DYNAMICS OF A TWO-SPECIES STAGE-STRUCTURED
MODEL INCORPORATING STATE-DEPENDENT
MATURATION DELAYS

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Abstract. This paper is devoted to a cooperative model composed of two species with stage structure and state-dependent maturation delays. Firstly, positivity and boundedness of solutions are addressed to describe the population survival and the natural restriction of limited resources. It is shown that for a given pair of positive initial functions, the two mature populations are uniformly bounded away from zero and that the two mature populations are bounded above only if the coupling strength is small enough. Moreover, if the coupling strength is large enough then the two mature populations tend to infinity as the time tends to infinity. In particular, the positivity of the two immature populations has been established under some additional conditions. Secondly, the existence and patterns of equilibria are investigated by means of degree theory and Lyapunov-Schmidt reduction. Thirdly, the local stability of the equilibria is also discussed through a formal linearization. Fourthly, the global behavior of solutions is discussed and the explicit bounds for the eventual behaviors of the two mature populations and two immature populations are obtained. Finally, global asymptotical stability is investigated by using the comparison principle of the state-dependent delay equations.

1. Introduction. Time-delay in a natural ecosystem has been widely considered since Hutchison proposed a Logistic model with time-delay (see e.g. [22] [29] [30] [31]). Furthermore, most species go through two or more stages from birth to death, and species at two stages may have different behaviors. Thus stage structure is considered in population according to the natural phenomenon. Gurney, Blythe, and Nisbet [13] proposed a time delay growth model of blowflies. They verified solutions of the time delay model according with the data in blowflies growth experiments by Nicholson (see [20]). This implies that time delay and stage structure are necessary to be introduced into population research such that the model is more realistic.

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Since then, stage structure time delay population models of various types have been investigated by many researchers (see e.g., [7, 8, 14, 19, 20, 21, 28, 32, 33]).

Due to the influence of circumstances such as resources and interaction, however, the constant time delay is not reasonable any more (see [1, 4, 10, 12, 17, 18]). Aiello, Freedman, and Wu [3] have already considered a system with a state-dependent delay and two stages, motivated by their knowledge about whale and seal populations. They proposed the following state-dependent delay model

$$\begin{align*}
\dot{v}(t) &= \alpha u(t) - \gamma v(t) - \alpha e^{-\gamma \tau(v+u)} u(t - \tau(v+u)), \\
\dot{u}(t) &= \alpha e^{-\gamma \tau(v+u)} u(t - \tau(v+u)) - \beta u^2(t),
\end{align*}$$

(1)

where $v(t)$ and $u(t)$ represent the immature and mature populations densities, respectively; the parameters $\alpha$ and $\gamma$ represent the birth rate and death rate of immatures, respectively; $\beta$ represents the mature death and overcrowding rate. The state-dependent time delay $\tau(v+u)$ is taken to be an increasing differentiable function of the total population $(v + u)$ so that $\tau'(v+u) \geq 0$ and $\tau_m \leq \tau(v+u) \leq \tau_M$ with $\tau(0) = \tau_m$ and $\tau(+\infty) = \tau_M$. These assumptions imply that the maturation time for the species depends on the total number of them (matures plus immatures) around. The greater the number of individuals present, the longer they will take to mature. This assumption is known to be realistic in the case of Antarctic whale and seal populations [3]. Lowering the number of whales apparently causes the remaining whales to mature more quickly (presumably because there is more food for the remaining whales). Since both immature and mature whales need food, this is the motivation for having the maturation delay depending on the sum $v + u$ of the immature and mature populations. The term $\alpha e^{-\gamma \tau(v+u)} u(t - \tau(v+u))$ appearing in both equations of system (1) represents the density of individuals survive to leave the immature and just enter the mature class. Aiello, Freedman, and Wu [3] found that there always exists a positive equilibrium, and obtained criteria for uniqueness as well as local asymptotic stability. In particular, Aiello, Freedman, and Wu [3] obtained bounds for the eventual behavior of $u(t)$ and $v(t)$. Since then, more and more researchers have worked on state-dependent time delay population models; see, for example, [1, 4, 5, 19, 35]. Recently, Al-Omari and Gourley [4] derived and studied a stage-dependent population model with state-dependent time delay where the immature birth rate is taken to be a general function of the mature population and is commonly seen in social animals, including humans (see e.g., [11, 23, 24]). Lv and Yuan [24] investigated a system consisting of two cooperative mature species by assuming that each immature population density $v_i$ depends on the mature population density $u_i$ and that the time delay $\tau$ is just a function of $u_i$ not the sum $u_i + v_i$. Namely, Lv and Yuan [24] discussed the stability of the equilibria of the following system with a state-dependent delay

$$\begin{align*}
\frac{du_1}{dt} &= \alpha_1 e^{-\gamma_1 \tau(u_1)} u_1(t - \tau(u_1)) - \beta_1 u_1^2 + \mu_1 u_1 u_2, \\
\frac{du_2}{dt} &= \alpha_2 e^{-\gamma_2 \tau(u_2)} u_2(t - \tau(u_2)) - \beta_2 u_2^2 + \mu_2 u_1 u_2,
\end{align*}$$

(2)
where \( u_1 \) and \( u_2 \) represent the densities of the two cooperative mature species, \( \mu_1 \) and \( \mu_2 \) are positive interspecific cooperative effects of the classical Lotka-Volterra kind. Similarly to [3] and [4], Lv and Yuan [24] analyzed the positivity and boundedness of solutions of (2). Moreover, by using the comparison principle, Lv and Yuan [24] obtained a stability criterion both from local and global points of view.

Motivated by Aiello, Freedman, and Wu [3], Lv and Yuan [24], in this paper we shall investigate the following system of two cooperative species with a delay depending on the total populations

\[
\begin{aligned}
\frac{du_1}{dt} &= \alpha u_1 - \gamma v_1 - \alpha e^{-\gamma \tau(z_1)} u_1(t - \tau(z_1)), \\
\frac{du_2}{dt} &= \alpha e^{-\gamma \tau(z_1)} u_1(t - \tau(z_1)) - \beta u_1^2 + \mu u_1 u_2, \\
\frac{dv_1}{dt} &= \alpha u_2 - \gamma v_2 - \alpha e^{-\gamma \tau(z_2)} u_2(t - \tau(z_2)), \\
\frac{dv_2}{dt} &= \alpha e^{-\gamma \tau(z_2)} u_2(t - \tau(z_2)) - \beta u_2^2 + \mu u_1 u_2,
\end{aligned}
\]

(3)

where \( z_i = u_i + v_i \), \( v_i \) and \( u_i \) \((i = 1, 2)\) are the densities of the cooperative immature and mature species at time \( t \), respectively; \( \alpha \) is the birth rate; \( \gamma \) is the death rate of the immature and \( \beta \) is the mature death and overcrowding rate, as in the logistic equation; \( \mu \) is the interspecific cooperative effect of the classical Lotka-Volterra kind.

Throughout this paper, we always assume that \( \alpha, \beta, \gamma, \mu \) are all positive constants. Similarly to [3], the state-dependent time delay \( \tau(z_i) \) is taken to be an increasing differentiable function of the total population \( z_i = u_i + v_i \) so that \( \tau'(z_i) \geq 0 \), \( \tau''(z_i) \leq 0 \), and \( \tau_m \leq \tau(z_i) \leq \tau_M \) with \( \tau(0) = \tau_m \) and \( \tau(\pm \infty) = \tau_M \), \( i = 1, 2 \). The initial condition for (3) is

\[
\begin{aligned}
&u_i(s) = \varphi_i(s) \geq 0 \quad \text{for all } s \in [-\tau_M, 0], \quad i = 1, 2, \\
v_i(0) = \psi_i(0) \geq 0, \quad i = 1, 2,
\end{aligned}
\]

with

\[
\psi_i(0) = \int_{-\tau_i}^{0} \alpha \varphi_i(s) e^{\gamma s} ds, \quad i = 1, 2,
\]

which is the number of immatures that have survived to time \( t = 0 \). Here, \( \tau_i \) is the maturation time of the \( i \)-th species at \( t = 0 \), and the lower limit on the integral is \( -\tau_i \) because anyone of the \( i \)-th species born before that time will have matured before time \( t = 0 \). Since \( \tau_i \) is the maturation time at \( t = 0 \), \( \tau_i \) is given by \( \tau_i = \tau(u_i(0) + v_i(0)) \), i.e.,

\[
\tau_i = \tau \left( \varphi_i(0) + \int_{-\tau_i}^{0} \alpha \varphi_i(s) e^{\gamma s} ds \right), \quad i = 1, 2.
\]

Note that \( \tau_i \) \((i = 1, 2)\) appear on both the left- and right-hand sides of the above equation, so that \( \tau_i \) \((i = 1, 2)\) are determined implicitly.

For our model to make sense, i.e., to exclude the possibility of adults becoming immatures except by birth, we need to find conditions ensuring that for each \( i = 1, 2 \), \( t - \tau(z_i(t)) \) is an increasing function of \( t \) as \( t \) increases. Namely, we need \( \tau'(u_i + v_i)(\dot{v}_i + \dot{u}_i) < 1, \ i = 1, 2 \), which is equivalent to

\[
\tau'(u_i + v_i)(\alpha u_i - \gamma v_i - \beta u_1^2 + \mu u_1 u_2) < 1, \quad i = 1, 2.
\]

In section 2, we will consider the positivity and boundedness of solutions to (3) and shall find that if \( \beta > \mu \) then \( 0 \leq u_i \leq u_+ := \alpha e^{-\gamma \tau_M}/(\beta - \mu) \) and \( v_i \geq 0 \) for all
Let $t$ be a positive constant, then there exist some $i = 1, 2$. In this case, we have
\[ \alpha u_i - \gamma v_i - \beta u_i^2 + \mu v u_2 \leq (\alpha + \mu u_1) u_i(t) - \beta u_i^2(t) \leq \frac{(\alpha + \mu u_1)^2}{4\beta}. \]

Therefore, if $\beta > \mu$ and $\beta^*(z_i) < 4\beta/(\alpha + \mu u_1)^2$, then $t - \beta^*(z_i(t))$ is strictly increasing.

Compared with [3] and [24], our theoretical results are more accurate and our method is completely different. In particular, we shall employ degree theory and Lyapunov-Schmidt reduction to investigate the existence and patterns of equilibria. Moreover, we find out the relationship among uniqueness, local asymptotical stability and global asymptotical stability of equilibria. Two auxiliary systems and comparison principles are introduced to prove the global asymptotical stability of the synchronous equilibrium point. By replacing certain variables of $u$ with parameters, we obtain the monotonicity and attractiveness of solutions for the auxiliary systems.

This paper is organized as follows: in section 2, the positivity and boundedness of all solutions of system (3) are obtained. In section 3, we first investigate the existence of synchronous equilibria by means of degree theory. Then we employ Lyapunov-Schmidt reduction to discuss the existence of asynchronous equilibria. Section 4 is devoted to the stability of equilibria, especially the synchronous ones. In section 5, we examine the global behavior of solutions and in section 6 we investigate the global asymptotical stability by introducing two auxiliary systems and using the comparison principle of the state-dependent delay equations. Moreover, we illustrate our results with some numerical simulations. Finally, some conclusions and discussions are made in Section 7.

2. Positivity and boundedness. Since the solutions of system (3) represent populations and we also anticipate that limited resources will place a natural restriction to how many individuals can survive, we need address positivity and boundedness of the solution of the system.

**Theorem 2.1.** If $\varphi_1(t) > 0$ and $\varphi_2(t) > 0$ for $-\tau_M \leq t \leq 0$, then $u_1(t) > 0$ and $u_2(t) > 0$ for all $t > 0$.

**Proof.** Suppose that $u_i(t) = 0$ for some value of $t$ and $i \in \{1, 2\}$. Since $u_i(t) = \varphi_i(t) > 0$ for $-\tau_M \leq t \leq 0$, if such a value of $t$ exists, it is positive. Let $t^* = \inf\{t > 0| u_i(t) = 0\}$. Note that $\tau(z_i) > 0$ and $t^* - \tau(z_i(t^*)) < t^*$, then it follows from the definition of $t^*$ that $u_i(t^* - \tau(z_i(t^*))) > 0$. Then from system (3) we have $\dot{u}_i(t^*) = \alpha e^{-\gamma}\tau(z_i(t^*))u_i(t^* - \tau(z_i(t^*))) > 0$, giving a contradiction. Therefore no such $t^*$ exists.

**Theorem 2.2.** If $\varphi_1(t) > 0$ and $\varphi_2(t) > 0$ for $-\tau_M \leq t \leq 0$, then there exists a positive constant $\delta$ depending on $(\varphi_1, \varphi_2)$ such that $u_1(t) > \delta$ and $u_2(t) > \delta$ for all $t \geq 0$.

**Proof.** Let
\[ \delta = \frac{1}{2} \min \left\{ \inf_{-\tau_M \leq t \leq 0} \varphi_1(t), \inf_{-\tau_M \leq t \leq 0} \varphi_2(t), \alpha \beta^{-1} e^{-\gamma \tau_M} \right\}. \]

Assume that there exist some $i \in \{1, 2\}$ such that $u_i(t^*) = \delta$, where $t^* = \inf\{t \geq 0| u_i(t) = \delta\}$. It follows from $u_i(0) = \varphi_i(0) \geq 2\delta$ and the continuity of
the two mature populations $u_i(t)$ that $t^* > 0$. Then
\[
\dot{u}_i(t^*) = \alpha e^{-\gamma \tau(z_i(t^*))} u_i(t^* - \tau(z_i(t^*))) - \beta u_i^2(t^*) + \mu u_1(t^*) u_2(t^*) \\
\geq \alpha e^{-\gamma \tau(z_i(t^*))} \delta - \beta \delta^2 \\
\geq \alpha e^{-\gamma \tau(z_i(t^*))} \delta - \frac{1}{2} \alpha e^{-\gamma \tau(z_i(t^*))} \delta \\
= \frac{1}{2} \alpha e^{-\gamma \tau(z_i(t^*))} \delta > 0,
\]
which contradicts the definition of $t^*$. Thus we complete the proof of this theorem.

Theorem 2.2 implies that for a given pair of positive initial functions $\varphi_1$ and $\varphi_2$, the two mature populations $u_1(t)$ and $u_2(t)$ are uniformly bounded away from zero. Now, we shall show that the two mature populations $u_1(t)$ and $u_2(t)$ are bounded when $\beta > \mu$.

**Theorem 2.3.** Assume that $\beta > \mu$, if $\varphi_1(t) > 0$ and $\varphi_2(t) > 0$ for $-\tau_M \leq t \leq 0$, then there exists $\Theta > 0$ depending on $(\varphi_1, \varphi_2)$ such that $u_1(t) \leq \Theta$ and $u_2(t) \leq \Theta$ for all $t \geq 0$.

**Proof.** Our proof is split into three cases. We start with the first case where both $u_1(t)$ and $u_2(t)$ are eventually monotonic. If both $u_1(t)$ and $u_2(t)$ are eventually decreasing then the conclusion of this theorem is obvious. Suppose that both $u_1(t)$ and $u_2(t)$ are eventually increasing, i.e., $\dot{u}_i(t) \geq 0$ for all $t > T$ for some $T \geq 0$. Then for $t > T + \tau_M$,
\[
0 \leq \dot{u}_i(t) \leq \alpha e^{-\gamma \tau_m} u_i(t) - \beta u_i^2(t) + \mu u_1(t) u_2(t).
\]
This means that $\beta u_1 - \mu u_2 \leq \alpha e^{-\gamma \tau_m}$ and $\beta u_2 - \mu u_1 \leq \alpha e^{-\gamma \tau_m}$ for all $t > T$. Thus, it follows from $\beta > \mu$, $u_1(t) > 0$, and $u_2(t) > 0$ that
\[
u_i(t) \leq u_+ \triangleq \alpha(\beta - \mu)^{-1} e^{-\gamma \tau_m}
\]
for all $t > T$ and $i \in \{1, 2\}$, giving us the desired result.

Next, we assume that both $u_1(t)$ and $u_2(t)$ are oscillatory. Suppose that there exist two sequences $\{t_n\}_{n=1}^\infty$ and $\{s_m\}_{m=1}^\infty$ such that $u_1(t_n) = u_2(s_m) = 0$, $u_1(t_n)$ and $u_2(s_m)$ are local maxima of $u_1$ and $u_2$, respectively, and that $u_1(t) \leq u_1(t_n)$ for all $0 < t < t_n$, and $u_2(t) \leq u_2(s_m)$ for all $0 < t < s_m$, $m, n \in \mathbb{N}$. Using a similar analysis at $t = t_n$ and $t = s_m$, we have
\[
\beta u_1(t_n) - \mu u_2(t_n) \leq \alpha e^{-\gamma \tau_m}, \quad \beta u_2(s_m) - \mu u_1(s_m) \leq \alpha e^{-\gamma \tau_m}. \quad (4)
\]
For any given $t_n$, we take $s_n = \max\{s_m | s_m \leq t_n\}$.

If $s_n = t_n$, then using similar arguments as the first case, we see that $u_1(t) \leq u_+$ and $u_2(t) \leq u_+$ for all $t < t_n$.

If $s_n < t_n$ and $u_2(s_n) \leq u_2(t_n)$, then $\dot{u}_2(t_n) > 0$ and $u_2(t) \leq u_2(t_n)$ for all $t \leq t_n$. Otherwise, there is $t \in (s_n, t_n)$ such that $u_2(t) = 0$, which contradicts the definition of $s_n$. Thus, we have
\[
0 < \dot{u}_2(t_n) \leq \alpha e^{-\gamma \tau_m} u_2(t_n) - \beta u_2^2(t_n) + \mu u_1(t_n) u_2(t_n),
\]
which means that $\beta u_2(t_n) - \mu u_1(t_n) \leq \alpha e^{-\gamma \tau_m}$. This, together with the first inequality of (4) and a similar argument as the first case, implies that both $u_1(t)$ and $u_2(t)$ are bounded above.
If \( s_n < t_n \) and \( u_2(t_n) \leq u_2(s_n) \), then from the first inequality of (4) it follows that
\[
\beta u_1(s_n) - \mu u_2(s_n) \leq \beta u_1(t_n) - \mu u_2(t_n) \leq \alpha e^{-\gamma t_m}.
\]
Combining this with the second inequality of (4), we see that both \( u_1(t) \) and \( u_2(t) \) are bounded above.

Finally, we consider the case where one of \( u_1(t) \) and \( u_2(t) \) is oscillatory and the other is eventually monotonic. Without loss of generality, assume that \( u_1 \) is oscillatory and \( u_2 \) is eventually increasing because the other cases can be dealt with analogously. Thus, there exists a sequence \( \{t_n\}_{n=1}^{\infty} \) such that \( \dot{u}_1(t_n) = 0 \), \( u_1(t_n) \) are local maxima of \( u_1 \) and that \( u_1(t) \leq u_1(t_n) \) for all \( 0 < t < t_n, \ n \in \mathbb{N} \). It follows that \( \beta u_1(t_n) - \mu u_2(t_n) \leq \alpha e^{-\gamma t_m} \). For the same sequence \( \{t_n\} \) introduced above, it follows from the eventual monotonicity of \( u_2 \) that there exists \( N > 0 \) such that \( u_2(t_n) \geq 0 \) for all \( n > N \), and hence that \( \beta u_2(t_n) - \mu u_1(t_n) \leq \alpha e^{-\gamma t_m} \) for all \( n > N \). Hence, we immediately conclude that both \( u_1(t) \) and \( u_2(t) \) are bounded above. Choosing \( \Theta = \max\{\sup_{-\tau M \leq t \leq 0} \varphi_1(t), \sup_{-\tau M \leq t \leq 0} \varphi_2(t), u_+\} \), we complete the proof of the theorem. \( \square \)

Theorem 2.3 implies that the two mature populations \( u_1 \) and \( u_2 \) are bounded above when the coupling strength \( \mu \) is small (i.e., \( \beta > \mu \)). The following theorem states that \( u_1 \) and \( u_2 \) are unbounded when the coupling strength \( \mu \) is large enough (i.e., \( \beta < \mu \)).

**Theorem 2.4.** Assume that \( \beta < \mu \), if \( \varphi_1(t) > 0 \) and \( \varphi_2(t) > 0 \) for \( -\tau M \leq t \leq 0 \), then the two mature populations \( u_1(t) \) and \( u_2(t) \) satisfy \( u_1(t) \to +\infty \) and \( u_2(t) \to +\infty \) as \( t \to +\infty \).

**Proof.** It follows from (4) that \( u_1(t) \geq x(t) \) and \( u_2(t) \geq y(t) \) for all \( t > 0 \), where \((x(t), y(t))\) is a solution to the following system
\[
\begin{align*}
\dot{x} &= x(\mu y - \beta x), \\
\dot{y} &= y(\mu x - \beta y), \\
x(0) &= \varphi_1(0) > 0, \quad y(0) = \varphi_2(0) > 0.
\end{align*}
\]
It is easy to see that \( x(t) > 0 \) and \( y(t) > 0 \) for all \( t > 0 \). Note that
\[
\frac{d(x - y)^2}{dt} = -2\beta(x + y)(x - y)^2 < 0.
\]
Then every solution of (5) with initial values is asymptotically synchronous, i.e., \( \lim_{t \to \infty} [x(t) - y(t)]^2 = 0 \). In other words, every solution of (5) with initial values \( x(0) > 0 \) and \( y(0) > 0 \) tends to some solution \( u(t) \) of the following equation
\[
\dot{u} = (\mu - \beta)u^2.
\]
Obviously, \( u(t) \to +\infty \) as \( t \to +\infty \), which implies that \( x(t) \to +\infty \) and \( y(t) \to +\infty \) as \( t \to +\infty \), and hence that \( u_1(t) \to +\infty \) and \( u_2(t) \to +\infty \) as \( t \to +\infty \). \( \square \)

We shall now prove that \( v_1(t) \) and \( v_2(t) \) are bounded above by a number that depends on the initial conditions when \( \beta > \mu \).

**Theorem 2.5.** Assume that \( \beta > \mu \), if \( \varphi_1(t) > 0 \) and \( \varphi_2(t) > 0 \) for \( -\tau M \leq t \leq 0 \), then there exists a positive constant \( V \) depending on \((\varphi_1, \varphi_2)\) such that \( v_1(t) < V \) and \( v_2(t) < V \) for all \( t \geq 0 \).
Theorem 2.6. Suppose that lower bound $\delta$ theorem, proving positivity of $v$ to establish the positivity of $\beta > \mu$ all bounded above when $v$ the equation for $v$. Then integrating the equation for $v(t)$ of system we get

$$v(t) = e^{-\gamma t}v(0) + \alpha e^{-\gamma t} \int_0^t e^{\gamma s} u_i(s)ds - \alpha e^{-\gamma t} \int_0^t e^{\gamma s} e^{-\gamma \tau(z_i(s))} u_i(s - \tau(z_i(s)))ds$$

$$< e^{-\gamma t}v(0) + \alpha e^{-\gamma t} \int_0^t e^{\gamma s} u_i(s)ds$$

$$\leq e^{-\gamma t}v(0) + \alpha e^{-\gamma t} \int_0^t \Theta e^{\gamma s}ds$$

$$= e^{-\gamma t}v(0) + \alpha e^{-\gamma t} \int_0^t \Theta e^{\gamma s}ds$$

$$< v(0) + \alpha e^{-\gamma t} \Theta < \mathcal{V}, \quad i = 1, 2.$$ 

This completes the proof. 

Proof. First, let $\mathcal{V} = v_1(0) + v_2(0) + \alpha \gamma^{-1} \Theta$. Since $v_i(0) = \int_{-\tau_i}^{t_0} \alpha \varphi_i(s)e^{\gamma s}ds$ for $i = 1, 2$, $\mathcal{V}$ is indeed a functional depending only on $\varphi_1$ and $\varphi_2$. Then integrating the equation for $v_i(t)$ of system we get

$$v_i(t) = e^{-\gamma t}v_i(0) + \alpha e^{-\gamma t} \int_0^t e^{\gamma s} u_i(s)ds - \alpha e^{-\gamma t} \int_0^t e^{\gamma s} e^{-\gamma \tau(z_i(s))} u_i(s - \tau(z_i(s)))ds$$

$$< e^{-\gamma t}v_i(0) + \alpha e^{-\gamma t} \int_0^t e^{\gamma s} u_i(s)ds$$

$$\leq e^{-\gamma t}v_i(0) + \alpha e^{-\gamma t} \int_0^t \Theta e^{\gamma s}ds$$

$$= e^{-\gamma t}v_i(0) + \alpha e^{-\gamma t} \int_0^t \Theta e^{\gamma s}ds$$

$$< v_i(0) + \alpha e^{-\gamma t} \Theta < \mathcal{V}, \quad i = 1, 2.$$ 

We have proved that $u_1$ and $u_2$ remain positive and that $u_1$, $v_1$, $u_2$, and $v_2$ are all bounded above when $\beta > \mu$. This leaves the question of whether it is possible to establish the positivity of $v_1$ and $v_2$. As we shall see in the proof of the following theorem, proving positivity of $v_1$ and $v_2$ depends on our having a strictly positive lower bound $\delta$ and an upper bound $\Theta$ for $u_1$ and $u_2$.

Theorem 2.6. Suppose that $\beta > \mu$ and $\tau'(z_i) < 4\beta/(\alpha + \mu u_+)^2$, $i = 1, 2$ and that $\tau'(z_i) > 0$ ($i = 1, 2$) are small enough so that

$$\delta \int_{t-\tau_m}^t e^{\gamma s} ds > \Theta \int_{-\tau_i}^{t-\tau_m} \frac{(\alpha + \mu u_+)^2 \tau'(z_i)}{4\beta - (\alpha + \mu u_+)^2 \tau'(z_i)} e^{\gamma s} ds, \quad i = 1, 2$$

for all values of $t$. Then $v_1(t) > 0$ and $v_2(t) > 0$ for all $t \geq 0$.

Proof. Assume that $v_i(t) = 0$ for some value of $t$ and $i$. Define $t_i^* = \inf\{t > 0|v_i(t) = 0\}$. Since $v_i(0) > 0$, then $t_i^* > 0$ by continuity. Then integrating the first equation of system we get

$$v_i(t_i^*) = e^{-\gamma t_i^*}v_i(0) + \alpha e^{-\gamma t_i^*} \int_0^{t_i^*} e^{\gamma s} u_i(s)ds$$

$$- \alpha e^{-\gamma t_i^*} \int_0^{t_i^*} e^{\gamma s} e^{-\gamma \tau(z_i(s))} u_i(s - \tau(z_i(s)))ds.$$ 

Since $v_i(t_i^*) = 0$ and $v_i(0) = \int_{-\tau_i}^{0} \alpha \varphi_i(s)e^{\gamma s}ds$, the above expression is equivalent to

$$\int_{-\tau_i}^{t_i^*} e^{\gamma s} u_i(s)ds = \int_0^{t_i^*} e^{-\gamma \tau(z_i(s))} u_i(s - \tau(z_i(s)))ds. \quad (7)$$

Substituting $r = s - \tau(z(s))$ into and then changing $r$ for $s$, noting that $1 - \tau'(z_i)\dot{z}_i(s) > 0$ since $t - \tau(z(t))$ is an increasing function of $t$, we get

$$\int_{-\tau_i}^{t_i^*} e^{\gamma s} u_i(s)ds = \int_0^{t_i^*-\tau(z_i(t_i^*)))} e^{\gamma s} u_i(s)ds \leq \int_0^{t_i^*-\tau_m} e^{\gamma s} u_i(s)ds \int_0^{t_i^*-\tau_m} e^{\gamma s} u_i(s)ds.$$
Remark 1. To prove that the state-dependent time delay is essential, we need to show that there are additional restrictions either on the initial conditions or on the delay \( v \) of Theorem 2.6, both of them are only sufficient conditions ensuring the positivity of the state-dependent time delay. The following is a corollary of Theorem 2.6.

Corollary 1. Suppose that \( f \) satisfies the hypothesis of this theorem, so no such \( t^*_i \) exists and hence \( v_i(t) > 0 \) for all \( t > 0 \). This proves the theorem.

Finally, combining with those above inequalities, we have

\[
\delta \int_{t_i^* - \tau_m}^{t_i^*} e^{\gamma s} ds \leq \Theta \int_{-\tau_i}^{t_i^* - \tau_m} \frac{\tau'(z_i(s))}{1 - \tau'(z_i(s))} e^{\gamma s} ds.
\]

This contradicts the hypothesis of this theorem, so no such \( t^*_i \) exists and hence \( v_i(t) > 0 \) for all \( t > 0 \). This proves the theorem.

**Remark 1.** To prove \( v_i(t) > 0 \) for all \( t \) and \( i \), it seems impossible without placing additional restrictions either on the initial conditions or on the delay \( \tau(z_i) \). For example, if \( \tau'(z_i) \equiv 0 \), it has been shown in [2] that \( v_i(t) \) is positive for all \( t \). In Theorem 2.6, we give a set of initial conditions on \( \tau(z_i) \), while maintaining the essential character of the state-dependent time delay. The following is a corollary of Theorem 2.6, both of them are only sufficient conditions ensuring the positivity of \( v_i(t) \).

**Corollary 1.** Suppose that \( \beta > \mu \) and \( e^{\gamma \tau_m} \leq 1/\Theta \), then \( v_1(t) > 0 \) and \( v_2(t) > 0 \) for all \( t > 0 \).

**Proof.** From the proof of Theorem 2.2 we know that (7) holds for such \( t_i^* < \infty \). The left-hand side of (7) satisfies

\[
\int_{-\tau_i}^{t_i^*} e^{\gamma s} u_i(s) ds \geq \delta^{-1} \left( e^{\gamma t_i^*} - e^{-\gamma \tau_i} \right) \triangleq f_1(t_i^*)
\]

by Theorem 2.3 and integration. Similarly, the right-hand side satisfies

\[
\int_0^{t_i^*} e^{-\gamma \tau(z_i(s))} u_i(s - \tau(z_i(s))) ds \leq \Theta^{-1} e^{-\gamma \tau_m} \left( e^{\gamma t_i^*} - 1 \right) \triangleq f_2(t_i^*).
\]

It follows that \( f_1(t^*) \leq f_2(t^*) \). On the other hand, \( f_1'(t) = \delta e^{\gamma t} \) and \( f_2'(t) = \Theta e^{-\gamma \tau_m} e^{\gamma t} \), then we have \( f_2'(t) \leq f_1'(t) \) for all \( t \) since \( e^{-\gamma \tau_m} \leq 1/\Theta \). Thus, \( f_2(t) \leq f_1(t) \) for all \( t \).
where $Z_{\beta > \mu}$.

Theorem 3.2. System (3) has exactly one nontrivial synchronous equilibrium if

Thus, we have the following result.

3. Existence and patterns of equilibria. The purpose of this section is to investigate the existence and patterns of equilibria $(v_1, u_1, v_2, u_2)$ of system (3), which satisfy

$$
\begin{align*}
\alpha u_1 - \gamma v_1 - \alpha e^{-\gamma(u_1+v_1)}u_1 &= 0, \\
\alpha e^{-\gamma(u_1+v_1)}u_1 - \beta u_1^2 + \mu u_1 u_2 &= 0, \\
\alpha u_2 - \gamma v_2 - \alpha e^{-\gamma(u_2+v_2)}u_2 &= 0, \\
\alpha e^{-\gamma(u_2+v_2)}u_2 - \beta u_2^2 + \mu u_1 u_2 &= 0.
\end{align*}
$$

(8)

It follows from the first and third equations of (8) that

$$
v_1 = g(u_1, u_2), \quad v_2 = g(u_2, u_1),
$$

where $g: \mathbb{R}^2 \to \mathbb{R}$ is defined as

$$
g(x, y) = \frac{1}{\gamma} (\alpha x - \beta x^2 + \mu xy)
$$

for all $x, y \in \mathbb{R}$. Thus, system (8) can be reduced to

$$
\begin{align*}
\alpha e^{-\gamma(u_1+g(u_1,u_2))} - \beta u_1 + \mu u_2 &= 0, \\
\alpha e^{-\gamma(u_2+g(u_2,u_1))} - \beta u_2 + \mu u_1 &= 0,
\end{align*}
$$

(9)

which is obviously $\mathbb{Z}_2$-equivariant. This implies that if $(v_1, u_1, v_2, u_2)$ is an equilibrium of system (3), then so is $(v_2, u_2, v_1, u_1)$. It is clear that system (3) has an equilibrium $E_0(0,0,0,0)$. If system (3) has a positive equilibrium $(v_1, u_1, v_2, u_2)$, i.e., $u_1, u_2, v_1, v_2 > 0$, then it follows from (9) that

$$
\beta u_1 > \mu u_2 \geq 0, \quad \beta u_2 > \mu u_1 \geq 0,
$$

and hence that $\beta^2 u_1 u_2 > \mu^2 u_1 u_2$, i.e., $\beta > \mu$. Thus, we obtain the following result.

**Theorem 3.1.** System (3) has no positive equilibria if $\beta \leq \mu$.

In what follows, we shall investigate the existence, pattern, and multiplicity of equilibria of system (3) with $\beta > \mu$. The first of our interest is the existence and multiplicity of synchronous equilibria of the form $(v, u, v, u)$, where $v = g(u, u)$ and $u$ satisfies $\alpha e^{-\gamma (u+g(u,u))} - (\beta - \mu) u = 0$. Let $\Omega = \{ u \in \mathbb{R} | 0 < u < \alpha (\beta - \mu)^{-1} (1 + e^{-\gamma M}) \} \subset \mathbb{R}$ and $f: \overline{\Omega} \to \mathbb{R}$ be a continuous mapping defined as

$$
f(u) = \alpha e^{-\gamma (u+g(u,u))} - (\beta - \mu) u, \quad u \in \overline{\Omega}.
$$

(10)

Note that

$$
\begin{align*}
f'(u) &= -\alpha e^{-\gamma (u+g(u,u))} \tau'(u+g(u,u)) [\gamma + \alpha - 2(\beta - \mu) u] - (\beta - \mu), \\
f''(u) &= -\alpha e^{-\gamma (u+g(u,u))} [\tau'(u+g(u,u))]^2 [\gamma + \alpha - 2(\beta - \mu) u]^2 \\
&\quad - \alpha \gamma^{-1} e^{-\gamma (u+g(u,u))} \tau''(u+g(u,u)) [\gamma + \alpha - 2(\beta - \mu) u]^2 \\
&\quad + 2(\beta - \mu) \alpha e^{-\gamma (u+g(u,u))} \tau'(u+g(u,u)) > 0
\end{align*}
$$

for all $u \in \overline{\Omega}$. This implies that the graph of the curve $y = f(u)$ is concave upwards. Thus, we have the following result.

**Theorem 3.2.** System (3) has exactly one nontrivial synchronous equilibrium if and only if $\beta > \mu$. 


Proof. If \( \beta \leq \mu \) then \( ae^{-\gamma t(u+g(u,u))} - (\beta - \mu)u > 0 \) for all \( u > 0 \). This means that system (3) has no nontrivial synchronous equilibria. In what follows, we show that system (3) has at least one nontrivial synchronous equilibrium if \( \beta > \mu \). We first seek for a simpler \( G: \Omega \rightarrow \mathbb{R} \) such that the integer \( \text{deg}(f, \Omega) \) can be calculated by \( \text{deg}(G, \Omega) \). For this purpose, we have to define a continuous mapping \( H: [0,1] \times \Omega \rightarrow \mathbb{R} \) such that \( H(1,u) = f(u), H(0,u) = G(u) \), and \( H(t, u) \neq 0 \) for all \( (t, u) \in [0,1] \times \partial \Omega \). This kind of \( H \) is called \( \Omega \)-admissible homotopy. Then by homotopy invariance, we can reach our expectancy. Define \( H: [0,1] \times \Omega \rightarrow \mathbb{R} \) as

\[
H(t, u) = ae^{-\gamma t(u+g(u,u))} - (\beta - \mu)u
\]

for all \((t, u) \in [0,1] \times \Omega\). Thus, we have \( G(u) = \alpha - (\beta - \mu)u \). For \( u \in \partial \Omega \), we have either \( u = 0 \) or \( u = \alpha(\beta - \mu)^{-1}(1 + e^{-\gamma t M}) \). Note that

\[
H(t, 0) = ae^{-\gamma t(0)} > 0, \quad H(t, \alpha(\beta - \mu)^{-1}(1 + e^{-\gamma t M})) \leq \alpha - \alpha(1 + e^{-\gamma t M}) < 0.
\]

It turns out that \( H(t, u) \) is a \( \Omega \)-admissible homotopy. Thus, by homotopy invariance, \( \text{deg}(f, \Omega) = \text{deg}(H(1, \cdot), \Omega) = \text{deg}(H(0, \cdot), \Omega) = \text{deg}(G, \Omega) \). Note that

\[
\text{deg}(G, \Omega) = \text{sign}(\mu - \beta) = -1.
\]

This implies that \( f \) has at least one zero point in \( \Omega \), and hence that system (3) has at least one synchronous equilibrium \((v^*, u^*, v^*, u^*)\) with \((u^*, v^*)\) satisfying \( v^* = g(u^*, v^*) \) and \( f(u^*) = 0 \).

Finally, it follows from \( f''(u) > 0 \) for all \( u \in \Omega \) that \( f \) has exactly one or two different zeros in \( \Omega \) if \( \beta > \mu \). In fact, if \( f \) has exactly two different zeros in \( \Omega \), then \( \text{deg}(f, \Omega) = 0 \), which contradicts \( \text{deg}(f, \Omega) = -1 \). Therefore, \( f \) has exactly one zero in \( \Omega \) when \( \beta > \mu \). Namely, if \( \beta > \mu \) then system (3) has exactly one nontrivial synchronous equilibrium.

Theorem 3.2 implies that system (3) has a unique nontrivial synchronous equilibrium \((v^*, u^*, v^*, u^*)\). Note that \( f(u^*) = 0 \) and \( u^* < \alpha/(\beta - \mu) \), then we have \( f''(u^*) = (\mu - \beta) \{u^* \cdot \tau'(z^*) [\gamma + \alpha - (\beta - \mu)u^*] + 1 \} \), where \( z^* = u^* + g(u^*, u^*) \). It follows from the proof of Theorem 3.2 that \( f''(u^*) < 0 \) and hence that

\[
u^* \cdot \tau'(z^*) [2(\beta - \mu)u^* - (\gamma + \alpha)] < 1. \tag{11}\]

Remark 2. Following Theorem 4.1 of Aiello, Freedman, and Wu [3], we need one of the following assumptions to ensure that system (3) with \( \beta > \mu \) has exactly one synchronous equilibrium \((v^*, u^*, v^*, u^*)\) since \( \alpha > (\beta - \mu)u^* \):

(i): \( \gamma > \alpha \);
(ii): \( u^* < \frac{\alpha + \gamma}{2(\beta - \mu)} \);
(iii): \( \tau'(u^* + g(u^*, u^*)) < \frac{1}{u^* - (\beta - \mu)u^* - (\gamma + \alpha)} \) and \( u^* > \frac{\alpha + \gamma}{2(\beta - \mu)} \).

In view of Theorem 3.2 we see that neither of the above three assumptions is necessary.

Next, we consider the existence of boundary equilibria. For an equilibrium \((v_1, u_1, v_2, u_2)\) of system (3), if \( u_1 = 0 \) then \( v_1 = 0 \). This means that the boundary equilibria of system (3) takes the form \((v, u, 0, 0)\) or \((0, 0, v, u)\) with the nonzero vector \((u, v)\) satisfying

\[
u = \alpha e^{-\gamma t(u+g(u,0))}, \quad v = g(u,0). \tag{12}\]

Using a similar argument as Theorem 3.2 we have the following results.
where $Y$ is symmetric and we have the following decompositions:

Thus, the second equation of (14) can be rewritten as

$$
\mathcal{G}(x, y, \eta) \triangleq (I - P)F(u^*p + xq + yp, \eta) = 0.
$$
Notice that $\mathcal{G}(0, 0, \eta) = 0$ and $\mathcal{G}_\eta(0, 0, 0) = (I - P)\mathcal{L}_0 p = \mathcal{L}_0 p$. Applying the implicit function theorem, we obtain a positive constant $\delta$ and a continuous differential $\mathbb{Z}_2$-equivariant map $W$ such that $W(-x, \eta) = -W(x, \eta)$ for all $x \in (-\delta, \delta)$, and

$$(I - P)F(u^* p + xq + W(x, \eta)p, \eta) = 0.$$ 

Substituting $y = W(x, \eta)$ into the first equation of (14), we have

$$B(x, \eta) = PF(u^* p + xq + W(x, \eta)p, \eta) = 0.$$ 

Hence we reduce the original problem to the problem of finding zeros of the map $B$. Moreover, $B(-x, \eta) = -B(x, \eta)$ for all $x \in (-\delta, \delta)$. Define $\mathcal{G} : (-\delta, \delta) \times \mathbb{R} \to \mathbb{R}$ by $\mathcal{G}(x, \eta) = q \cdot B(x, \eta)$. Then $\mathcal{G}(-x, \eta) = -\mathcal{G}(x, \eta)$ for all $x \in (-\delta, \delta)$. It is easy to see that $\mathcal{G}(x, \eta) = x(-2\eta + \omega x^2 + o(x^2))$, where

$$\omega = \frac{(\beta + \mu)\beta}{3(\beta - \mu)^2 u^*} \left\{ 1 - \frac{3\gamma(z^*)^2}{\gamma[z(z^*)]} + \frac{\gamma^2[z(z^*)]}{\gamma^2[z(z^*)]^{3/2}} \right\} + 2(\beta + \mu)^2 \left\{ \frac{z(z^*)}{\gamma[z(z^*)]} - \frac{\gamma(z^*)}{\gamma[z(z^*)]} \right\}.$$ 

Thus, if $\omega \neq 0$ then the zeros $x$ of $\mathcal{G}(\cdot, \eta)$ undergo a pitchfork bifurcation near $x = 0$. Namely, if $\omega < 0$ (respectively, $> 0$) then there exist a constant $\delta > 0$ and a continuously differentiable mapping $x_0$ from $(0, \delta)$ (respectively, $(-\delta, 0)$) to $\mathbb{R}$ such that $\mathcal{G}(x, \eta)$ has three zeros: $0$ and $\pm x_0(\eta)$. Obviously, $x_0(\eta) = \sqrt{2\eta/\omega} + o(\eta)$.

The zero point $x = 0$ corresponds to the synchronous equilibrium $(v^*, u^*, v^*, u^*)$ of system $[3]$, while the zeros $x_0(\eta)$ and $-x_0(\eta)$ correspond to asynchronous equilibria $(v^+(\eta), u^-(\eta), v^-\eta, u^-\eta)$ and $(v^-\eta, u^-\eta, v^+\eta, u^+\eta)$, respectively, where

$$u^\pm(\eta) = u^* \pm x_0(\eta) \pm W(x_0(\eta), \eta), \quad v^\pm(\eta) = g(u^\pm(\eta), u^\mp(\eta)).$$

Thus, we obtain the following result.

**Theorem 3.4.**

(i): Assume that $\beta > \mu$. If $\tau'(z^*) = 0$ or $\alpha + \gamma > 2\beta u^*$ and $\tau'(z^*) > 0$ then system $[3]$ has exactly one interior equilibrium, i.e., the synchronous equilibrium $(v^*, u^*, v^*, u^*)$.

(ii): If there exists positive constants $\alpha$, $\beta$, $\gamma$, $\mu$ such that $\beta > \mu$ and $\omega > 0$ (respectively, $< 0$) and $\eta \triangleq \beta + \mu + (\beta - \mu)(\gamma + \alpha - 2\beta u^*)\tau'(z^*)u^*$ is sufficiently close to $0$, then there exist a constant $\delta > 0$ and four continuously differentiable mappings $u^\pm$ and $v^\pm$ from $(0, \delta)$ (respectively, $(-\delta, 0)$) to $\mathbb{R}$ such that $[3]$ has two asynchronous equilibria $(u^+(\eta), v^+(\eta), u^-(\eta), v^-(\eta))$ and $(u^-\eta, v^-\eta, u^+\eta, v^+\eta))$, which satisfy $u^\pm(\eta) \to u^*$ and $v^\pm(\eta) \to v^*$ as $\eta \to 0$.

Note that $(\beta - \mu)u^* = 2\alpha e^{-\gamma \tau(m)} < 2\alpha e^{-\gamma \tau(m)}$. Hence, if $(\alpha + \gamma)(\beta - \mu) > 2\alpha e^{-\gamma \tau(m)}$ and $\tau'(z^*) > 0$ then

$$\alpha + \gamma - 2\beta u^* = \alpha + \gamma - \frac{2\alpha e^{-\gamma \tau(m)}}{\beta - \mu} > \alpha + \gamma - \frac{2\alpha e^{-\gamma \tau(m)}}{\beta - \mu} > 0.$$ 

This, together with Theorem [3.4(i)], implies that we obtain the following result.

**Corollary 2.** If $(\beta - \mu)(\gamma + \alpha) > 2\alpha e^{-\gamma \tau(m)}$ and $\tau'(z^*) > 0$ then system $[3]$ has exactly one interior equilibrium, i.e., the synchronous equilibrium $(v^*, u^*, v^*, u^*)$. 
4. Linearized stability. In this section, we will investigate the local stability of the three types of equilibria. Linearizing an system with state-dependent delay is not completely straightforward because the delay is a function depending on the state variables \( u_i \) and \( v_i \). The local stability of equilibria of state-dependent delay differential equations was studied in [6, 16]. It was shown that generically the behaviour of the state-dependent delay except for its value has no effect on the stability of an equilibrium, and that a local linearization is valid by treating the delay function as a constant at the equilibrium point. Hence to study the local stability of an equilibrium \( E(v_i^0, u_i^0, v_i^0, u_i^0) \) of (3), we linearize (3) at \( E(v_i^0, u_i^0, v_i^0, u_i^0) \) by treating the two delays \( \tau(u_1 + v_1) \) and \( \tau(u_2 + v_2) \) as \( \tau(v_i^0 + u_i^0) \) and \( \tau(v_i^0 + u_i^0) \), respectively. The resulting linear system is a differential equation with two constant delays:

\[
\dot{X}(t) = BX(t) + B_1X(t - \tau(z_1^0)) + B_2X(t - \tau(z_2^0))
\]

for \( X(t) = (v_1(t), u_1(t), v_2(t), u_2(t))^T \in C([0, \tau_M]; \mathbb{R}^4) = C_{4, \tau_M} \), where

\[
B = \begin{bmatrix}
-\gamma + \xi_1^0 & -\xi_1^0 & \alpha + \xi_1^0 & 0 \\
-\xi_1^0 & -\xi_1^0 & 0 & 0 \\
0 & 0 & 0 & -\gamma + \xi_2^0 \\
0 & 0 & -\xi_2^0 & 0
\end{bmatrix},
\]

\[
B_1 = \begin{bmatrix}
0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 \\
-\alpha e^{-\gamma t(z_i^0)} & 0 & 0 & 0
\end{bmatrix},
\]

\[
B_2 = \begin{bmatrix}
0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 \\
0 & 0 & -\alpha e^{-\gamma t(z_i^0)} & 0 \\
0 & 0 & 0 & -\alpha e^{-\gamma t(z_i^0)}
\end{bmatrix}
\]

and \( \xi_i^0 = \alpha\gamma e^{-\gamma t(z_i^0)} \xi_i^0, z_i^0 = u_i^0 + v_i^0 \). This leads to the following characteristic equation

\[
\det(\lambda I - B - B_1 e^{-\lambda t(z_i^0)} - B_2 e^{-\lambda t(z_i^0)}) = 0.
\]

For the extinction equilibrium \( E_0(0, 0, 0, 0) \), (16) reduces to

\[
(\lambda + \gamma)(\lambda - \alpha e^{(\gamma + \lambda)\tau_m}) = 0.
\]

Clearly \( \lambda = -\gamma \) is one of these eigenvalues. All the other eigenvalues \( \lambda \) satisfy the equation \( \lambda = \alpha e^{(\gamma + \lambda)\tau_m} \), which always has a real, positive solution. Hence \( E_0 \) is unstable.

For the boundary equilibrium \( E_1(v_0, u_0, 0, 0) \) with its existence guaranteed by Theorem 3.3, the eigenvalues \( \lambda \) are the roots of the equation

\[
\left[ (\lambda + \gamma - \xi_0)(\lambda + \xi_0 + 2\beta u_0 - \alpha e^{-(\gamma + \lambda)\tau(z_0)}) - \xi_0(-\alpha + \alpha e^{-(\gamma + \lambda)\tau(z_0)}) \right] \\
\times (\lambda + \gamma) \left( \lambda - \mu u_0 - \alpha e^{-(\gamma + \lambda)\tau_m} \right) = 0,
\]

where \( \xi_0 = \alpha\gamma e^{-(\gamma + \lambda)\tau(z_0)} u_0 \) and \( z_0 = u_0 + v_0 \). Some eigenvalues are given by \( \lambda = \mu u_0 + \alpha e^{-(\gamma + \lambda)\tau_m} \), where, clearly, \( \text{Re}\lambda > 0 \) and hence \( E_1 \) is unstable. Similarly, we can show that \( E_2(0, 0, v_0, u_0) \) is also unstable. That means the two species depend on each other, and they cannot survive without the other one.

Now, we consider the stability at the synchronous equilibrium \( E^*(v^*, u^*, v^*, u^*) \) under the assumption that \( \beta > \mu \). The characteristic equation (16) can be reduced to

\[
\Delta_+(\lambda) \cdot \Delta_-(\lambda) = 0,
\]

\( \Delta_+ \) and \( \Delta_- \) are the characteristic multipliers at the boundary equilibrium and the extinction equilibrium, respectively.
where
\[
\Delta_\pm (\lambda) = (\lambda + \gamma - \xi') (\lambda + \xi + 2\beta u^* - \mu u^* - \alpha e^{-(\gamma + \lambda)\tau(z^*)}) \\
- \xi' (-\alpha + \alpha e^{-(\gamma + \lambda)\tau(z^*)} - \xi) \pm (\lambda + \gamma - \xi)\mu u^*,
\]
and \(\xi' = \alpha e^{-\gamma(z^*)}r'(z^*)u^*\) and \(z^* = u^* + v^*\). Then the eigenvalues are given by the solutions of \(\Delta_\pm (\lambda) = 0\). As stated in Section 1, \(\tau'(z^*) \geq 0\), so we divide the analysis of stability into two parts: \(\tau'(z^*) = 0\) and \(\tau'(z^*) > 0\).

**Theorem 4.1.** If \(\beta > \mu\) and \(\tau'(z^*) = 0\) then the synchronous equilibrium \(E^*\) is locally asymptotically stable.

**Proof.** If \(\tau'(z^*) = 0\), the characteristic equation (16) can be rewritten as
\[
(\lambda + \gamma)^2 \left((\lambda + 2\beta u^* - \mu u^* - \alpha e^{-(\gamma + \lambda)\tau(z^*)})^2 - (\mu u^*)^2 \right) = 0.
\]
Obviously, \(\lambda = -\gamma\) is an eigenvalue, and some of the others are given by
\[
\lambda + 2\beta u^* - \alpha e^{-(\gamma + \lambda)\tau(z^*)} = 0.
\]
Then we compute the real parts and get
\[
\text{Re}\lambda + 2\beta u^* - 2\mu u^* = (\beta - \mu) u^* \text{cos} (\text{Im}\lambda \tau(z^*)) \; e^{-\text{Re}\lambda \tau(z^*)} \leq (\beta - \mu) u^*;
\]
and hence \(\text{Re}\lambda \leq -(\beta + \mu) u^* < 0\). The remaining eigenvalues \(\lambda\) are given by
\[
\lambda + 2\beta u^* - \alpha e^{-(\gamma + \lambda)\tau(z^*)} = 0.
\]
Using the same method we see that
\[
\text{Re}\lambda + 2\beta u^* - 2\mu u^* = (\beta - \mu) u^* \text{cos} (\text{Im}\lambda \tau(z^*)) \; e^{-\text{Re}\lambda \tau(z^*)} \leq (\beta - \mu) u^*;
\]
and hence \(\text{Re}\lambda \leq -(\beta - \mu) u^* < 0\). Thus, we complete the proof. \(\Box\)

We now consider the case where \(\tau'(z^*) > 0\). First we investigate the solutions \(\lambda\) to \(\Delta_\pm (\lambda) = 0\), i.e.,
\[
\lambda^2 + (\gamma + 2\beta u^*)\lambda + \gamma u^* (\tau'(z^*) u^* (\beta - \mu) (\alpha + \gamma - 2\beta u^*) + 2\beta) \\
- (\lambda + \gamma) (\beta - \mu) e^{-\lambda\tau(z^*)} u^* = 0.
\]
Let \(\lambda = a + ib\), then separating it into real and imaginary parts, we get
\[
a^2 - b^2 + (\gamma + 2\beta u^*) a + \zeta = (\beta - \mu) u^* e^{-\alpha \tau(z^*)} \left((a + \gamma) \cos b \tau(z^*) + b \sin b \tau(z^*)\right),
\]
\[
2ab + (\gamma + 2\beta u^*) b = (\beta - \mu) u^* e^{-\alpha \tau(z^*)} \left(b \cos b \tau(z^*) - (a + \gamma) \sin b \tau(z^*)\right),
\]
where \(\zeta = \gamma u^* (\tau'(z^*) u^* (\beta - \mu) (\alpha + \gamma - 2\beta u^*) + 2\beta)\). From Theorem 4.1 we know that \(E^*\) is asymptotically stable if \(\tau'(z^*) = 0\). Now suppose that \(\tau'(z^*) > 0\) and seek for the value of \(\zeta\) such that \(a = 0\), i.e., \(E^*\) loses its stability. Then (18) becomes
\[
-b^2 + \zeta = (\beta - \mu) u^* \left(\gamma \cos b \tau(z^*) + b \sin b \tau(z^*)\right),
\]
\[
(\gamma + 2\beta u^*) b = (\beta - \mu) u^* \left(b \cos b \tau(z^*) - \gamma \sin b \tau(z^*)\right).
\]
Squaring and adding the above two equations yield
\[
b^4 + [(\gamma + 2\beta u^*)^2 - (\beta - \mu)^2 (u^*)^2 - 2\zeta] b^2 + \zeta^2 - (\beta - \mu)^2 (u^*)^2 \gamma^2 = 0. \quad (19)
\]
For such $\zeta$ to exist, \[19\] must have real roots $b$. After substituting for $\zeta$ and rearranging, we see that $b$ is a zero of the following function

$$h_1(b) = \left( b^2 - \gamma (\beta - \mu)(u^*)^2(\alpha + \gamma - 2\beta u^*)\tau'(z^*) \right)^2$$

$$+ \left( \gamma^2 + (4\beta^2 - (\beta - \mu)^2)(u^*)^2 \right) b^2$$

$$+ \gamma^2 (4\beta^2 - (\beta - \mu)^2)(u^*)^2 + 4\beta(\beta - \mu)\gamma^2(u^*)^3(\alpha + \gamma - 2\beta u^*)\tau'(z^*).$$

For this function, we have the following observation.

**Lemma 4.2.** $h_1(b) > 0$ for all $b \in \mathbb{R}$ if

$$2\beta u^* - \alpha - \gamma)u^* \tau'(z^*) < \frac{\beta + \mu}{\beta - \mu}.$$

**Proof.** Note that $\beta > \mu$ and $4\beta^2 - (\beta - \mu)^2 > 0$. Observe that $u^* > 0$ and $\tau'(z^*) > 0$ and that the first three terms in $h_1(b)$ are always positive. Thus, if $u^* < \frac{\alpha + \gamma}{2\beta}$ then the last term is also positive, and hence $h_1(b^2) > 0$.

If $u^* > \frac{\alpha + \gamma}{2\beta}$, then $-\gamma (\beta - \mu)(u^*)^2(\alpha + \gamma - 2\beta u^*)\tau'(z^*) > 0$. Obviously, $h_1(b)$ obtains its minimum value when $b = 0$. Namely,

$$h_1(b) \geq h_1(0) = \gamma^2 \left[ (\beta - \mu)^2 \rho^2 + 4\beta(\beta - \mu)\rho + 4\beta^2 - (\beta - \mu)^2 \right],$$

where $\rho = u^*(\alpha + \gamma - 2\beta u^*)\tau'(z^*)$. It is easy to see that $h_1(0) > 0$ when $\rho > -\frac{\beta + \mu}{\beta - \mu}$.

It follows that $\rho > -\frac{\beta + \mu}{\beta - \mu}$ that $2(\beta u^* - \alpha - \gamma)u^* \tau'(z^*) < \frac{\beta + \mu}{\beta - \mu}$. So if $\beta > \mu$ and $2(\beta u^* - \alpha - \gamma)u^* \tau'(z^*) < \beta - \mu$, then $h_1(b) > 0$ for all $b \in \mathbb{R}$. \[\square\]

Analogously, the eigenvalues $\lambda$ satisfying $\Delta_-(\lambda) = 0$ can be discussed by considering the existence of zeros of the following function

$$h_2(b) = \left( b^2 - \gamma (\beta - \mu)(u^*)^2(\alpha + \gamma - 2\beta u^*)\tau'(z^*) \right)^2 + \left( \gamma^2 + 3(\beta - \mu)^2 \right) b^2$$

$$+ 3\gamma^2 (\beta - \mu)^2(u^*)^2 + 4(\beta - \mu)\gamma^2(u^*)^3(\alpha + \gamma - 2\beta u^*) \tau'(z^*).$$

Similarly to Lemma 4.2 we have $h_2(b) > 0$ for all $b \in \mathbb{R}$ if

$$\beta > \mu, \quad u^* [2(\beta - \mu)u^* - \alpha - \gamma] \tau'(z^*) < 1.$$

Thus, it follows from (11) that we have the following observation.

**Lemma 4.3.** If $\beta > \mu$ then $h_2(b) > 0$ for all $b \in \mathbb{R}$.

In view of Lemmas 4.2 and 4.3, we see that under the condition (20), $h_1(b) > 0$ and $h_2(b) > 0$ for all $b \in \mathbb{R}$. That is to say, (19) has no real solutions $b$. Hence no such $\zeta$ exists such that one of $\Delta_\pm(\cdot)$ has a purely imaginary zero. We conclude that under the condition (20), it is impossible for one of $\Delta_\pm(\cdot)$ to have a purely imaginary zero. According to Theorem 3.1, we notice that each zero of $\Delta_\pm(\cdot)$ has negative real parts when $\tau'(z^*) = 0$. By the continuity of $\tau'(\cdot)$, we see that each zero of $\Delta_\pm(\cdot)$ has negative real parts for every choice of $\tau'(z^*) > 0$. Namely, we obtain the following result.

**Theorem 4.4.** The synchronous equilibrium $E^*$ is locally asymptotically stable if $\beta > \mu$ and (20) is satisfied.

If $(\beta - \mu)(\gamma + \alpha) > 2\alpha \beta$ then $(2\beta u^* - \alpha - \gamma) < 0$ and $[2(\beta - \mu)u^* - \alpha - \gamma] < 0$. This, together with Theorem 5.3(1), yields the following corollary immediately.
Corollary 3. The synchronous equilibrium $E^*$ is locally asymptotically stable if one of the following assumptions holds:

(i): $\beta > \mu$ and $\tau(u) \equiv \tau(0)$ for all $u \geq 0$;
(ii): $\beta > \mu$, $\alpha + \gamma > 2\beta u^*$, and $\tau'(z^*) > 0$;
(iii): $(\beta - \mu)(\gamma + \alpha) > 2\alpha\beta e^{-\gamma \tau M}$ and $\tau'(z^*) > 0$.

5. Global behaviors. In this section, we shall discuss the global behavior of solutions of the model (3), and obtain explicit bounds for the eventual behaviors of $u_i(t)$ and $v_i(t)$, $i = 1, 2$. Throughout this section, we always assume that $\beta > \mu$, since from Theorem 2.4, we know that the solutions are unbounded when $\beta < \mu$.

For convenience, let

$$u = \frac{\alpha e^{-\gamma \tau M}}{\beta - \mu}.$$  

(21)

Theorem 5.1. Assume that $\beta > \mu$. Let $(v_1(t), u_1(t), v_2(t), u_2(t))$ be a solution of (3).

(i): If there exists $t_1 \geq -\tau_m$ such that $u_i(t) \leq u_+ \text{ for all } i \in \{1, 2\}$ and $t_1 < t < t_1 + \tau_M$, then $u_i(t) \leq u_+$ for all $t \geq t_1$, where $u_+$ is defined as (21).

(ii): If there exist some $i \in \{1, 2\}$ and $t_2 \geq -\tau_m$ such that $u_i(t) \geq \alpha^i \beta^{-1} e^{-\gamma \tau M}$ for all $t_2 < t \leq t_2 + \tau_M$, then $u_i(t) \geq \alpha^i \beta^{-1} e^{-\gamma \tau M}$ for all $t \geq t_2$.

Proof. (i) Without loss of generality, we suppose that there exists $t^* > t_1 + \tau_M$ such that $u_1(t^*) = u_+, u_2(t^*) < u_+$, but $u_1(t) \leq u_+$ for $t_1 \leq t < t^*$, where $u_1(t^*) \geq 0$. It follows from (3) that

$$\dot{u}_1(t^*) = \alpha e^{-\gamma \tau(z_1)}u_1(t^* - \tau(z_1)) - \beta u_1^2(t^*) + \mu u_1(t^*)u_2(t^*)$$

$$< \alpha e^{-\gamma \tau(z_1)}u_1(t^* - \tau(z_1)) - \beta u_1^2(t^*) + \mu u_1(t^*)u_+$$

$$= \alpha e^{-\gamma \tau(z_1)}u_1(t^* - \tau(z_1)) - (\beta - \mu)u_+^2$$

$$\leq \alpha e^{-\gamma \tau_m}(u_1(t^* - \tau(z_1)) - u_+)$$

$$< 0$$

since $t^* - \tau(z_1) < t^*$. This is a contradiction. And the other cases can be discussed similarly.

(ii) For either $i = 1$ or $i = 2$, the result can be obtained with an analogous method in (i), since

$$\dot{u}_i(t) \geq \alpha e^{-\gamma \tau(z_i)}u_i(t - \tau(z_i)) - \beta u_i^2(t).$$

This completes the proof.

Remark 4. This theorem means that if the mature population remains below or above a certain value depending on $\tau_m$ and $\tau_M$ for length of time $\tau_M$, it will do so from then on.

The following result gives the state bounds on the eventual behaviour of $u_i(t)$, independent of admissible initial conditions.

Theorem 5.2. Assume that $\beta > \mu$. Let $(v_1(t), u_1(t), v_2(t), u_2(t))$ be a solution of (3). Then

$$u_- \leq \liminf_{t \to \infty} u_i(t) \leq \limsup_{t \to \infty} u_i(t) \leq u_+,$$

where $u_\pm$ are defined as (21).
Proof. We distinguish three cases to complete the proof of this theorem. The first case is that both \( u_1(t) \) and \( u_2(t) \) are eventually monotonic and bounded. In this case, there exists \( 0 < \bar{u}_i < \infty \) such that \( \lim_{t \to \infty} u_i(t) = \bar{u}_i \) and \( \lim_{t \to \infty} \dot{u}_i(t) = 0, \ i = 1, 2 \). Hence from (3), taking the limit superior as \( t \to \infty \), we have

\[
\begin{align*}
\bar{u}_1 \left( \alpha e^{-\gamma \tau M} - \beta \bar{u}_1 + \mu \bar{u}_2 \right) & \leq 0 \leq \bar{u}_1 \left( \alpha e^{-\gamma \tau m} - \beta \bar{u}_1 + \mu \bar{u}_2 \right), \\
\bar{u}_2 \left( \alpha e^{-\gamma \tau M} - \beta \bar{u}_2 + \mu \bar{u}_1 \right) & \leq 0 \leq \bar{u}_2 \left( \alpha e^{-\gamma \tau m} - \beta \bar{u}_2 + \mu \bar{u}_1 \right),
\end{align*}
\]

from which we have \( u_- \leq \bar{u}_i \leq u_+, \ i = 1, 2 \).

Next, we consider the case where both \( u_1(t) \) and \( u_2(t) \) are oscillatory. We only show that \( \limsup_{t \to \infty} u_i(t) \leq u_+ \) for \( i = 1, 2 \), because the other inequalities follow analogously. Define two sequences \( t_n \) and \( s_m \) as those times for which \( u_1(t) \) and \( u_2(t) \) achieve their local maxima, respectively, i.e., \( \dot{u}_1(t_n) = 0, \ \dot{u}_1(t_n) < 0, \ u_2(s_m) = 0, \ \dot{u}_2(s_m) < 0 \). Let

\[
\bar{u}_1 = \limsup_{n \to \infty} u_1(t_n), \quad \bar{u}_2 = \limsup_{m \to \infty} u_2(s_m),
\]

then \( \limsup_{t \to \infty} u_i(t) = \bar{u}_i, \ i = 1, 2 \). If \( \bar{u}_i \leq u_+ \) for \( i = 1, 2 \), we are done. Hence assume that

\[
\bar{u}_i > u_+ \quad (22)
\]

is true for at least one of \( i = 1, 2 \).

If (22) holds for only \( i = 1 \) and \( u_2 \leq u_+ \), we now choose a subsequence of \( \{t_n\}_{n=1}^\infty \), relabelled as \( t_k \) such that \( \lim_{k \to \infty} u_1(t_k) = \bar{u}_1 \) and \( t_k + 1 \geq t_k + \gamma \tau M \). Then choose a subsequence of \( t_k \), relabelled so that \( \lim_{k \to \infty} z_1(t_k) = \hat{z}_1, \ \hat{z}_1 = \limsup_{k \to \infty} z_1^k \), \( z_1^k = u_1(t_k) + v_1(t_k) \). Then let \( u_1^# = \limsup_{k \to \infty} u_1(t_k - \tau(z_1^k)) \) for this subsequence \( t_k \), we choose a subsequence of \( t_k \), once again relabelled \( t_k \), such that \( \lim_{k \to \infty} u_1(t_k - \tau(z_1^k)) = u_1^# \) and \( \bar{u}_2 = \limsup_{k \to \infty} u_2(t_k) \). At last, we choose a final subsequence of \( t_k \), once again relabelled \( t_k \), such that \( \lim_{k \to \infty} u_2(t_k) = \bar{u}_2 \). Obviously, we have \( \bar{u}_2 \leq \bar{u}_2 \), since \( \bar{u}_2 \) is just a limit of subsequence of \( u_2 \). Then from (3) and (22), taking the limit as \( k \to \infty \),

\[
0 = \alpha e^{-\gamma \tau \hat{z}_1} u_1^# - \beta \bar{u}_1^2 + \mu \bar{u}_1 \bar{u}_2 \\
\leq \alpha e^{-\gamma \tau \bar{u}_1} u_1^# - \beta \bar{u}_1 u_+ + \mu \bar{u}_1 u_+ \\
\leq \alpha e^{-\gamma \tau m} (u_1^# - \bar{u}_1). \quad (23)
\]

If \( u_1^# \leq \bar{u}_1 \), we get a contradiction. Hence we suppose that \( u_1^# > \bar{u}_1 \). Then we have that, for each \( k \), we can choose a value \( t_p \), such that \( \dot{u}_1(t_p) = 0, \ \dot{u}_1(t_p) < 0, \ \limsup_{p \to \infty} u_1(t_p) \geq u_1^# > \bar{u}_1 \), which contradicts the definition of \( \bar{u}_1 \), so \( u_1^# \neq \bar{u}_1 \) cannot be true. If (22) is valid for \( \bar{u}_2 \), the same arguments can be done with subsequence \( s_k \).

If (22) holds for both \( i = 1 \) and \( 2 \), we assume that \( \bar{u}_1 \geq \bar{u}_2 > u_+ \), because the case where \( \bar{u}_2 \geq \bar{u}_1 > u_+ \) can be dealt with analogously. Similarly to (23), we have

\[
0 = \alpha e^{-\gamma \tau \bar{u}_1} u_1^# - \beta \bar{u}_1^2 + \mu \bar{u}_1 \bar{u}_2 \\
\leq \alpha e^{-\gamma \tau \bar{u}_1} u_1^# - \beta \bar{u}_1^2 + \mu \bar{u}_1^2 \\
\leq \alpha e^{-\gamma \tau m} (u_1^# - \bar{u}_1).
\]

Using a similar argument, we see that this is also a contradiction. Therefore, if both \( u_1(t) \) and \( u_2(t) \) are oscillatory then \( \limsup_{t \to \infty} u_i(t) \leq u_+ \).

Finally, we need to consider the case where one of \( u_1(t) \) and \( u_2(t) \) is oscillatory and the other is eventually monotone. Without loss of generality, suppose that \( u_1(t) \)
is oscillatory and $u_2(t)$ is eventually monotone. Using a similar argument as above, we also have (23), since $u_2(t)$ is monotone and bounded. Thus, $\limsup_{t \to \infty} u_i(t) \leq u_+ = i = 1, 2$. This completes the proof.

We now use the estimates obtained in Theorem 5.2 to obtain estimates on $v_1$ and $v_2$. We first note that there is a $T(\epsilon) > 0$ large enough such that

$$u_- - \epsilon < u_i(t) < u_+ + \epsilon$$

(24)

for any given $\epsilon > 0$ whenever $t > T$. And the equation of $v_i(t)$, $i = 1, 2$ from (3) can be written in the integral form

$$v_i(t) = e^{-\gamma(t-T)} \left( v_i(T) + \alpha \int_{T}^{t} e^{-\gamma(s-T)} \left( u_i(s) - e^{-\gamma\tau(z(s))}u_i(s-\tau(z(s))) \right) ds \right).$$

(25)

**Theorem 5.3.** Assume that $\beta > \mu$. Let $(v_1(t), u_1(t), v_2(t), u_2(t))$ be a solution of system (3). Then

$$\limsup_{t \to \infty} v_i(t) \leq \alpha^2 (\beta - \mu)^{-1} \gamma^{-1} \left( e^{-\gamma\tau_m} - e^{-2\gamma\tau_m} \right), \quad i = 1, 2.$$

**Theorem 5.4.** Assume that $\beta > \mu$ and $\tau_M < 2\tau_m$. Let $(v_1(t), u_1(t), v_2(t), u_2(t))$ be a solution of system (3). Then

$$\liminf_{t \to \infty} v_i(t) \geq \alpha^2 (\beta - \mu)^{-1} \gamma^{-1} \left( e^{-\gamma\tau_M} - e^{-2\gamma\tau_M} \right), \quad i = 1, 2.$$

The proofs for Theorems 5.3 and 5.4 are similar to those in [3] and hence are omitted. The condition $\tau_M < 2\tau_m$ is required for the lower bound to be positive.

6. **Global asymptotical stability.** In this section, we shall investigate the global asymptotical stability of the positive synchronous equilibrium when $E^*(v^*, u^*, v^*, u^*)$ of (3). For this purpose, we first consider the following system

$$v'(t) = \alpha u - \gamma v - \alpha \gamma e^{-\gamma\tau(u+v)},$$

$$u'(t) = \beta c u + \gamma v - \beta u^2 + c \mu u,$$

(26)

where function $\tau(\cdot)$ is the same to that in system (3), $c \geq 0$, $\alpha, \beta, \gamma$ are positive constants, $a \in [c_-, c_+]$, $b \in [c_-, c_+]$, and

$$c_+ = \frac{\alpha e^{-\gamma\tau_m} + c \mu}{\beta}, \quad c_- = \frac{\alpha e^{-\gamma\tau_M} + c \mu}{\beta}.$$

Note that (26) is a mixed quasi-monotone system (see [27, 34]). Firstly, we have the following observations.

**Lemma 6.1.** The set $\{(v, u) \in \mathbb{R}^2 \mid c_- < u < c_+\}$ is positively invariant.

**Lemma 6.2.** Assume that $a < b$ or $a > b$ and $2\tau_m \geq \tau_M$. Then system (26) has a positive equilibrium point $(\tilde{v}(a, b, c), \tilde{u}(a, b, c))$. More precisely,

(i): $c_- < \tilde{u}(a, b, c) < c_+$;
(ii): The positive equilibrium point $(\tilde{v}(a, b, c), \tilde{u}(a, b, c))$ is unique if $\alpha c_+ \tau'(c_-) e^{-\gamma\tau(c_-)} < 1$;
(iii): The positive equilibrium point $(\tilde{v}(a, b, c), \tilde{u}(a, b, c))$ is locally asymptotically stable and attracts all of the positive solutions of system (26) if $\alpha c_+ \tau'(c_-) e^{-\gamma\tau(c_-)} < 1$. 

Proof. Obviously, the equilibria \((v, u)\) of system (26) satisfy
\[
v = \frac{(b\alpha + ac\mu)u - a\beta u^2}{b\gamma}, \quad bae^{-\gamma(u+v)} - \beta u^2 + c\mu u = 0. \tag{27}
\]
Define \(\mathcal{F}: \mathbb{R} \times [c_-, c_+] \times [c_-, c_+] \times [0, \infty) \rightarrow \mathbb{R}\) as
\[
\mathcal{F}(u, a, b, c) = b\alpha \exp\left\{-\gamma\tau\left(\frac{(b\gamma + ba + ac\mu)u - a\beta u^2}{b\gamma}\right)\right\} - \beta u^2 + c\mu u.
\]
Note that
\[
\mathcal{F}(u, a, b, c) > bae^{-\gamma\tau M} - c_-ae^{-\gamma\tau M} = (b - c_-)ae^{-\gamma\tau M} \geq 0
\]
for all \(u \in [0, c_-]\), and
\[
\mathcal{F}(c_+, a, b, c) < \alpha(b - c_+)ae^{-\gamma\tau M} \leq 0.
\]
Thus, there exists some \(\hat{u}(a, b, c) \in (c_-, c_+)\) such that \(\mathcal{F}(\hat{u}(a, b, c), a, b, c) = 0\). It follows from (27) that
\[
\hat{v}(a, b, c) = \frac{(b\alpha + ac\mu)\hat{u}(a, b, c) - a\beta \hat{u}^2(a, b, c)}{b\gamma}.
\]
If \(a < b\) or \(a > b\) and \(2\tau_m \geq \tau_M\) then
\[
\frac{b\alpha}{a} + c\mu - \beta c_+ > \alpha\left[\frac{ae^{-\gamma\tau M} + c\mu}{ae^{-\gamma\tau M} + c\mu} - e^{-\gamma\tau_m}\right] \geq \alpha\left[e^{\gamma(\tau_m - \tau_M)} - e^{-\gamma\tau_m}\right] \geq 0,
\]
and hence
\[
c_- < \hat{u}(a, b, c) < c_+ < \frac{b\alpha + ac\mu}{a\beta}, \quad \hat{v}(a, b, c) > 0.
\]
Therefore, system (26) has a positive equilibrium point \((\hat{v}(a, b, c), \hat{u}(a, b, c))\).

If \(a\alpha + \tau\gamma\tau(e^{-\gamma\tau(c_-)}) < 1\) then \(a\alpha\tau\gamma\gamma\gamma(u)e^{-\gamma\tau(u)} < 1\) for all \(u > c_-\), and hence
\[
\mathcal{F}_u(u, a, b, c) \leq (c\mu - 2\beta u) \left[1 - a\alpha\tau\gamma\gamma\gamma(u) e^{-\gamma\tau(u)}\right]
\leq - [c\mu + 2\alpha e^{-\gamma\tau_M}] \left[1 - a\alpha\tau\gamma\gamma\gamma(u) e^{-\gamma\tau(u)}\right] < 0
\]
for all \(u \in (c_-, c_+)\). This implies that system (26) has exactly one positive equilibrium point \((\hat{v}(a, b, c), \hat{u}(a, b, c))\).

It is easy to see that trace and determinant of the linearized matrix of (26) at the positive equilibrium point \((\hat{v}(a, b, c), \hat{u}(a, b, c))\) are negative and positive, respectively, if \(a\alpha\tau\gamma\gamma\gamma(u, v) e^{-\gamma\tau(u,v)}(\hat{u}(a, b, c) + \hat{v}(a, b, c)) < 1\) Therefore, the positive equilibrium point \((\hat{v}(a, b, c), \hat{u}(a, b, c))\) is locally asymptotically stable if \(a\alpha\gamma\gamma\gamma(c_-) e^{-\gamma\tau(c_-)} < 1\). Note that the divergence of the vector field associated with (26) is
\[
-\gamma + (a - b)\alpha\gamma\tau\gamma\gamma\gamma(u + v)e^{-\gamma\tau(u+v)} - 2\beta u + c\mu,
\]
which is negative if \(a\alpha\gamma\gamma\gamma(u, v) e^{-\gamma\tau(u,v)} < 1\). This implies that system (26) has no periodic solutions lying in the set \(\{(v, u) \in \mathbb{R}^2|c_- < u < c_+\}\). Thus, the global attractivity of the positive equilibrium point \((\hat{v}(a, b, c), \hat{u}(a, b, c))\) follows from Lemma 6.1.

Note that \(\mathcal{F}(b, a, b, c) = b\hat{f}(a, b, c),\) where
\[
\hat{f}(a, b, c) \triangleq \alpha \exp\left\{-\gamma\tau\left(\frac{b\gamma + ba + ac\mu - a\beta}{\gamma}\right)\right\} - \beta b + c\mu
\]
Lemma 6.3. \(f\) that \(\hat{u}\) and hence that \(\hat{\beta}_{\infty}\) and \(\hat{c}\) thus \(\hat{\beta}_{\infty} \geq \hat{c}\).

In addition,
\[
\hat{f}(a,b,c) > 0.
\]

It is easy to see that \(\hat{f}(a,b,c)\) is strictly decreasing in \(a \in [c_-, c_+]\) and satisfies \(\hat{f}(c_-, c_+, c) > 0 > \hat{f}(c_+, c_+, c)\). Thus, there exists exactly one \(\hat{u}(c) \in (c_-, c_+)\) such that \(\hat{f}(\hat{u}(c), \hat{u}(c), c) = 0\). Therefore, we have the following observation.

**Lemma 6.3.** (i): If \(c_- \leq a < \hat{u}(c) < b \leq c_+\) and \(ac_+ \tau'(c_-) e^{-\gamma \tau(c_-)} < 1\) then
\[
a < \hat{u}(b,a,c) < b \quad \text{and} \quad a < \hat{u}(b,a,c) < b.
\]
(ii): If \(c_- \leq a < \hat{u}(c), c_- \leq a < b \leq c_+, \text{ and } \tau'(\hat{u}(c)) \hat{u}(c)(\beta \hat{u}(c) - c\mu) < \frac{(\hat{u}(c) - a)c_-}{b - a}, \text{ then } \hat{u}(c) > \hat{u}(b,a,c);
\]
(iii): If \(c_- \leq a < b \leq c_+ \text{ and } \tau'(\hat{u}(c)) \hat{u}(c)(\beta \hat{u}(c) - c\mu) < \frac{b - \hat{u}(c)}{b - a}, \text{ then } \hat{u}(c) < \hat{u}(a,b,c);
\]
(iv): If \(c_- \leq a < b \leq c_+ \text{ and } ac_+ \tau'(c_-) e^{-\gamma \tau(c_-)} < 1\) then \(c_- < \hat{u}(b,a,c) < \hat{u}(a,b,c) < c_+;
\]
(v): If \(c_- \leq a < b < \hat{u}(c) \text{ then } \hat{u}(a,b,c) < \hat{u}(c);
\]
(vi): If \(\hat{u}(c) < a < b \leq c_+ \text{ then } \hat{u}(b,a,c) > \hat{u}(c).
\]

**Proof.** For convenience, let \(\bar{u} = \hat{u}(a,b,c), \bar{u} = \hat{u}(b,a,c), \text{ and } \hat{u} = \hat{u}(c).\) It follows from \(ac_+ \tau'(c_-) e^{-\gamma \tau(c_-)} < 1\) that \(ac_+ \tau'(c_-) e^{-\gamma \tau(c_-)} < 1\) and hence \(\hat{f}(a,b,c) > 0\) and \(\hat{f}(a,b,c) < 0\). If \(c_- < a < \hat{u} < b < c_+\) then \(\hat{f}(a,b,c) < \hat{f}(b,a,c) < \hat{f}(c_+, a,c) < \hat{f}(b,a,c) \text{ and hence } \mathcal{F}(b,a,b,c) > 0 > \mathcal{F}(a,b,a,c), \text{ which implies that } \hat{u} < b \text{ and } a < \hat{u}.\) Note that
\[
\mathcal{F}(u,a,b,c) = [1 + u(c\mu - u\beta)\tau'(c_-)] \alpha \exp \left\{-\gamma \tau \left(\frac{(b\gamma + ba + ac\mu)u - a\beta u^2}{b\gamma}\right)\right\}
\]
\[
> [1 - ac_+ \tau'(c_-) e^{-\gamma \tau(c_-)}] \alpha \exp \left\{-\gamma \tau \left(\frac{(b\gamma + ba + ac\mu)u - a\beta u^2}{b\gamma}\right)\right\}
\]
\[
> 0
\]
for all \(u \in [c_-, c_+].\) This implies that
\[
\mathcal{F}(a,b,a,c) > \mathcal{F}(a,a,a,c) = \alpha \hat{f}(a,a,c) > 0,
\]
\[
\mathcal{F}(b,b,a,c) < \mathcal{F}(b,b,b,c) = b \hat{f}(b,b,c) < 0,
\]
and hence that \(\hat{u} > a \text{ and } \hat{u} < b.\) Note that
\[
\mathcal{F}(\hat{u},a,b,c)
\]
\[
> [b \exp \left\{\tau'(\hat{u}) \left(1 - \frac{a}{b}\right) \hat{u}(c\mu - \beta \hat{u}) - \hat{u}\right\} - \hat{u}] \alpha \exp \left\{-\gamma \tau \left(\frac{(\gamma + \alpha)\hat{u} + (c\mu + \beta \hat{u})\hat{u}}{\gamma}\right)\right\}
\]
\[
> [b - \hat{u} - (b-a)\tau'(\hat{u})\hat{u}(\beta \hat{u} - c\mu)] \alpha \exp \left\{-\gamma \tau \left(\frac{(\gamma + \alpha)\hat{u} + (c\mu + \beta \hat{u})\hat{u}}{\gamma}\right)\right\}.
\]
\[ F(\hat{u}, b, a, c) \]
\[ \leq \left[ a - \hat{u} \exp \left\{ -\tau'(\hat{u}) \left( 1 - \frac{b}{a} \right) \hat{u}(c\mu - \beta\hat{u}) \right\} \right] \alpha \exp \left\{ -\gamma \tau \left( \frac{(a\gamma + a\alpha + b\mu)\hat{u} - b\beta\hat{u}^2}{a\gamma} \right) \right\} \]
\[ \leq \left[ a - \hat{u} + \frac{\hat{u}}{a} (b - a) \tau'(\hat{u}) \hat{u}(\beta\hat{u} - c\mu) \right] \alpha \exp \left\{ -\gamma \tau \left( \frac{(a\gamma + a\alpha + b\mu)\hat{u} - b\beta\hat{u}^2}{a\gamma} \right) \right\}. \]

Thus, if \( c_- \leq a < \hat{u}(c) \) and \( c_- \leq a < b \leq c_+ \) and
\[ \tau'(\hat{u})\hat{u}(\beta\hat{u} - c\mu) < \frac{(\hat{u} - a)a}{(b - a)\hat{u}}, \]
then \( F(\hat{u}, b, a, c) < 0 \) and hence \( \hat{u} > \hat{u} \). If \( c_- \leq a < b \leq c_+ \) and
\[ \tau'(\hat{u})\hat{u}(\beta\hat{u} - c\mu) < \frac{b - \hat{u}}{b - a}, \]
then \( F(\hat{u}, a, b, c) > 0 \) and hence \( \hat{u} < \hat{u} \). Note that
\[ F(\hat{u}, a, b, c) \]
\[ \geq \left[ b \exp \left\{ \tau'(\hat{u}) \left( \frac{b}{a} - \frac{a}{b} \right) (c\mu\hat{u} - \beta\hat{u}^2) \right\} - a \right] \alpha \exp \left\{ -\gamma \tau \left( \frac{(a\gamma + a\alpha + b\mu)\hat{u} - b\beta\hat{u}^2}{a\gamma} \right) \right\} \]
\[ \geq \left[ b + \tau'(\hat{u}) \left( \frac{b^2}{a} - a \right) (c\mu\hat{u} - \beta\hat{u}^2) - a \right] \alpha \exp \left\{ -\gamma \tau \left( \frac{(a\gamma + a\alpha + b\mu)\hat{u} - b\beta\hat{u}^2}{a\gamma} \right) \right\} \]
\[ \geq (b - a) \left[ 1 + 2\tau'(\hat{u})(c\mu\hat{u} - \beta\hat{u}^2) \right] \alpha \exp \left\{ -\gamma \tau \left( \frac{(a\gamma + a\alpha + b\mu)\hat{u} - b\beta\hat{u}^2}{a\gamma} \right) \right\}. \]

Thus, if \( c_- \leq a < b \leq c_+ \) and \( 2ac_+\tau'(c_-)e^{-\gamma\tau_m} < 1 \) then \( F(\hat{u}, a, b, c) > 0 \), which implies that \( \hat{u} < \hat{u} \). Then
\[ F(\hat{u}, a, b, c) \]
\[ \leq \alpha \hat{u} \exp \left\{ -\gamma \tau \left( \frac{b\gamma}{b\gamma} (b\gamma + a\alpha + a\mu)\hat{u} - a\beta\hat{u}^2 \right) \right\} \]
\[ - \alpha \hat{u} \exp \left\{ -\gamma \tau \left( \frac{\gamma + a}{\gamma} (\gamma + a)\hat{u} + (c\mu - \beta\hat{u})\hat{u} \right) \right\} \]
\[ \leq \left[ \exp \left\{ \tau'(\theta) \left( 1 - \frac{a}{b} \right) \hat{u}(c\mu - \beta\hat{u}) \right\} - 1 \right] \alpha \hat{u} \exp \left\{ -\gamma \tau \left( \frac{(\gamma + a)\hat{u} + (c\mu - \beta\hat{u})\hat{u}}{\gamma} \right) \right\} \]
\[ < 0, \]
where \( \theta \) lies between \( [(b\gamma + a\alpha + a\mu)\hat{u} - a\beta\hat{u}^2]/(b\gamma) \) and \( [(\gamma + a)\hat{u} + (c\mu - \beta\hat{u})\hat{u}]/\gamma \). This implies that \( \hat{u}(a, b, c) < \hat{u}(c) \). Using a similar argument as above, we see that \( \hat{u}(b, a, c) > \hat{u}(c) \) if \( \hat{u}(c) < a < b \leq c_+ \). This completes the proof of this lemma. \( \square \)
Lemma 6.4. Define two sequences \( \{\overline{u}_n\}_{n=1}^{\infty} \) and \( \{\underline{u}_n\}_{n=1}^{\infty} \) as follows: 
\[ \overline{u}_1 = \tilde{u}(c_-, c_+, c), \quad \underline{u}_1 = \hat{u}(c_+, c_-, c), \]
and 
\[ \overline{u}_n = \tilde{u}(\overline{u}_{n-1}, \overline{u}_{n-1}, c), \quad \underline{u}_n = \hat{u}(\underline{u}_{n-1}, \underline{u}_{n-1}, c) \]  
for all \( n > 2 \). If 
\[ \alpha c_+ \tau'(c_-) e^{-\gamma \tau(c_-)} < \frac{1}{2} \]  
then 
\[ \lim_{n \to \infty} \overline{u}_n = \lim_{n \to \infty} \underline{u}_n = \hat{u}(c). \]

Proof. It follows from Lemma 6.3(i)(iv) that \( c_- < \underline{u}_n < \overline{u}_n < c_+ \) for all \( n \in \mathbb{N} \). Let 
\[ \underline{u}_- = \lim_{n \to \infty} \underline{u}_n, \quad \underline{u}_+ = \lim_{n \to \infty} \underline{u}_n, \quad \overline{u}_- = \lim_{n \to \infty} \overline{u}_n, \quad \overline{u}_+ = \lim_{n \to \infty} \overline{u}_n. \]

Obviously, we have \( \underline{u}_- < \underline{u}_+ \leq \overline{u}_- \leq \overline{u}_+ \). It follows from (28) that \( \overline{u}_+ \leq \tilde{u}(\overline{u}_+, \overline{u}_+, c) \) and \( \underline{u}_- \geq \hat{u}(\overline{u}_-, \underline{u}_-, c) \), and hence that 
\[ J(\overline{u}_+, \overline{u}_+, \overline{u}_+), \quad \underline{u}_- \geq \hat{u}(\overline{u}_-, \underline{u}_-, c), \]  
that is, 
\[ \hat{f}(\overline{u}_+, \overline{u}_+, \overline{u}_+) \geq \hat{f}(\underline{u}_+, \underline{u}_+, \underline{u}_+) \geq \hat{f}(\underline{u}_-, \underline{u}_-, \underline{u}_-). \]

Thus, we have \( \overline{u}_+ \leq \hat{u}(c) \leq \underline{u}_- \). Therefore, \( \underline{u}_- = \underline{u}_+ = \overline{u}_- = \overline{u}_+ = \hat{u}(c) \). This completes the proof of this lemma. \( \square \)

In what follows, consider the following system 
\[ \begin{align*}
v'(t) &= \alpha \mu - \gamma v - \alpha c_+ e^{-\gamma \tau(u+v)} u(t - \tau(u + v)), \\
u'(t) &= \alpha c_- e^{-\gamma \tau(u+v)} u(t - \tau(u + v)) - \beta u^2 + \gamma \mu u, 
\end{align*} \]  
where \( \gamma \) are positive constants, \( c \geq 0 \), and function \( \tau(\cdot) \) is the same to that of system (3). We have the following result on the existence, uniqueness, and global attractivity of a positive equilibrium point of system (30).

Lemma 6.5. System (30) has a positive equilibrium point \( (\hat{v}(c), \hat{u}(c)) \), where \( \hat{u}(c) \in (c_-, c_+) \) satisfies 
\[ \hat{f}(\hat{u}(c), \hat{u}(c), c) = 0 \quad \text{and} \quad \hat{v}(c) = \frac{[\alpha + c\mu - \beta \hat{u}(c)] \hat{u}(c)}{\gamma}. \]

Assume further that (29) holds, then the positive equilibrium point \( (\hat{v}(c), \hat{u}(c)) \) is unique and attracts all of the positive solutions of system (30).

Proof. It follows from the proof of Lemma 6.3 that we can obtain the existence and uniqueness of the positive equilibrium point \( (\hat{v}(c), \hat{u}(c)) \). In what follows, we only need to prove the global attractivity of the positive equilibrium point \( (\hat{v}(c), \hat{u}(c)) \).

Using a similar argument as that of [3], we see that 
\[ c_- < \liminf_{t \to \infty} u(t) \leq \limsup_{t \to \infty} u(t) < c_+, \]
then for all large enough \( t \), we have 
\[ \begin{align*}
v'(t) &> \alpha u - \gamma v - \alpha c_+ e^{-\gamma \tau(u+v)}, \\
u'(t) &> \alpha c_- e^{-\gamma \tau(u+v)} - \beta u^2 + \gamma \mu u, \\
v'(t) &< \alpha u - \gamma v - \alpha c_- e^{-\gamma \tau(u+v)}, \\
u'(t) &< \alpha c_+ e^{-\gamma \tau(u+v)} - \beta u^2 + \gamma \mu u. 
\end{align*} \]

Thus, we have 
\[ \underline{x}(t) < u(t) < \overline{x}(t), \quad \underline{y}(t) < v(t) < \overline{y}(t), \]  
(31)
where \((x, y, \bar{x}, \bar{y})\) is a solution to the following system

\[
\begin{align*}
x'(t) &= \alpha y - \gamma x - \alpha c_+ e^{-\gamma t} x + y, \\
y'(t) &= \alpha c_- e^{-\gamma t} x + \beta y^2 + c \mu y, \\
\bar{x}'(t) &= \alpha \bar{y} - \gamma \bar{x} - \alpha c_- e^{-\gamma t} \bar{x} + \bar{y}, \\
\bar{y}'(t) &= \alpha c_+ e^{-\gamma t} \bar{x} - \beta \bar{y}^2 + c \mu \bar{y}.
\end{align*}
\]

It follows from Lemma 3.3 that

\[
\lim_{t \to \infty} (x(t), y(t), \bar{x}(t), \bar{y}(t)) = (\bar{v}_1, \bar{u}_1, \bar{v}_1, \bar{u}_1),
\]

where

\[
\begin{align*}
\bar{v}_1 &= \tilde{v}(c_-, c_+, c), & \bar{u}_1 &= \tilde{u}(c_-, c_+, c), \\
\tilde{v}_1 &= \tilde{v}(c_+, c_-, c), & \tilde{u}_1 &= \tilde{u}(c_+, c_-, c).
\end{align*}
\]

It follows from (31) and Lemma 6.3 that

\[
\bar{u}_1 < \liminf_{t \to \infty} u(t) \leq \limsup_{t \to \infty} u(t) < \bar{v}_1, \quad \bar{u}_1 < \liminf_{t \to \infty} v(t) \leq \limsup_{t \to \infty} v(t) < \bar{v}_1
\]

and

\[
c_- < \bar{u}_1 < \tilde{u}(c) < \bar{v}_1.
\]

This process can be continued to construct four sequences \(\{\bar{v}_n\}_{n=1}^\infty, \{\bar{u}_n\}_{n=1}^\infty, \{\tilde{v}_n\}_{n=1}^\infty, \{\tilde{u}_n\}_{n=1}^\infty\), as follows:

\[
\begin{align*}
\bar{v}_n &= \tilde{v}(\bar{v}_{n-1}, \bar{u}_{n-1}, c), & \bar{u}_n &= \tilde{u}(\bar{v}_{n-1}, \bar{u}_{n-1}, c), \\
\tilde{v}_n &= \tilde{v}(\tilde{v}_{n-1}, \tilde{u}_{n-1}, c), & \tilde{u}_n &= \tilde{u}(\tilde{v}_{n-1}, \tilde{u}_{n-1}, c).
\end{align*}
\]

It follows from Lemma 6.4 that

\[
\liminf_{t \to \infty} u(t) = \limsup_{t \to \infty} u(t) = \tilde{u}(c), \quad \liminf_{t \to \infty} v(t) = \limsup_{t \to \infty} v(t) = \tilde{v}(c).
\]

Thus, the positive equilibrium point \((\tilde{v}(c), \tilde{u}(c))\) attracts all of the positive solutions of system (30). This completes the proof of this lemma.

Finally, we consider some properties of the function \(\tilde{u}(c)\) for \(c > 0\). Note that \(\tilde{u}(c)\) is the unique zero of the function \(\vartheta(c, \cdot)\), where \(\vartheta: [0, \infty) \times [u_-, u_+] \to \mathbb{R}\) is defined as

\[
\vartheta(x, c) = \alpha \exp \left\{ -\gamma \tau \left( \frac{\gamma + \alpha + c \mu - \beta x}{\gamma} \right) \right\} - \beta x + c \mu
\]

for \(c \geq 0\) and \(x \in [u_-, u_+]\), where \(u_\pm\) are defined as (21). If \(\alpha u_+ \tau'(u_-) e^{-\gamma \tau(u_-)} < 1\) then

\[
\vartheta_x(c, x) \leq \alpha \beta u_+ \tau'(u_-) e^{-\gamma \tau(u_-)} - \beta < 0,
\]

\[
\vartheta_c(c, x) \geq \mu - \alpha \mu u_+ \tau'(u_-) e^{-\gamma \tau(u_-)} > 0,
\]

and hence \(\tilde{u}(c)\) is increasing with respect to \(c\). Note that \(f(u) = \vartheta(u, u) = \tilde{f}(u, u, u)\), where function \(f\) is defined as (10). It follows from the proof of Theorem 3.2 that \(f\) has exactly one positive zero \(u^*\) when \(\beta > \mu\). Namely, \(\tilde{u}(u^*) = u^*\). Hence, \(f(u) > 0\) for all \(u \in [0, u^*]\), and \(f(u) < 0\) for all \(u \in [u^*, \frac{\alpha}{\beta - \mu}]\). If \(c > u^*\) then \(\tilde{u}(c) > \tilde{u}(u^*) = u^*\); if \(c < u^*\) then \(\tilde{u}(c) < \tilde{u}(u^*) = u^*\). In addition, we see that \(\tilde{u}(0) = 0\). Therefore, we have the following observation.

**Lemma 6.6.** Assume that \(\alpha u_+ \tau'(u_-) e^{-\gamma \tau(u_-)} < 1\), then

(i) \(\tilde{u}(c)\) is increasing with respect to \(c \geq 0\);
\[(ii): \text{If } c > u^* \text{ then } c > \hat{u}(c) > u^*;\]
\[(iii): \text{If } c < u^* \text{ then } c < \hat{u}(c) < u^*.\]

Now, we can state our main result on the global asymptotical stability of the positive synchronous equilibrium when \(E^*(v^*, u^*, v^*, u^*)\) of (3)

**Theorem 6.7.** The synchronous equilibrium \(E^*(v^*, u^*, v^*, u^*)\) is globally asymptotically stable if one of the following assumptions is satisfied:

(i): \(\beta > \mu\) and \(\tau(u) \equiv \tau(0)\) for all \(u \geq 0\);
(ii): \(\beta > \mu, \alpha + \gamma > 2\beta u^*, \text{ and } \alpha u_+ \tau'(u_-) e^{-\gamma \tau(u_-)} < \frac{1}{2}\);
(iii): \((\beta - \mu)(\gamma + \alpha) > 2\alpha \beta e^{-\gamma \tau_m} \text{ and } \alpha u_+ \tau'(u_-) e^{-\gamma \tau(u_-)} < \frac{1}{2}\).

**Proof.** If \(\alpha u_+ \tau'(u_-) e^{-\gamma \tau(u_-)} < \frac{1}{2}\) then there exists \(\sigma \in (0, \beta - \mu)\) such that

\[\alpha(u_+ + \varepsilon) \tau'(u_- - \varepsilon) e^{-\gamma \tau(u_- - \varepsilon)} < \frac{1}{2}\]

for all \(\varepsilon \in (0, \sigma)\). Furthermore, it follows from Corollary 3 that system (3) has exactly one interior equilibrium, i.e., the synchronous equilibrium \(E^*(v^*, u^*, v^*, u^*)\), which is locally asymptotically stable. So we only need to prove the global attractivity of \(E^*\). For each \(i = 1, 2\), let

\[\underline{v}_i = \limsup_{t \to \infty} u_i(t), \quad \bar{u}_i = \liminf_{t \to \infty} u_i(t),\]
and
\[\underline{v}_i = \limsup_{t \to \infty} v_i(t), \quad \bar{v}_i = \liminf_{t \to \infty} v_i(t).\]

In view of Theorem 5.2, we obtain \(u_\ell \leq \underline{u}_i \leq \bar{u}_i \leq u_+\) for \(i = 1, 2\). For each \(\varepsilon \in (0, \sigma)\), there exists \(t_0 > \tau_M\) such that \(u_i(t) > u_- - \varepsilon\) for all \(t > t_0, i = 1, 2\). Thus, we have

\[v_i'(t) = \alpha u_i - \gamma v_i - \alpha e^{-\gamma \tau(u_i + v_i)} u_i(t - (u_i + v_i))\]
\[u_i'(t) > \alpha e^{-\gamma \tau(u_i + v_i)} u_i(t - (u_i + v_i)) - \beta u_i^2 + \mu u_i(u_- - \varepsilon).\]

By comparison principle, \(u_i(t) \geq u_0(t)\) and \(v_i(t) \geq v_0(t)\) for all \(t > t_0\), where \((u_0(t), v_0(t))\) is the solution to the following equation

\[v_0'(t) = \alpha u_0 - \gamma v_0 - \alpha e^{-\gamma \tau(u_0 + v_0)} u_0(t - (u_0 + v_0)),\]
\[u_0'(t) = \alpha e^{-\gamma \tau(u_0 + v_0)} u_0(t - (u_0 + v_0)) - \beta u_0^2 + \mu u_0(u_- - \varepsilon),\]

with the initial values \(v_0(t_0) = v_i(t_0)\) and \(u_0(t) = \max\{u_i(t)\mid t \in [t_0 - \tau_M, t_0]\}\) for all \(t \in [t_0 - \tau_M, t_0]\). Thus, it follows from Lemma 6.5 that \(v_i \geq \hat{v}(u_- - \varepsilon)\) and \(u_i \geq \hat{u}(u_- - \varepsilon)\). Since this is true for any \(\varepsilon \in (0, \frac{1}{2} u_-)\), it follows that \(v_i \geq N_i^{u_i}\) and \(u_i \geq N_i^{v_i}\) for \(i = 1, 2\), where

\[N_i^{u_i} = \hat{v}(u_-), \quad N_i^{v_i} = \hat{u}(u_-).\]

It follows from Lemma 6.6 that

\[0 < N_i^{v_i} < u^*, \quad i = 1, 2.\]

For each \(\varepsilon \in (0, \sigma)\), it follows from (32) that there exists \(t_1 > t_0\) such that \(u_2(t) \geq N_1^{u_2} - \varepsilon\) for all \(t > t_1\). Thus, we have

\[u_1'(t) \geq \alpha e^{-\gamma \tau(u_1 + v_1)} u_1(t - (u_1 + v_1)) - \beta u_1^2 + \mu u_1(N_1^{v_2} - \varepsilon).\]
Again, by comparison principle, \( v_1(t) \geq v_{11}(t) \) and \( u_1(t) \geq u_{11}(t) \) for all \( t > t_1 \), where \( (v_{11}(t), u_{11}(t)) \) is the solution to the following system

\[
\begin{align*}
v'_{11}(t) &= \alpha u_{11} - \gamma v_{11} - \alpha e^{-\gamma(u_{11} + v_{11})} u_{11} (t - \tau (u_{11} + v_{11})), \\
u'_{11}(t) &= \alpha e^{-\gamma(u_{11} + v_{11})} u_{11} (t - \tau (u_{11} + v_{11})) - \beta u_{11}^2 + \mu u_{11} (N_{11}^{u_{11}} - \varepsilon),
\end{align*}
\]

with the initial values \( v_{11}(t_1) = v(t_1) \) and \( u_{11}(t) = \max\{u_1(t) | t \in [t_1 - \tau, t_1] \} \) for all \( t \in [t_1 - \tau, t_1] \). In view of Lemma 6.6 we have \( \lim_{t \to \infty} v_{11}(t) = \hat{v}(N_1^{u_1} - \varepsilon) \) and \( \lim_{t \to \infty} u_{11}(t) = \hat{u}(N_1^{u_1} - \varepsilon) \). Thus, we have \( v_1 \geq \hat{v}(N_1^{u_1} - \varepsilon) \) and \( u_1 \geq \hat{u}(N_1^{u_1} - \varepsilon) \). Since this is true for any \( \varepsilon \in (0, \beta - \mu) \), it follows that \( v_1 \geq N_2^{u_1} \) and \( u_1 \geq N_2^{u_1} \), where

\[
N_2^{u_1} = \hat{v}(N_1^{u_1}), \quad N_2^{u_2} = \hat{u}(N_1^{u_2}).
\]

Similarly, we have \( \bar{v}_2 \geq N_2^{u_2} \) and \( \bar{u}_2 \geq N_2^{u_2} \), where

\[
N_2^{u_2} = \hat{v}(N_1^{u_2}), \quad N_2^{u_2} = \hat{u}(N_1^{u_2}).
\]

This process can be continued to construct four sequences \( \{N_n^{u_1}\}_{n=1}^{\infty}, \{N_n^{u_1}\}_{n=1}^{\infty}, \{N_n^{u_2}\}_{n=1}^{\infty}, \text{ and } \{N_n^{u_2}\}_{n=1}^{\infty} \) as follows

\[
\begin{align*}
N_n^{u_1} &= \hat{v}(N_{n-1}^{u_1}), \quad N_n^{u_2} = \hat{u}(N_{n-1}^{u_2}), \\
N_{n+1}^{u_1} &= \hat{v}(N_{n}^{u_1}), \quad N_{n+1}^{u_2} = \hat{u}(N_{n}^{u_2}).
\end{align*}
\]

(34)

It follows from Lemma 6.6 that

\[
N_n^{u_1} < N_n^{u_2} < u^*, \quad n \geq 2, \quad i = 1, 2.
\]

(35)

Hence both \( \{N_n^{u_1}\}_{n=1}^{\infty} \) and \( \{N_n^{u_2}\}_{n=1}^{\infty} \) are monotonically increasing. It follows that \( N_1 = \lim_{n \to \infty} N_n^{u_1} \) and \( N_2 = \lim_{n \to \infty} N_n^{u_2} \) exist. Thus, we have \( N_1 = \hat{u}(N_2) \) and \( N_2 = \hat{u}(N_1) \), which, together with Lemma 6.6 implies that

\[
N_1 = N_2 = u^*.
\]

(36)

On the other hand, it follows from Theorem 5.2 that for each \( \varepsilon \in (0, \sigma) \), there exists \( t_0^* > \tau \) such that \( u_1(t) \leq u_+ + \varepsilon \) and \( u_2(t) \leq u_+ + \varepsilon \) for all \( t > t_0^* \). Thus, we have

\[
\begin{align*}
v'_1(t) &= \alpha u_1 - \gamma v_1 - \alpha e^{-\gamma(u_1 + v_1)} u_1 (t - \tau (u_1 + v_1)), \\
u'_1(t) &= \alpha e^{-\gamma(u_1 + v_1)} u_1 (t - \tau (u_1 + v_1)) - \beta u_1^2 + \mu u_1 (u_+ + \varepsilon).
\end{align*}
\]

Also, by comparison principle and Lemma 6.5 we get \( \bar{v}_1 \leq \hat{v}(u_+ + \varepsilon) \) and \( \bar{u}_1 \leq \hat{u}(u_+ + \varepsilon) \). Since this is true for any \( \varepsilon \in (0, \sigma) \), it follows that \( \bar{v}_1 \leq M_1^{u_1} \leq \hat{v}(u_+) \) and \( \bar{u}_1 \leq M_1^{u_1} \leq \hat{u}(u_+) \). It follows from Lemma 6.6 that \( u_+ \geq M_1^{u_1} \geq u^* \). Then it follows that there exists \( t_2 > t_0^* \) such that \( u_2(t) \leq M_2^{u_2} \leq \varepsilon \) for all \( t > t_2 \). Thus,

\[
\begin{align*}
u'_2(t) &\leq \alpha e^{-\gamma(u_1 + v_1)} u_2 (t - \tau (u_1 + v_1)) - \beta u_2^2 + \mu u_2 (M_1^{u_2} + \varepsilon).
\end{align*}
\]

Using similar arguments as above, we obtain four sequences \( \{M_n^{u_1}\}_{n=1}^{\infty}, \{M_n^{u_2}\}_{n=1}^{\infty}, \{M_n^{u_2}\}_{n=1}^{\infty}, \text{ and } \{M_n^{u_2}\}_{n=1}^{\infty} \) as follows

\[
\begin{align*}
M_n^{u_1} &= \hat{v}(M_{n-1}^{u_1}), \quad M_n^{u_2} = \hat{u}(M_{n-1}^{u_2}), \\
M_{n+1}^{u_1} &= \hat{v}(M_{n}^{u_1}), \quad M_{n+1}^{u_2} = \hat{u}(M_{n}^{u_2}),
\end{align*}
\]

(37)

which satisfy \( M_{n-1}^{u_1} \geq M_n^{u_1} \geq u^*, \quad i = 1, 2 \), i.e., both \( \{M_n^{u_1}\}_{n=1}^{\infty} \) and \( \{M_n^{u_2}\}_{n=1}^{\infty} \) are monotonically decreasing. It follows that \( M_1 = \lim_{n \to \infty} M_n^{u_1} \) and \( M_2 = \lim_{n \to \infty} M_n^{u_2} \).
lim_{n \to \infty} M_n^{u_2} exist. Thus, we have \(M_1 = \hat{u}(M_2)\) and \(M_2 = \hat{u}(M_1)\), which, together with Lemma 6.6 implies that

\[ M_1 = M_2 = u^*. \]  

(38)

It follows from (34), (36), (37) and (38) that

\[
\lim_{n \to \infty} N_n^{u_i} = \lim_{n \to \infty} M_n^{u_i} = u^*, \quad \lim_{n \to \infty} N_n^{v_i} = \lim_{n \to \infty} M_n^{v_i} = v^*, \quad i = 1, 2.
\]

Therefore,

\[
\liminf_{t \to \infty} u_i(t) = \limsup_{t \to \infty} u_i(t) = u^*, \quad \liminf_{t \to \infty} v_i(t) = \limsup_{t \to \infty} v_i(t) = v^*, \quad i = 1, 2,
\]

that is,

\[
\lim_{t \to \infty} u_i(t) = u^*, \quad \lim_{t \to \infty} v_i(t) = v^*, \quad i = 1, 2.
\]

Thus we complete the proof.

\[\square\]

**Remark 5.** Corollary 3 states that the synchronous equilibrium \(E^*(v^*, u^*, v^*, u^*)\) is locally asymptotically stable if \((\beta - \mu)(\gamma + \alpha) > 2\alpha\beta \varepsilon^{-\gamma \tau_m}\) and \(\tau'(z^*) > 0\). Assume further that \(\alpha u + z' \tau'(u) \varepsilon^{-\gamma \tau(u-)} < \frac{1}{2}\), then Theorem 6.7 means that \(E^*(v^*, u^*, v^*, u^*)\) is globally asymptotically stable. It is interesting to see what happens to the case where \(\alpha u + z' \tau'(u) \varepsilon^{-\gamma \tau(u-)} \geq \frac{1}{2}\). In fact, in this case, all the solutions of (3) with positive initial values eventually stay in a positively invariant set (see Theorems 5.2, 5.3 and 5.4), some of which maybe tend to \(E^*\) and the others maybe not. If the delay function \(\tau(\cdot)\) of system (3) is a constant function then it follows from Theorem 6.7 that \(E^*(v^*, u^*, v^*, u^*)\) is globally asymptotically stable if \(\beta > \mu\).

Let us now give some numerical simulations to illustrate the above results. Throughout this section we always take \(\tau(x) = 12 - 9e^{-0.1x}\). It is easy to check that \(\tau'(x) > 0, \tau''(x) < 0, \tau_m = 3, \tau_M = 12\), which satisfy all the conditions stated in the previous sections. Firstly, take \(\alpha = 2, \gamma = 0.1, \mu = 0.1\), and \(\beta = 0.365\), then it follows from Theorem 3.2 that system (3) has a unique synchronous equilibrium \(E^*(v^*, u^*, v^*, u^*)\) satisfying \(2 < u^* < 2.5\) and \(30 < v^* < 35\). Note that \(\alpha + \gamma - 2\beta u^* = 2.1 - 0.73u^* > 0.275\), then the synchronous equilibrium \(E^*(v^*, u^*, v^*, u^*)\) is locally asymptotically stable (see Theorem 4.4). Moreover, \(\alpha u^* \tau'(u^* + v^*) e^{-\gamma \tau(u^* + v^*)} < 0.0326 < \frac{1}{2}, \) which together with Theorem 6.7 implies that \(E^*(v^*, u^*, v^*, u^*)\) is globally asymptotically stable (see Figure 1).

Next, take \(\alpha = 1.5, \gamma = 0.2, \mu = 0.1\), and \(\beta = 0.365\), then it follows from Theorem 3.2 that system (3) has a unique synchronous equilibrium \(E^*(v^*, u^*, v^*, u^*)\) satisfying \(u^* \approx 1.2\) and \(v^* \approx 6.5\). Note that \(\alpha + \gamma - 2\beta u^* = 3.7 - 0.73u^* \approx 2.824 > 0\) and \(\alpha u^* \tau'(u^* + v^*) e^{-\gamma \tau(u^* + v^*)} \approx 0.0463 < \frac{1}{2}\). It follows from Theorem 6.7 that the synchronous equilibrium \(E^*(v^*, u^*, v^*, u^*)\) is globally asymptotically stable (see Figure 2).

From Figures 1 and 2, we see that all solutions converge to a positive, synchronous, and globally asymptotically stable equilibrium point even though the birth rate and death rate are quite different.

Finally, take \(\alpha = 2, \gamma = 0.1, \mu = 0.4\), and \(\beta = 0.365\). It follows from Theorem 2.4 that every solution of (3) tends to infinity as \(t\) tends to infinity (see Figure 3).
Figure 1. Simulations of system (3) illustrate that the synchronous equilibrium is globally asymptotically stable, where $\alpha = 2, \gamma = 0.1, \mu = 0.1, \beta = 0.365$.

Figure 2. Simulations of system (3) illustrate that the synchronous equilibrium is globally asymptotically stable, where $\alpha = 1.5, \gamma = 0.2, \mu = 0.1, \beta = 0.365$.

Figure 3. Simulations of system (3) illustrate that every solution of (3) is asymptotically synchronous and tends to infinity as $t$ tends to infinity, where $\alpha = 2, \gamma = 0.1, \mu = 0.4, \beta = 0.365$. 
7. Conclusions and discussions. In this paper, we have investigated a cooperative model composed of two identical species with stage structure and state-dependent maturation delays. Despite the low number of units, two-species networks with delay often display the same dynamical behaviors as large networks and, can thus be used as prototypes for us to understand the dynamics of large networks with delayed feedback. Much has been done when the function the delay is constant. When the delay is state-dependent, however, results in the aforementioned work can not be verified as the dynamical systems theory which usually requires the associated semi-flow is continuously differentiable with respect to its initial conditions.

In this paper, we are mainly concerned with the coexistence of the two species. In particular, the existence, patterns, and nonexistence of nonnegative equilibria have been established. Based on our investigation, we may hope to reveal some interesting phenomena of pattern formation in population ecology. The main results of Sections 4 and 5 are the stability analysis of equilibria and the global behaviors of solutions. Moreover, we investigate the global asymptotical stability by introducing two auxiliary systems and using the comparison principle of the state-dependent delay equations. On the one hand, these theoretical results are important for complementing the experimental and numerical observations made in populations population ecological systems, in order to understand the mechanisms underlying the state-dependent delay differential systems dynamics better. On the other hand, the results obtained in this paper suggest that the state-dependent delay plays a very important role on the dynamical behaviors of population system. A properly chosen state-dependent delay can stabilize the system, produce new equilibria, change the stability of the equilibria, and produce much more complex dynamical behaviors. Therefore, state-dependent delay may be used as a simple but efficient switch to control the dynamical behaviors of a system. This paper is only a first step toward networks modeling with state-dependent delays, which can describe more realistic complex networks. There are also some limitations in our model, for example, the two species are identical and the delay function is the same. So future work regarding this topic will include, for example, the dynamics of the following coupled system with state-dependent delay:

\[
\begin{align*}
\frac{dv_i}{dt} &= \alpha_i u_i - \gamma_i v_i - \alpha_i e^{-\gamma_i \tau_i(z_i)} u_i(t - \tau_i(z_i)), \\
\frac{du_1}{dt} &= \alpha_1 e^{-\gamma_1 \tau_1(z_1)} u_1(t - \tau_1(z_1)) - \beta_1 u_1^2 + \mu_1 u_1 u_2, \\
\frac{dv_2}{dt} &= \alpha_2 u_2 - \gamma_2 v_2 - \alpha_2 e^{-\gamma_2 \tau_2(z_2)} u_2(t - \tau_2(z_2)), \\
\frac{du_2}{dt} &= \alpha_2 e^{-\gamma_2 \tau_2(z_2)} u_2(t - \tau_2(z_2)) - \beta_2 u_2^2 + \mu_2 u_1 u_2, 
\end{align*}
\] (39)

where \( z_i = u_i + v_i, \alpha_i, \beta_i, \gamma_i, \mu_i \) are all positive constants, the state-dependent time delay functions \( \tau_i(z_i) \) are taken to be an increasing differentiable function of the total population \( z_i \), so that \( \tau_i'(z_i) \geq 0, \tau_i''(z_i) \leq 0 \), and \( \tau_m \leq \tau_i(z_i) \leq \tau_M \) with \( \tau_i(0) = \tau_m, \tau_i(+\infty) = \tau_M \), \( i = 1, 2 \). The initial condition for (3) is

\[
\begin{align*}
u_i(s) &= \varphi_i(s) \geq 0 \quad \text{for all} \quad s \in [-\tau_M, 0], \quad i = 1, 2, \\
v_i(0) &= \psi_i(0) \geq 0, \quad i = 1, 2,
\end{align*}
\]
with
\[ \psi_i(0) = \int_{-\tau_i0}^{0} \alpha_i \varphi_i(s)e^{\gamma s}ds, \quad i = 1, 2, \]
which is the number of immatures that have survived to time \( t = 0 \). Here, \( \tau_i0 \) is the maturation time of the \( i \)th species at \( t = 0 \), and the lower limit on the integral is \( -\tau_i0 \) because anyone of the \( i \)th species born before that time will have matured before time \( t = 0 \). Since \( \tau_i0 \) is the maturation time at \( t = 0 \), \( \tau_i0 \) is given by \( \tau_i0 = \tau_i(u_i(0) + v_i(0)) \), i.e.,
\[ \tau_i0 = \tau_i \left( \varphi_i(0) + \int_{-\tau_i0}^{0} \alpha_i \varphi_i(s)e^{\gamma s}ds \right), \quad i = 1, 2. \]

Note that \( \tau_i0 \) (\( i = 1, 2 \)) appear on both the left- and right-hand sides of the above equation, so that \( \tau_i0 \) (\( i = 1, 2 \)) are determined implicitly. Using similar arguments as the proof of Theorems 2.1 and 2.2, we can conclude that for a given pair of positive initial functions \( \varphi_1 \) and \( \varphi_2 \) on \([-\tau_M, 0] \), the two mature populations \( u_1(t) \) and \( u_2(t) \) of system (39) are positive and uniformly bounded away from zero. Similar to Theorem 2.3, the two mature populations \( u_1(t) \) and \( u_2(t) \) and the two immature populations \( v_1(t) \) and \( v_2(t) \) are bounded above when \( \beta_1 > \mu_1 \) and \( \beta_2 > \mu_2 \).

Our another interest is the interaction between the two species maybe not excitationary. For example, the following system may display different dynamical behaviors as (39):
\[
\begin{align*}
\frac{dv_1}{dt} &= \alpha_1 u_1 - \gamma_1 v_1 - \alpha_1 e^{-\gamma_1 \tau_1(z_1)} u_1(t - \tau_1(z_1)), \\
\frac{du_1}{dt} &= \alpha_1 e^{-\gamma_1 \tau_1(z_1)} u_1(t - \tau_1(z_1)) - \beta_1 u_1^2 + \mu_1 u_1 u_2, \\
\frac{dv_2}{dt} &= \alpha_2 u_2 - \gamma_2 v_2 - \alpha_2 e^{-\gamma_2 \tau_2(z_2)} u_2(t - \tau_2(z_2)), \\
\frac{du_2}{dt} &= \alpha_2 e^{-\gamma_2 \tau_2(z_2)} u_2(t - \tau_2(z_2)) - \beta_2 u_2^2 - \mu_2 u_1 u_2,
\end{align*}
\]
where $z_i = u_i + v_i$, $\alpha_i$, $\beta_i$, $\gamma_i$, $\mu_i$ are all positive constants, the delay functions $\tau_i(z_i)$ are taken to be the same to that of (39). In (41), we may expect for the existence of bifurcation phenomena and mode interactions. As a result of codimension two mode interaction, the primary branches may undergo secondary bifurcations to branches of mixed-mode solutions. Moreover, the primary branches above may undergo secondary Hopf bifurcations leading to periodic solutions (or quasi-periodic solutions) with trivial spatial isotropy and nontrivial spatiotemporal symmetry. In particular, we may expect that secondary branches of periodic solutions undergo further bifurcations leading to chaotic dynamics. Unfortunately, no systematic method is in the flavor of bifurcation theory for the analysis of the dynamics of state-dependent delay differential equations.

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