tau_{ij} = 0$. However, we show by examples that the solutions of system (1.1) can be unbounded under condition (C1) when condition (C2) fails.

2. **The Main Results.** We need the following two lemmas for the proof of our main results.

LEMMA 2.1 [8]. Every solution $x(t)$ of system (1.1) exists in the interval $[T, +\infty]$ and remains positive for all $t \geq T$.

LEMMA 2.2. In competitive case ($a_{12} < 0$ and $a_{21} < 0$), if $a_i - a_{ii} > 0$ $(i = 1, 2)$, then any solution of (1.1) with initial condition (1.2) is ultimately bounded. That is, there exist $M_1 > 0,\ M_2 > 0$ such that

$$\limsup_{t\to+\infty} x_1(t) \leq M_1, \quad \limsup_{t\to+\infty} x_2(t) \leq M_2,$$

where $M_1 = \frac{|r_1|+1}{a_1 - a_{11}^+}$, $M_2 = \frac{|r_2|+1}{a_2 - a_{22}^+}$ $(a_{11}^+ = \max(a_{11}, 0),\ a_{22}^+ = \max(a_{22}, 0))$. Further, if $\phi_i(t) \leq M_i$, $t \in [-\tau, 0]$ $(i = 1, 2)$, then $x_i(t) \leq M_i$ for all $t \geq 0$.

Proof. The proof of the former part is similar to that in [12]. We show the latter claim. Otherwise, there exists $\bar{t} > 0$, such that

$$x_i(\bar{t}) = \frac{|r_i| + 1}{a_i - a_{ii}^+} \quad \text{and} \quad \dot{x}_i(\bar{t}) > 0,$$

$$x_i(t) < \frac{|r_i| + 1}{a_i - a_{ii}^+}, \quad \forall\ t \in [-\tau, \bar{t}).$$

But

$$\begin{aligned} \dot{x}_i(\bar{t}) &\leq x_i(\bar{t})[|r_i| - a_i x_i(\bar{t}) + a_{ii}^+ x_i(\bar{t} - \tau_{ii})] \\ &\leq x_i(\bar{t})[|r_i| - a_i \tfrac{|r_i|+1}{a_i - a_{ii}^+} + a_{ii}^+ \tfrac{|r_i|+1}{a_i - a_{ii}^+}] \\ &= -x_i(\bar{t}) < 0, \end{aligned}$$

which is contradictory to $\dot{x}_i(\bar{t}) > 0$. Thus, the proof of Lemma 2.2 is completed.

THEOREM 2.1. In competitive case ($a_{12} < 0$ and $a_{21} < 0$), if $a_i - a_{ii} > 0$ $(i = 1, 2)$, system (1.1) is permanent if and only if condition (C1) holds.

Proof. Sufficiency. Consider two continuous functionals

$$\begin{aligned} V_1(t) = \quad & x_1(t)^{a_2 - a_{22}} x_2(t)^{a_{12}} \exp\left[a_{12}\left(a_{21}\int_{t-\tau_{21}}^t x_1(s)ds + a_{22}\int_{t-\tau_{22}}^t x_2(s)ds\right)\right. \\ & \left. +(a_2 - a_{22})\left(a_{11}\int_{t-\tau_{11}}^t x_1(s)ds + a_{12}\int_{t-\tau_{12}}^t x_2(s)ds\right)\right], \end{aligned} \tag{2.1}$$

and

$$\begin{aligned} V_2(t) = \quad & x_1(t)^{a_{21}} x_2(t)^{a_1 - a_{11}} \exp\left[a_{21}\left(a_{11}\int_{t-\tau_{11}}^t x_1(s)ds + a_{12}\int_{t-\tau_{12}}^t x_2(s)ds\right)\right. \\ & \left. +(a_1 - a_{11})\left(a_{21}\int_{t-\tau_{21}}^t x_1(s)ds + a_{22}\int_{t-\tau_{22}}^t x_2(s)ds\right)\right]. \end{aligned} \tag{2.2}$$

Then, we have

$$\dot{V}_i(t) = V_i(t)(\Delta_i - \Delta x_i(t)),\ i = 1,\ 2, \tag{2.3}$$

where

$$\begin{aligned} &\Delta_1 = r_1(a_2 - a_{22}) + r_2 a_{12}, \\ &\Delta_2 = r_2(a_1 - a_{11}) + r_1 a_{21}, \\ &\Delta = (a_1 - a_{11})(a_2 - a_{22}) - a_{12}a_{21}. \end{aligned}$$

Note that $\Delta > 0$ by condition (C1) and hence $\Delta_1 > 0,\ \Delta_2 > 0$ by condition (1.3).

Let $h_i = \dfrac{\Delta_i}{2\Delta} = \dfrac{1}{2}x_i^*$; if $x_i(t) \le h_i$, then

$$\dot{V}_i(t) \ge \frac{1}{2}V_i(t)\Delta_i. \tag{2.4}$$

Then it follows from Lemma 2.2 that there exists some sufficiently large $t_0 > T$, such that for $t \ge t_0$.

$$0 < x_i(t) \le M,\ i = 1,\ 2.$$

Here M=max$\{M_1, M_2\}$. Then for $t \ge t_0 + \tau$, we have

$$\underline{m}_1 x_1(t)^{a_2-a_{22}} x_2(t)^{a_{12}} \le V_1(t) \le \overline{m}_1 x_1(t)^{a_2-a_{22}} x_2(t)^{a_{12}}, \tag{2.5}$$

$$\underline{m}_2 x_1(t)^{a_{21}} x_2(t)^{a_1-a_{11}} \le V_2(t) \le \overline{m}_2 x_1(t)^{a_{21}} x_2(t)^{a_1-a_{11}}, \tag{2.6}$$

where

$$\begin{aligned}
\underline{m}_1 &= \exp\left[(-|a_2 - a_{22}||a_{11}| + |a_2 - a_{22}|a_{12} - a_{12}a_{21} + a_{12}|a_{22}|)M\tau\right],\\
\overline{m}_1 &= \exp\left[(|a_2 - a_{22}||a_{11}| - |a_2 - a_{22}|a_{12} + a_{12}a_{21} - a_{12}|a_{22}|)M\tau\right],\\
\underline{m}_2 &= \exp\left[(a_{21}|a_{11}| - a_{21}a_{12} + |a_1 - a_{11}|a_{21} - |a_1 - a_{11}||a_{22}|)M\tau\right],\\
\overline{m}_2 &= \exp\left[(-a_{21}|a_{11}| + a_{21}a_{12} - |a_1 - a_{11}|a_{21} + |a_1 - a_{11}||a_{22}|)M\tau\right].
\end{aligned}$$

Then, the remaining parts are similar to [6]. Thus the proof of the sufficiency for the theorem is completed.

Proof. Necessity. Assume the assertion is false. That is, let system (1.1) be permanent but condition (C1) fails, implying that $\Delta < 0$ and furthermore that $\Delta_1 < 0$ and $\Delta_2 < 0$ by the existence of a unique positive equilibrium. Here

$$\begin{aligned}
\Delta_1 &= r_1(a_2 - a_{22}) + r_2 a_{12},\\
\Delta_2 &= r_2(a_1 - a_{11}) + r_1 a_{21},\\
\Delta &= (a_1 - a_{11})(a_2 - a_{22}) - a_{12}a_{21}.
\end{aligned}$$

By (2.3), we have

$$\dot{V}_1(t) = V_1(t)(\Delta_1 - \Delta x_1(t)). \tag{2.7}$$

Let

$$0 < \phi_i(t) < \min\{M_i/2,\ x_i^*/2\},\quad \forall t \in [-\tau,\ 0]. \tag{2.8}$$

Then by Lemma 2.2,

$$0 < x_i(t) \le M = \max\{M_1,\ M_2\},\quad \forall\ t \ge 0,\quad (i = 1, 2). \tag{2.9}$$

Furthermore, let

$$x_1(0) < (\underline{m}_1/\overline{m}_1)^{\frac{1}{a_2-a_{22}}} (M/x_2(0))^{\frac{a_{12}}{a_2-a_{22}}} (x_1^*/2). \tag{2.10}$$

Here

$$\begin{aligned}
\underline{m}_1 &= \exp\left[(-|a_2 - a_{22}||a_{11}| + |a_2 - a_{22}|a_{12} - a_{12}a_{21} + a_{12}|a_{22}|)M\tau\right],\\
\overline{m}_1 &= \exp\left[(|a_2 - a_{22}||a_{11}| - |a_2 - a_{22}|a_{12} + a_{12}a_{21} - a_{12}|a_{22}|)M\tau\right].
\end{aligned}$$

Then, we have

$$\underline{m}_1 x_1(t)^{a_2-a_{22}} x_2(t)^{a_{12}} \le V_1(t) \le \overline{m}_1 x_1(t)^{a_2-a_{22}} x_2(t)^{a_{12}}. \tag{2.11}$$

By (2.8), we have

$$\dot{V}_1(0) < \Delta V_1(0)\frac{x_1^*}{2} < 0. \tag{2.12}$$

Now, we show that $\dot{V}_1(t) < 0$, for $t \geq 0$. Otherwise, there exists t_1, such that $\dot{V}_1(t_1) = 0$, and $\dot{V}_1(t) < 0$, for $t \in [0, t_1)$. Thus, by (2.9), (2.11) and (2.12)

$$\underline{m}_1 x_1(t)^{a_2 - a_{22}} M^{a_{12}} \leq V_1(t) < V_1(0) \leq \overline{m}_1 x_1(0)^{a_2 - a_{22}} x_2(0)^{a_{12}}, \quad \forall t \in [0, t_1]. \tag{2.13}$$

Since $a_2 - a_{22} > 0$, then by (2.10), we have for $t \in [0, t_1]$,

$$\begin{aligned} x_1(t) &< (\overline{m}_1/\underline{m}_1)^{\frac{1}{a_2 - a_{22}}} \left(\tfrac{x_2(0)}{M}\right)^{\frac{a_{12}}{a_2 - a_{22}}} x_1(0) \\ &< (\overline{m}_1/\underline{m}_1)^{\frac{1}{a_2 - a_{22}}} \left(\tfrac{x_2(0)}{M}\right)^{\frac{a_{12}}{a_2 - a_{22}}} (\underline{m}_1/\overline{m}_1)^{\frac{1}{a_2 - a_{22}}} \left(\tfrac{M}{x_2(0)}\right)^{\frac{a_{12}}{a_2 - a_{22}}} \cdot \tfrac{x_1^*}{2} \\ &= \frac{x_1^*}{2}. \end{aligned} \tag{2.14}$$

Thus,

$$\dot{V}_1(t) < \Delta V_1(t) \frac{x_1^*}{2} < 0, \quad \text{for} \quad t \in [0, t_1]. \tag{2.15}$$

Especially, $\dot{V}_1(t_1) < 0$, which contradicts the assumption that $\dot{V}_1(t_1) = 0$.

So we have shown that for all $t \geq 0$, $\dot{V}_1(t) < 0$. Then for all $t \geq 0$, by using the same procedure as in (2.13) — (2.15), we obtain that

$$\dot{V}_1(t) < \Delta V_1(t) \frac{x_1^*}{2} < 0, \quad \text{for} \quad t \geq 0, \tag{2.16}$$

which implies

$$V_1(t) \to 0 \quad \text{as} \quad t \to +\infty, \tag{2.17}$$

contradicting to the permanence of (1.1).

The necessity for the theorem has been proved and hence the proof of Theorem 2.1 is completed.

The sufficient part is similar to Lu and Takeuchi [6] and Wang and Ma [14]. The necessary part is modified from Liu and Chen [4].

Note that the conditions for a competitive system to be permanent are independent of the delays.

In [8], Muroya proves the following boundedness result for cooperative system (1.1).

LEMMA 2.3 [8]. In cooperative case ($a_{12} > 0$ and $a_{21} > 0$), condition (C2) implies the upper boundedness of system (1.1).

In fact, we can obtain a stronger result as follows.

THEOREM 2.2. In cooperative case ($a_{12} > 0$ and $a_{21} > 0$), if $r_i > 0$ $(i = 1, 2)$, condition (C2) implies the permanence of system (1.1).

Proof. By Lemma 2.3, we know that there is a constant $M_i' > 0$ such that for sufficiently large t, any solution $x(t) = (x_1(t), x_2(t))$ to (1.1) satisfies $0 < x_i(t) \leq M_i'$.

In the following we show that each $x_i(t)$ is eventually bounded below by a positive constant.

From (1.1), we have

$$\dot{x}_i(t) \geq x_i(t)[r_i - a_i M_i' + a_{ii}^- M_i'], \quad (i = 1, 2).$$

By integrating it from $t - \tau_{ii}$ to t, we obtain

$$x_i(t) \geq x_i(t - \tau_{ii}) \exp[(r_i - a_i M_i' + a_{ii}^- M_i')\tau_{ii}], \quad (i = 1, 2);$$

thus

$$x_i(t-\tau_{ii}) \le x_i(t)\exp[-(r_i - a_iM_i' + a_{ii}^-M_i')\tau_{ii}], \quad (i=1,2).$$

Substituting it into (1.1), we have

$$\dot{x}_i(t) \ge x_i(t)[r_i - (a_i - a_{ii}^- \exp[-(r_i - a_iM_i' + a_{ii}^-M_i')\tau_{ii}])x_i(t)], \quad (i=1,2).$$

Denote $k_i = a_i - a_{ii}^- \exp[-(r_i - a_iM_i' + a_{ii}^-M_i')\tau_{ii}]$. Then $a_{ii}^- = \min\{a_{ii}, 0\} \le 0$ implies $k_i > 0$. Thus

$$\dot{x}_i(t) \ge x_i(t)[r_i - k_ix_i(t)], \quad (i=1,2).$$

Hence, we have

$$\liminf_{t\to+\infty} x_i(t) \ge \frac{r_i}{k_i} > 0, \quad (i=1,2).$$

The proof is completed.

Remark 2.1. Under the assumption of the existence of a unique positive equilibrium, the sufficient conditions for the permanence of system (1.1) in [8] are given as

$$\begin{cases} r_1 + \dfrac{a_{11}r_1}{a_1} + \dfrac{a_{12}r_2}{a_2} > 0 \\ r_2 + \dfrac{a_{21}r_1}{a_1} + \dfrac{a_{22}r_2}{a_2} > 0 \end{cases} \tag{2.18}$$

where $a_{ij} < 0\,(i \ne j)$, $a_i > 0$, $a_{ii} \le 0\,(i,j=1,2)$. It is not difficult to show that condition (2.18) is stronger than condition (C1). Moreover, the conditions for the permanence of system (1.1) provided in [9] are under the assumption of $a_i > 0\,(i=1,2)$, which seems unnecessary by Theorems 2.1 and 2.2.

Remark 2.2. Suppose that system (1.1) has a unique positive equilibrium. Condition (C1) implies the permanence for the system in the competitive case if $a_i - a_{ii} > 0\,(i,j=1,2)$. In fact, in the proof of theorem 2.1, it is positiveness of the equilibrium and condition (C1) that give the permanence. Furthermore, positiveness of the equilibrium can be ensured by condition (C1) and the following:

$$\textbf{Condition(E)}: \begin{cases} r_1(a_2 - a_{22}) + r_2a_{12} > 0, \\ r_2(a_1 - a_{11}) + r_1a_{21} > 0. \end{cases}$$

Thus, with the hypothesis of $a_i - a_{ii} > 0\,(i=1,2)$, conditions (C1) and (E) are sufficient for the permanence of system (1.1) in the competitive case. Conversely, the permanence of the system, which implies the existence of a unique positive equilibrium, guarantees that conditions (C1) and (E) hold. Therefore, without the assumption of the existence, we have

Theorem 2.3. In competitive case ($a_{12} < 0$ and $a_{21} < 0$), if $a_i - a_{ii} > 0$ ($i = 1,2$), system (1.1) is permanent if and only if conditions (C1) and (E) hold.

Since condition (C2) implies condition (C1), by a similar analysis we can obtain the following consequence for the cooperative system.

Theorem 2.4. In cooperative case ($a_{12} > 0$ and $a_{21} > 0$), if $r_i > 0$ ($i = 1, 2$), conditions (C2) and (E) imply the permanence of system (1.1).

Subsequently, we shall show by examples that condition (C1) can not ensure the permanence for cooperative systems.

Example 2.1.

$$\begin{aligned} \dot{x}_1(t) &= x_1(t)\left[1 - \frac{1}{2}x_1(t) - \frac{1}{2}e^3x_1(t-3) + ex_2(t-1)\right], \\ \dot{x}_2(t) &= x_2(t)\left[1 - \frac{1}{2}x_2(t) + ex_1(t-1) - \frac{1}{2}e^4x_2(t-4)\right]. \end{aligned} \tag{2.19}$$

Clearly, for system (2.19), condition (C1) is satisfied, but conditon (C2) fails. There is an unbounded solution $(x_1(t), x_2(t)) = (e^t, e^t)$ with initial condition $\phi_i(t) = e^t \ \ (i = 1,\ 2)$ for the system. In this case, both delayed intraspecific competitions are present. The following example shows that even if one of the species is delayed intraspecific cooperative, the system can also have an unbounded solution.

EXAMPLE 2.2.

$$\begin{aligned} \dot{x}_1(t) &= x_1(t)\left[1 - \frac{1}{2}x_1(t) - \frac{1}{2}e^7 x_1(t-7) + e x_2(t-1)\right], \\ \dot{x}_2(t) &= x_2(t)\left[1 - 5x_2(t) + \frac{9}{2}e x_1(t-1) + \frac{1}{2}e^2 x_2(t-2)\right]. \end{aligned} \tag{2.20}$$

Obviously, the unbounded solution given in Example 2.1 is also an unbounded one for system (2.20).

We have known that condition (C1) ensures the global attractivity of system (1.1) if the diagonal delays are small enough, which implies the permanence of the system. However, the permanence for system (1.1) may be destroyed with large diagonal delays even if condition (C1) is satisfied. Hence, we can deduce that the sharp permanence conditions for system (1.1) in the cooperative case must be associated with the diagonal delays.

3. Concluding Remarks.

We have shown that the conditions for the permanence of system (1.1) in competitive or prey-predator cases are similar to that for system (1.1) without delays. But in the cooperative case, the conditions should be stronger than that of other two cases.

In the prey-predator case, without the assumption of $a_i - a_{ii} > 0$, the positive equilibrium of system (1.1) may be globally attractive or unstable when $\tau_{ij} = 0 \ \ (i, j = 1, 2)$. It can be inferred that conditions for the permanence of system (1.1) are not easy to get in this case, and we leave this as a future research topic.

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