

A STAGE STRUCTURED PREDATOR-PREY MODEL WITH TIME DELAYS

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ABSTRACT. In this paper, a stage structured predator-prey system with two time delays (maturation delay and gestation delay) is studied. Qualitative analysis of the model such as the stability of equilibria and Hopf bifurcation is provided. By using an iterative technique and comparison arguments, sufficient conditions are derived for the global asymptotical stability of the positive equilibrium and the boundary equilibrium of the model. The special case where one of the delays can be ignored is considered, and sufficient conditions are obtained for the occurrence of a Hopf bifurcation of periodic solutions when the gestation delay is varied. It is also shown that varying the maturation delay does not affect the stability of the positive equilibrium.

1. Introduction. This paper presents the model development and analysis of predation involving species with stage structures and gestation delays. This study is motivated by the distinct characteristics at different stages of growth and development of the prey population. Such differences induced by stage structures of the prey species should not be ignored since, for example, the immature individuals cannot reproduce, while the mature may have greater survival capability in addition to their fecundity.

Stage-structured predator-prey models have received substantial in the literature [1, 2, 4–14]. Aiello and Freedman [1] proposed and studied the following now well-known single species model with structured delay

$$\begin{aligned}\dot{x}_{im}(t) &= \alpha x_m(t) - \gamma x_{im}(t) - \alpha e^{-\gamma\tau} x_m(t - \tau), \\ \dot{x}_m(t) &= \alpha e^{-\gamma\tau} x_m(t - \tau) - \beta x_m^2(t),\end{aligned}$$

where $x_{im}(t)$ and $x_m(t)$ are densities of the immature and the mature populations, respectively. This model has then been extended to cover

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situations involving multi-species interaction [6–14]. Especially, in [13], Xu and Ma studied a delayed predator-prey system with stage-structure for the prey and time delay due to the gestation of the predator. However, they neglected maturation delay for the prey. In [9], Song and Chen investigated a model of two species predator-prey with stage structure and harvesting for prey and obtained sufficient conditions for global asymptotic stability of the nonnegative equilibria. In [7, 8], the authors examined a predator prey Lotka-Volterra system with two time delays (maturation delays of prey and predator), and obtained global asymptotic stability of the unique positive equilibrium. However, in [7, 8, 9], they only considered maturation delays but not gestation delay for the predator.

In this paper, we assume that the prey has two stages and that only mature individuals can reproduce. The model does involve two time delays: gestation and maturation delays. Using an iteration technique and a comparison argument, we establish, in Section 3, global asymptotical stability of the positive equilibrium under the assumption that the product of intra-specific coefficients is greater than the product of inter-specific coefficients and the boundary equilibrium. We also discuss, in Section 4, special cases where one of the delays is ignored. In particular, we obtain sufficient conditions for the occurrence of a Hopf bifurcation of stable periodic solutions when the maturation delay is zero, and we illustrate this result with some numerical simulations. We also in this section show that varying the maturation delay does not affect the stability of the positive equilibrium. Some concluding remarks are given in the final section.

2. Model. We consider the case where the prey has two stages. The model takes the form

$$\begin{aligned}
 \dot{x}_{im}(t) &= bx_m(t) - d_1x_{im}(t) - be^{-d_1\tau_1}x_m(t - \tau_1), \\
 \dot{x}_m(t) &= be^{-d_1\tau_1}x_m(t - \tau_1) - a_1x_m^2(t) - px_m(t)y(t), \\
 \dot{y}(t) &= kpx_m(t - \tau_2)y(t - \tau_2) - d_2y(t) - a_2y^2(t),
 \end{aligned}
 \tag{1}$$

where $x_{im}(t)$ and $x_m(t)$ represent the densities of the immature and the mature of prey at time t , respectively, while $y(t)$ represents the density of the predator at time t . The model is derived under the following assumptions:

(a) The prey population: the birth of the immature population is proportional to the existing mature population with a proportionality $b > 0$; the death of the immature population is proportional to the existing immature population with a proportionality $d_1 > 0$; $\tau_1 > 0$ denotes the length of time from the birth to the maturity of the prey. The term $be^{-d_1\tau_1}x_m(t-\tau_1)$ stands for the number of the immature who were born at time $t-\tau_1$ and still survive at time t and are transferred from the immature stage to the mature stage at time t . a_1 is the intra-specific competition rate of the mature population.

(b) The predator population: the growth of the species is of a Lotka-Volterra nature. The predator feed only on the mature prey. $d_2 > 0$ is the death rate of the predator; $a_2 > 0$ is the intra-specific competition rate of the predator; $p > 0$ is the capture rate of the predator; $k > 0$ is the conversion rate of nutrients into the reproduction of the predator; $\tau_2 \geq 0$ is a constant delay due to the gestation of the predator, that is, mature adult predators.

The initial conditions for system (1) are

$$(2) \quad \begin{aligned} x_{im}(\theta) &= \varphi_1(\theta) & x_m(\theta) &= \varphi_2(\theta), & y(\theta) &= \psi(\theta), \\ \varphi_1(\theta) &\geq 0, & \varphi_2(\theta) &\geq 0, & \psi(\theta) &\geq 0, & \theta \in [-\tau, 0], \\ \varphi_1(0) &> 0, & \varphi_2(0) &> 0, & \psi(0) &> 0, \end{aligned}$$

where $\tau = \max\{\tau_1, \tau_2\}$, $R_+^3 = \{(x_1, x_2, x_3) \mid x_j \geq 0, j = 1, 2, 3\}$ and $\phi = (\varphi_1, \varphi_2, \psi) \in C([-\tau, 0], R_+^3)$.

It is biologically realistic to require the following matching condition:

$$(3) \quad x_{im}(0) = \int_{-\tau_1}^0 be^{d_1s}\varphi_2(s) ds.$$

Using (3) and the first equation of system (1), we get

$$(4) \quad x_{im}(t) = \int_{t-\tau_1}^t be^{d_1(s-t)}x_m(s) ds.$$

Theorem 2.1. *If (2) and (3) hold, then the solutions of system (1) with given initial conditions are positive for all $t \geq 0$.*

Proof. Let $(x_{im}(t), x_m(t), y(t))$ be a solution of system (1) with initial conditions (2) and (3). First we show $x_m(t) > 0$ for all $t \geq 0$. Otherwise, at least a $t_1 > 0$ must exist such that $x_m(t_1) = 0$. Denoting $t_0 = \inf \{t > 0 \mid x_m(t) = 0\}$, then $t_0 > 0$ and from the second equation of system (1), we get

$$\dot{x}_m(t_0) = \begin{cases} be^{-d_1\tau_1}\varphi_2(t_0 - \tau_1) > 0 & 0 \leq t_0 \leq \tau_1, \\ be^{-d_1\tau_1}x_m(t_0 - \tau_1) > 0 & t_0 > \tau_1, \end{cases}$$

a contradiction to the definition of t_0 . Hence, $x_m(t) > 0$ for all $t \geq 0$.

Similarly, we get $y(t) > 0$ for all $t \geq 0$.

It follows from (4) and $x_m(t) > 0$ for all $t \geq 0$ that

$$x_{im}(t) = \int_{t-\tau_1}^t be^{d_1(s-t)}x_m(s) ds > 0,$$

for all $t \geq 0$. \square

3. Global asymptotic stability. In this section, we discuss global asymptotic stability of the positive equilibrium and the boundary equilibrium of system (1).

By setting $\dot{x}_{im} = \dot{x}_m = \dot{y} = 0$ in system (1), we observe that there are two nonnegative equilibria: $E_0(0, 0, 0)$ and $E_1(x_{im}^0, x_m^0, 0)$, where

$$x_{im}^0 = \frac{b^2 e^{-d_1\tau_1}(1 - e^{-d_1\tau_1})}{a_1 d_1}, \quad x_m^0 = \frac{be^{-d_1\tau_1}}{a_1}.$$

Further, if the following condition

$$(H1) \quad bkp e^{-d_1\tau_1} > a_1 d_2$$

holds, then system (1) has a unique positive equilibrium $E^*(x_{im}^*, x_m^*, y^*)$, where

$$(5) \quad \begin{aligned} x_{im}^* &= \frac{b(1 - e^{-d_1\tau_1})(a_2 be^{-d_1\tau_1} + d_2 p)}{d_1(a_1 a_2 + kp^2)}, \\ x_m^* &= \frac{a_2 be^{-d_1\tau_1} + d_2 p}{a_1 a_2 + kp^2}, \\ y^* &= \frac{bkpe^{-d_1\tau_1} - a_1 d_2}{a_1 a_2 + kp^2}. \end{aligned}$$

We need the following well-known results.

Lemma 3.1 [7]. *The roots of equation $\lambda + 2be^{-d\tau} - be^{-\tau(\lambda+d)} = 0$, with $b, d, \tau > 0$, have negative real parts.*

Lemma 3.2 [8]. *Consider the following equation*

$$\dot{x}(t) = ax(t - \tau) - bx(t) - cx^2(t),$$

where a, b, c and τ are positive constants and $x(t) > 0$ for all $t \in [-\tau, 0]$. We have

- (i) If $a > b$, then $\lim_{t \rightarrow +\infty} x(t) = (a - b)/c$;
- (ii) If $a < b$, then $\lim_{t \rightarrow +\infty} x(t) = 0$.

Theorem 3.1. *The equilibrium E_0 is unstable. Under condition (H1), the equilibrium E_1 is unstable.*

Proof. The characteristic equation of equilibrium E_0 is

$$(\lambda + d_1)(\lambda + d_2)(\lambda - be^{-\tau_1(\lambda+d_1)}) = 0.$$

Clearly, $\lambda = -d_1$ and $\lambda = -d_2$ are always two negative zeros. All other eigenvalues are given by the solutions of $\lambda - be^{-\tau_1(\lambda+d_1)} = 0$. To show that a positive zero exists, we notice that the graph of $y = \lambda$ and $y = be^{-\tau_1(\lambda+d_1)}$ must intersect at a positive value of λ . Hence, the equilibrium E_0 is unstable.

The characteristic equation of the equilibrium E_1 is

$$(\lambda + d_1)(\lambda + 2be^{-d_1\tau_1} - be^{-\tau_1(\lambda+d_1)}) \left(\lambda + d_2 - \frac{bkpe^{-(d_1\tau_1+\lambda\tau_2)}}{a_1} \right) = 0.$$

Clearly, $\lambda = -d_1$ is always a negative zero. By Lemma 3.1, the solutions of $\lambda + 2be^{-d_1\tau_1} - be^{-\tau_1(\lambda+d_1)} = 0$ have only negative real parts. All other zeros are given by the solutions of $\lambda = \frac{bkpe^{-(d_1\tau_1+\lambda\tau_2)}}{a_1} - d_2$. We will show that a positive zero exists if $bkpe^{-d_1\tau_1} > a_1d_2$. In fact, if

we set $f(\lambda) = \lambda + d_2 - bkp e^{-(d_1\tau_1 + \lambda\tau_2)}/a_1$, then we get

$$\begin{aligned} f'(\lambda) &= 1 + \frac{bkp\tau_2 e^{-(d_1\tau_1 + \lambda\tau_2)}}{a_1} > 0, \\ f(0) &= \frac{a_1 d_2 - bkp e^{-d_1\tau_1}}{a_1} < 0, \\ \lim_{t \rightarrow +\infty} f(\lambda) &= +\infty. \end{aligned}$$

So $f(\lambda) = 0$ has a positive real part. Consequently, (H1) implies that the equilibrium E_1 is unstable. This completes the proof of Theorem 3.1. \square

Theorem 3.2. *If assumptions (H1) and*

(H2) $a_1 a_2 > kp^2$

hold, then the positive equilibrium E^ is globally asymptotically stable.*

Proof. First we show that E^* is locally asymptotically stable.

The characteristic equation of the equilibrium E^* is

$$\begin{aligned} (\lambda + d_1)[(\lambda + py^* + 2a_1x_m^* - be^{-\tau_1(\lambda+d_1)})(\lambda + d_2 + 2a_2y^* - kpx_m^* e^{-\lambda\tau_2}) \\ + kp^2x_m^*y^* e^{-\lambda\tau_2}] = 0. \end{aligned}$$

Clearly, $\lambda = -d_1$ is always a negative zero. We denote

$$\begin{aligned} g(\lambda) &= (\lambda + py^* + 2a_1x_m^* - be^{-\tau_1(\lambda+d_1)})(\lambda + d_2 + 2a_2y^* - kpx_m^* e^{-\lambda\tau_2}) \\ &\quad + kp^2x_m^*y^* e^{-\lambda\tau_2}. \end{aligned}$$

We only need to prove that the solutions of $g(\lambda) = 0$ have only negative real parts. Let $\lambda = \xi + i\eta$ (here ξ and η are real). We get

$$\begin{aligned} g(\lambda) &= (\xi + i\eta + py^* + 2a_1x_m^* - be^{-\tau_1(\xi+d_1+i\eta)})(\xi + i\eta + d_2 + 2a_2y^* \\ &\quad - kpx_m^* e^{-\tau_2(\xi+i\eta)}) + kp^2x_m^*y^* e^{-\tau_2(\xi+i\eta)} \\ &= (B_1 + A_1i)(B_2 + A_2i) + (B_3 + A_3i) = 0, \end{aligned}$$

where

$$\begin{aligned} A_1 &= \eta + be^{-\tau_1(d_1+\xi)} \sin(\eta\tau_1), \\ A_2 &= \eta + kpx_m^* e^{-\xi\tau_2} \sin(\eta\tau_2), \\ A_3 &= -kp^2x_m^*y^* e^{-\xi\tau_2} \sin(\eta\tau_2), \\ B_1 &= \xi + py^* + 2a_1x_m^* - be^{-\tau_1(d_1+\xi)} \cos(\eta\tau_1), \\ B_2 &= \xi + d_2 + 2a_2y^* - kpx_m^* e^{-\xi\tau_2} \cos(\eta\tau_2), \\ B_3 &= kp^2x_m^*y^* e^{-\xi\tau_2} \cos(\eta\tau_2). \end{aligned}$$

From the above, we get

$$B_3 = A_1A_2 - B_1B_2, \quad A_3 = -A_1B_2 - A_2B_1.$$

So, we have

$$B_3^2 + A_3^2 = (kp^2x_m^*y^* e^{-\xi\tau_2})^2,$$

and

$$\begin{aligned} B_3^2 + A_3^2 &= (A_1A_2 - B_1B_2)^2 + (-A_1B_2 - A_2B_1)^2 \\ &= (A_1A_2)^2 + (B_1B_2)^2 + (A_1B_2)^2 + (A_2B_1)^2. \end{aligned}$$

So, $(B_1B_2)^2 \leq B_3^2 + A_3^2$.

If $\xi \geq 0$, then

$$(B_1B_2)^2 \leq B_3^2 + A_3^2 \leq (kp^2x_m^*y^*)^2.$$

But

$$\begin{aligned} B_1 &\geq py^* + 2a_1x_m^* - be^{-d_1\tau_1} \\ &= (py^* + a_1x_m^* - be^{-d_1\tau_1}) + a_1x_m^* = a_1x_m^* > 0, \\ B_2 &\geq d_2 + 2a_2y^* - kpx_m^* \\ &= (d_2 + a_2y^* - kpx_m^*) + a_2y^* = a_2y^* > 0. \end{aligned}$$

Thus, $B_1B_2 \geq a_1a_2x_m^*y^* > 0$. From assumption (H2), it is easy to get $(B_1B_2)^2 > (kp^2x_m^*y^*)^2$, which is a contradiction to the above inequality. Thus, $\xi < 0$. This implies that λ has negative real part. Therefore, E^* is locally asymptotically stable.

Next, we prove that E^* is globally attractive using an iteration technique.

Assume that $(x_{im}(t), x_m(t), y(t))$ is a positive solution of system (1) with initial condition (2). Let

$$\begin{aligned} U_m &= \limsup_{t \rightarrow +\infty} \sup x_m(t), & V_m &= \liminf_{t \rightarrow +\infty} \inf x_m(t), \\ U_y &= \limsup_{t \rightarrow +\infty} \sup y(t), & V_y &= \liminf_{t \rightarrow +\infty} \inf y(t). \end{aligned}$$

In the following, we shall show that $U_m = V_m = x_m^*$, $U_y = V_y = y^*$.

From the second equation of system (1), we can get

$$\dot{x}_m(t) \leq be^{-d_1\tau_1} x_m(t - \tau_1) - a_1 x_m^2(t).$$

Therefore, by Lemma 3.2, we derive that

$$U_m = \limsup_{t \rightarrow +\infty} \sup x_m(t) \leq \frac{be^{-d_1\tau_1}}{a_1} := M_1^{x_m}.$$

Then, for $\varepsilon > 0$ sufficiently small, a $T_1 > 0$ exists such that if $t > T_1 + \tau$, $x_m(t) \leq M_1^{x_m} + \varepsilon$. We therefore derive from the third equation of system (1) that for $t > T_1 + \tau$,

$$\dot{y}(t) \leq kp(M_1^{x_m} + \varepsilon)y(t - \tau_2) - d_2y(t) - a_2y^2(t).$$

Consider the following auxiliary equation

$$\dot{v}(t) = kp(M_1^{x_m} + \varepsilon)v(t - \tau_2) - d_2v(t) - a_2v^2(t).$$

Since (H1) holds, by Lemma 3.2 we derive that

$$\limsup_{t \rightarrow +\infty} v(t) = \frac{kp(M_1^{x_m} + \varepsilon) - d_2}{a_2}.$$

By comparison, we obtain that

$$U_y = \limsup_{t \rightarrow +\infty} \sup y(t) \leq \frac{kp(M_1^{x_m} + \varepsilon) - d_2}{a_2}.$$

Since this is true for arbitrary $\varepsilon > 0$, it follows that

$$U_y \leq \frac{kpM_1^{x_m} - d_2}{a_2} := M_1^y.$$

Hence, for $\varepsilon > 0$ sufficiently small, there exists a $T_2 > T_1 + \tau$ such that if $t > T_2 + \tau$, $y(t) \leq M_1^y + \varepsilon$.

For $\varepsilon > 0$ sufficiently small, we derive from the second equation of system (1) that, for $t > T_2 + \tau$,

$$\dot{x}_m(t) \geq be^{-d_1\tau_1}x_m(t - \tau_1) - p(M_1^y + \varepsilon)x_m(t) - a_1x_m^2(t).$$

By comparison, we obtain that

$$V_m = \liminf_{t \rightarrow +\infty} \inf x_m(t) \geq \frac{be^{-d_1\tau_1} - p(M_1^y + \varepsilon)}{a_1}.$$

Since this is true for arbitrary $\varepsilon > 0$ sufficiently small, we conclude that $V_m \geq N_1^{x_m}$, where

$$N_1^{x_m} = \frac{be^{-d_1\tau_1} - pM_1^y}{a_1}.$$

Therefore, for $\varepsilon > 0$ sufficiently small, there exists a $T_3 > T_2 + \tau$ such that if $t > T_3 + \tau$, $x_m(t) \geq N_1^{x_m} - \varepsilon$.

For $\varepsilon > 0$ sufficiently small, we derive from the third equation of system (1) that, for $t > T_3 + \tau$,

$$\dot{y}(t) \geq kp(N_1^{x_m} - \varepsilon)y(t - \tau_2) - d_2y(t) - a_2y^2(t).$$

By comparison, we obtain that

$$V_y = \liminf_{t \rightarrow +\infty} \inf y(t) \geq \frac{kp(N_1^{x_m} - \varepsilon) - d_2}{a_2}.$$

Since this is true for arbitrary $\varepsilon > 0$, we conclude that $V_y \geq N_1^y$, where

$$N_1^y = \frac{kpN_1^{x_m} - d_2}{a_2}.$$

Hence, for $\varepsilon > 0$ sufficiently small, there exists a $T_4 > T_3 + \tau$ such that if $t > T_4 + \tau$, $y(t) \geq N_1^y - \varepsilon$.

For $\varepsilon > 0$ sufficiently small, it follows from the second equation of system (1) that for $t > T_4 + \tau$,

$$\dot{x}_m(t) \leq be^{-d_1\tau_1}x_m(t - \tau_1) - p(N_1^y - \varepsilon)x_m(t) - a_1x_m^2(t).$$

By comparison, we obtain that

$$U_m = \limsup_{t \rightarrow +\infty} \sup x_m(t) \leq \frac{be^{-d_1\tau_1} - p(N_1^y - \varepsilon)}{a_1}.$$

Since this is true for arbitrary $\varepsilon > 0$ sufficiently small, we conclude that $U_m \leq M_2^{x_m}$, where

$$M_2^{x_m} = \frac{be^{-d_1\tau_1} - pN_1^y}{a_1}.$$

Therefore, for $\varepsilon > 0$ sufficiently small, there exists a $T_5 > T_4 + \tau$ such that if $t > T_5 + \tau$, $x_m(t) \leq M_2^{x_m} + \varepsilon$.

For $\varepsilon > 0$ sufficiently small, it follows from the third equation of system (1) that, for $t > T_5 + \tau$,

$$\dot{y}(t) \leq kp(M_2^{x_m} + \varepsilon)y(t - \tau_2) - d_2y(t) - a_2y^2(t).$$

By comparison, we obtain that

$$U_y = \limsup_{t \rightarrow +\infty} \sup y(t) \leq \frac{kp(M_2^{x_m} + \varepsilon) - d_2}{a_2}.$$

Since this is true for arbitrary $\varepsilon > 0$, we conclude that $U_y \leq M_2^y$, where

$$M_2^y = \frac{kpM_2^{x_m} - d_2}{a_2}.$$

Hence, for $\varepsilon > 0$ sufficiently small, there exists a $T_6 > T_5 + \tau$ such that, if $t > T_6 + \tau$, $y(t) \leq M_2^y + \varepsilon$.

Continuing this process, we obtain four sequences $M_n^{x_m}$, $N_n^{x_m}$, M_n^y and N_n^y , $n = 1, 2, \dots$, such that for $n \geq 2$,

$$(6) \quad \begin{aligned} M_{n+1}^{x_m} &= \frac{be^{-d_1\tau_1} - pN_n^y}{a_1}, & N_n^{x_m} &= \frac{be^{-d_1\tau_1} - pM_n^y}{a_1}, \\ M_n^y &= \frac{kpM_n^{x_m} - d_2}{a_2}, & N_n^y &= \frac{kpN_n^{x_m} - d_2}{a_2}. \end{aligned}$$

Clearly, we have

$$N_n^{x_m} \leq V_m \leq U_m \leq M_n^{x_m}, \quad N_n^y \leq V_y \leq U_y \leq M_n^y.$$

It follows from (6) that

$$(7) \quad M_{n+1}^{x_m} = \frac{(a_2be^{-d_1\tau_1} + d_2p)(a_1a_2 - kp^2)}{a_1^2a_2^2} + \frac{k^2p^4}{a_1^2a_2^2}M_n^{x_m}.$$

Obviously $M_n^{x_m} \geq x_m^*$. It follows from (H2) $a_1a_2 > kp^2$ and (7) that

$$\begin{aligned} M_{n+1}^{x_m} - M_n^{x_m} &= \frac{(a_2be^{-d_1\tau_1} + d_2p)(a_1a_2 - kp^2)}{a_1^2a_2^2} + \frac{k^2p^4 - a_1^2a_2^2}{a_1^2a_2^2}M_n^{x_m} \\ &\leq \frac{(a_2be^{-d_1\tau_1} + d_2p)(a_1a_2 - kp^2)}{a_1^2a_2^2} + \frac{k^2p^4 - a_1^2a_2^2}{a_1^2a_2^2}x_m^* = 0. \end{aligned}$$

So, the sequence $M_n^{x_m}$ is monotonically decreasing. It follows that $\lim_{t \rightarrow +\infty} M_n^{x_m}$ exists. Taking $n \rightarrow +\infty$, we obtain from (7) that

$$(8) \quad \lim_{t \rightarrow +\infty} M_n^{x_m} = \frac{a_2be^{-d_1\tau_1} + d_2p}{a_1a_2 + kp^2} = x_m^*.$$

Similarly, we derive that

$$(9) \quad \lim_{t \rightarrow +\infty} N_n^{x_m} = x_m^*, \quad \lim_{t \rightarrow +\infty} M_n^y = y^*, \quad \lim_{t \rightarrow +\infty} N_n^y = y^*.$$

It follows from (8) and (9) that

$$U_m = V_m = x_m^*, \quad U_y = V_y = y^*.$$

We therefore have

$$\lim_{t \rightarrow +\infty} x_m(t) = x_m^*, \quad \lim_{t \rightarrow +\infty} y(t) = y^*.$$

Using L'Hospital's rule, it follows from (4) that

$$\begin{aligned} \lim_{t \rightarrow +\infty} x_{im}(t) &= \lim_{t \rightarrow +\infty} \frac{\int_{t-\tau_1}^t be^{d_1s}x_m(s) ds}{e^{d_1t}} \\ &= \lim_{t \rightarrow +\infty} \frac{be^{d_1t}x_m(t) - be^{d_1(t-\tau_1)}x_m(t-\tau_1)}{d_1e^{d_1t}} \\ &= \frac{b(1 - e^{-d_1\tau_1})}{d_1}x_m^* = x_{im}^*. \end{aligned}$$

This completes the proof of Theorem 3.2. \square

Therefore, if conditions (H1) and (H2) hold, we conclude that the unique positive equilibrium E^* is globally asymptotically stable. Biologically, condition (H2) means the product of intra-specific coefficients is greater than the product of inter-specific coefficients. Note that condition (H2) is not relevant to the birth rate b , the death rates d_1 and d_2 of immature prey and predator, the maturation delay τ_1 and the gestation delay τ_2 . It is only relevant to the intra-specific competition rate a_1, a_2 of the mature prey and predator, the capturing rate p , as well as the effective consumption rate kp of system (1).

Theorem 3.3. *If assumption*

$$(H3) \quad bkpe^{-d_1\tau_1} < a_1d_2$$

holds, then the equilibrium $E_1(x_{im}^0, x_m^0, 0)$ is globally asymptotically stable.

Proof. First, we show that the equilibrium E_1 is locally asymptotically stable. The characteristic equation of the equilibrium E_1 is

$$(\lambda + d_1)(\lambda + 2be^{-d_1\tau_1} - be^{-\tau_1(\lambda+d_1)})\left(\lambda + d_2 - \frac{bkpe^{-(d_1\tau_1+\lambda\tau_2)}}{a_1}\right) = 0.$$

Clearly, $\lambda = -d_1$ is always a negative eigenvalue. By Lemma 3.1, the solutions of $\lambda + 2be^{-d_1\tau_1} - be^{-\tau_1(\lambda+d_1)} = 0$ only have negative real parts. Next, we will prove that, under assumption (H3), all roots of the equation $\lambda + d_2 - bkpe^{-(d_1\tau_1+\lambda\tau_2)}/a_1 = 0$ have negative real parts. Let $\lambda = \xi + i\eta$ (here ξ, η are real). Then we get

$$\begin{aligned} \xi + d_2 - \frac{bkpe^{-d_1\tau_1}e^{-\xi\tau_2}\cos(\eta\tau_2)}{a_1} &= 0, \\ \eta + \frac{bkpe^{-d_1\tau_1}e^{-\xi\tau_2}\sin(\eta\tau_2)}{a_1} &= 0. \end{aligned}$$

From the above two equations, we deduce that

$$(10) \quad \left(\frac{bkpe^{-d_1\tau_1}e^{-\xi\tau_2}}{a_1}\right)^2 = (\xi + d_2)^2 + \eta^2.$$

If $\xi \geq 0$ and assumption (H3) holds, we get

$$(\xi + d_2)^2 + \eta^2 \geq \left(\xi + \frac{bkpe^{-d_1\tau_1}}{a_1}\right)^2 + \eta^2 > \left(\frac{bkpe^{-d_1\tau_1}}{a_1}\right)^2.$$

It follows from equation (10) that

$$(\xi + d_2)^2 + \eta^2 \leq \left(\frac{bkpe^{-d_1\tau_1}}{a_1} \right)^2.$$

It is a contradiction. So, $\xi < 0$. Therefore, E_1 is locally asymptotically stable.

In the following, we show that E_1 is globally attractive. From the second equation of system (1), we get

$$\dot{x}_m(t) \leq be^{-d_1\tau_1}x_m(t - \tau_1) - a_1x_m^2(t).$$

By comparison, we obtain that

$$(11) \quad \limsup_{t \rightarrow +\infty} \sup x_m(t) \leq \frac{be^{-d_1\tau_1}}{a_1} := R^{x_m}.$$

Under assumption (H3), we can choose $\varepsilon > 0$ sufficiently small such that

$$(12) \quad kp \left(\frac{be^{-d_1\tau_1}}{a_1} + \varepsilon \right) - d_2 < 0.$$

Hence, for $\varepsilon > 0$ sufficiently small satisfying (12), there exists a $T_1 > 0$ such that if $t > T_1 + \tau$, $x_m(t) \leq R^{x_m} + \varepsilon$. We therefore derive from the third equation of system (1) that, for $t > T_1 + \tau$,

$$\dot{y}(t) \leq kp(R^{x_m} + \varepsilon)y(t - \tau_2) - d_2y(t) - a_2y^2(t).$$

Consider the following auxiliary equation

$$\dot{v}(t) = kp(R^{x_m} + \varepsilon)v(t - \tau_2) - d_2v(t) - a_2v^2(t).$$

Since (12) holds, by Lemma 3.2 we derive that $\limsup_{t \rightarrow +\infty} v(t) = 0$. By comparison, we obtain $\limsup_{t \rightarrow +\infty} \sup y(t) = 0$. Hence, for $\varepsilon > 0$ sufficiently small satisfying (12), there exists a $T_2 > T_1 + \tau$ such that if $t > T_2 + \tau$, $y(t) < \varepsilon$.

It follows from the second equation of system (1) that, for $t > T_2 + \tau$,

$$\dot{x}_m(t) \geq be^{-d_1\tau_1}x_m(t - \tau_1) - \varepsilon px_m(t) - a_1x_m^2(t).$$

By comparison, we obtain that

$$\liminf_{t \rightarrow +\infty} \inf x_m(t) \geq \frac{be^{-d_1\tau_1} - \varepsilon p}{a_1}.$$

Since $\varepsilon > 0$ is arbitrarily small, we conclude that

$$\liminf_{t \rightarrow +\infty} \inf x_m(t) \geq \frac{be^{-d_1\tau_1}}{a_1},$$

which, together with (11), yields

$$\lim_{t \rightarrow +\infty} x_m(t) = \frac{be^{-d_1\tau_1}}{a_1} = x_m^0.$$

Using L'Hospital's rule, it follows from (4) that

$$\begin{aligned} \lim_{t \rightarrow +\infty} x_{im}(t) &= \lim_{t \rightarrow +\infty} \frac{\int_{t-\tau_1}^t be^{d_1s} x_m(s) ds}{e^{d_1t}} \\ &= \lim_{t \rightarrow +\infty} \frac{be^{d_1t} x_m(t) - be^{d_1(t-\tau_1)} x_m(t-\tau_1)}{d_1 e^{d_1t}} \\ &= \frac{b(1 - e^{-d_1\tau_1})}{d_1} x_m^0 = x_{im}^0. \end{aligned}$$

This completes the proof of Theorem 3.3. \square

4. Existence of Hopf bifurcation. As noted earlier, the dynamics of system (1) is determined by the following subsystem

$$\begin{aligned} \dot{x}_m(t) &= be^{-d_1\tau_1} x_m(t - \tau_1) - a_1 x_m^2(t) - px_m(t)y(t), \\ \dot{y}(t) &= kpx_m(t - \tau_2)y(t - \tau_2) - d_2y(t) - a_2y^2(t). \end{aligned}$$

In this section, we focus on two special cases where either $\tau_1 = 0$ or $\tau_2 = 0$.

4.1. Case 1. $\tau_1 = 0$. The corresponding subsystem is

$$(13) \quad \begin{aligned} \dot{x}_m(t) &= bx_m(t) - a_1 x_m^2(t) - px_m(t)y(t), \\ \dot{y}(t) &= kpx_m(t - \tau_2)y(t - \tau_2) - d_2y(t) - a_2y^2(t). \end{aligned}$$

As shown earlier, if $bkp > a_1d_2$ and the assumption (H1) hold when $\tau_1 = 0$, system (13) has a unique positive equilibrium $E^*(x_m^*, y^*)$ given by

$$(14) \quad x_m^* = \frac{a_2b + d_2p}{a_1a_2 + kp^2}, \quad y^* = \frac{bkp - a_1d_2}{a_1a_2 + kp^2}.$$

The characteristic equation at the equilibrium E^* is

$$(15) \quad \lambda^2 + A\lambda + B = (C\lambda + D)e^{-\lambda\tau_2},$$

where

$$A = (kp + a_1)x_m^* + a_2y^* > 0, \quad B = a_1x_m^*(kpx_m^* + a_2y^*) > 0, \\ C = kpx_m^* > 0, \quad D = kpx_m^*(2a_1x_m^* - b).$$

Theorem 4.1. *If*

$$4a_1kpx_m^* < a_1d_2 + bkp, \quad A^2D^2 - B^2C^2 - 2BD^2 > 0,$$

then as τ_2 increases from zero, there is a value τ_{20} such that the unique positive equilibrium E^ is locally asymptotically stable when $\tau_2 \in [0, \tau_{20})$ and unstable when $\tau_2 > \tau_{20}$. Furthermore, system (13) undergoes Hopf bifurcation at E^* when $\tau_2 = \tau_{20}$.*

Proof. Obviously, for $\tau_2 = 0$, equation (15) yields

$$(16) \quad \lambda^2 + (A - C)\lambda + (B - D) = 0,$$

where

$$A - C = a_1x_m^* + a_2y^* > 0, \quad B - D = x_m^*(bkp - a_1d_2) > 0.$$

Equation (16) has roots with negative real parts; therefore, the positive equilibrium E^* is locally asymptotically stable when $\tau_2 = 0$.

Now we check when there is a unique pair of purely imaginary roots $\pm i\omega_0$ for characteristic equation (15) at the positive equilibrium E^* .

If $\lambda = i\omega$ with $\omega > 0$ is a root of equation (15), then by separating real and imaginary parts, we have the following

$$(17) \quad \begin{aligned} B - \omega^2 &= D \cos(\omega\tau_2) + C\omega \sin(\omega\tau_2), \\ A\omega &= C\omega \cos(\omega\tau_2) - D \sin(\omega\tau_2). \end{aligned}$$

Squaring and adding both equations of (17), we get

$$(18) \quad \omega^4 + (A^2 - 2B - C^2)\omega^2 + (B^2 - D^2) = 0,$$

where

$$\begin{aligned} A^2 - 2B - C^2 &= 2a_2kpx_m^*y^* + (a_1x_m^*)^2 + (a_2y^*)^2 > 0, \\ B - D &= x_m^*(bkp - a_1d_2) > 0, \quad B + D = x_m^*(4a_1kpx_m^* - a_1d_2 - bkp). \end{aligned}$$

As $4a_1kpx_m^* < a_1d_2 + bkp$ means $B^2 - D^2 < 0$, we conclude that there is a unique positive ω_0 satisfying equation (18). Therefore, the characteristic equation (15) has a pair of purely imaginary roots $\pm i\omega_0$. From equation (17) it follows that the corresponding τ value, τ_{2n} , to the given ω_0 is

$$\tau_{2n} = \frac{1}{\omega_0} \arccos \left\{ \frac{(B - \omega_0^2)D + AC\omega_0^2}{C^2\omega_0^2 + D^2} \right\} + \frac{2n\pi}{\omega_0}, \quad n = 0, 1, 2, \dots$$

For $\tau_2 = 0$, E^* is stable. Hence by Butler's lemma [3], E^* remains stable for $\tau_2 < \tau_{20}$.

Now we would like to show

$$\left. \frac{d(\operatorname{Re}\lambda)}{d\tau_2} \right|_{\tau_2 = \tau_{2n}} > 0.$$

This will signify that at least one eigenvalue exists with positive real part for $\tau_2 > \tau_{2n}$. Now differentiating equation (15) with respect τ_2 , we get

$$\left[2\lambda + A - e^{-\lambda\tau_2}(C - C\lambda\tau_2 - D\tau_2) \right] \frac{d\lambda}{d\tau_2} = -\lambda(C\lambda + D)e^{-\lambda\tau_2}.$$

That is,

$$\begin{aligned} \left(\frac{d\lambda}{d\tau_2}\right)^{-1} &= \frac{2\lambda + A - e^{-\lambda\tau_2}(C - C\lambda\tau_2 - D\tau_2)}{-\lambda(C\lambda + D)e^{-\lambda\tau_2}} \\ &= \frac{2\lambda + A}{-\lambda(C\lambda + D)e^{-\lambda\tau_2}} + \frac{C}{\lambda(C\lambda + D)} - \frac{\tau_2}{\lambda} \\ &= \frac{\lambda^2 - B}{-\lambda^2(\lambda^2 + A\lambda + B)} - \frac{D}{\lambda^2(C\lambda + D)} - \frac{\tau_2}{\lambda}. \end{aligned}$$

Thus,

$$\begin{aligned} &\text{sign} \left\{ \frac{d(\text{Re } \lambda)}{d\tau_2} \right\}_{\lambda=i\omega_0} \\ &= \text{sign} \left\{ \text{Re} \left(\frac{d\lambda}{d\tau_2} \right)^{-1} \right\}_{\lambda=i\omega_0} \\ &= \text{sign} \left\{ \text{Re} \left[\frac{\lambda^2 - B}{-\lambda^2(\lambda^2 + A\lambda + B)} \right]_{\lambda=i\omega_0} - \text{Re} \left[\frac{D}{\lambda^2(C\lambda + D)} \right]_{\lambda=i\omega_0} \right\} \\ &= \text{sign} \left\{ \text{Re} \left[\frac{-B - \omega^2}{\omega^2(B - \omega^2 + A\omega i)} + \frac{D}{\omega^2(D + C\omega i)} \right] \right\} \\ &= \text{sign} \left\{ \frac{C^2\omega^4 + 2D^2\omega^2 + (A^2D^2 - B^2C^2 - 2BD^2)}{(D^2 + C^2\omega^2)[(B - \omega^2)^2 + A^2\omega^2]} \right\}. \end{aligned}$$

We can rewrite the numerator as follows. Let

$$V = \omega^2, f(\omega) = C^2\omega^4 + 2D^2\omega^2 + (A^2D^2 - B^2C^2 - 2BD^2).$$

Then,

$$f(V) = C^2V^2 + 2D^2V + (A^2D^2 - B^2C^2 - 2BD^2)$$

and

$$f'(V) = 2C^2V + 2D^2 > 0, \quad (V > 0),$$

which means that $f(\omega)$ is monotonically increasing on $[0, +\infty)$. We know $f(0) = A^2D^2 - B^2C^2 - 2BD^2 > 0$ and we have $f(\omega) > 0$ for $\omega > 0$. Then we obtain

$$\left. \frac{d(\text{Re } \lambda)}{d\tau_2} \right|_{\tau_2=\tau_{2n}, \omega=\omega_0} > 0.$$

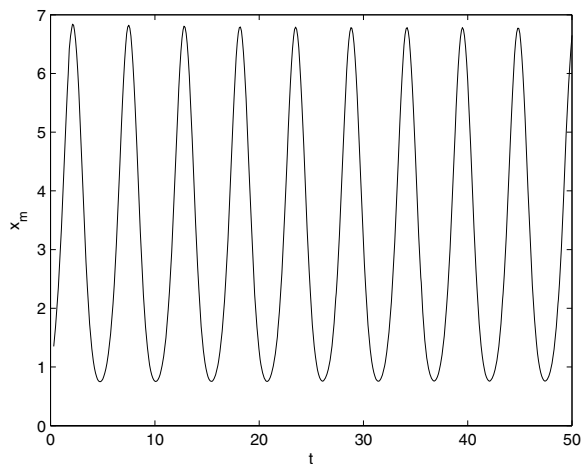


FIGURE 1. x_m as a function of t for system (13) with $\tau_2 = 0.9500 > \tau_{20}$, indicating that a Hopf bifurcation of stable periodic solutions from E^* occurs.

Therefore, the transversality condition holds and Hopf bifurcation occurs at $\tau_2 = \tau_{2n}$, $\omega = \omega_0$. This completes the proof of Theorem 4.1. \square

Here are some numerical simulations: where $b = 3$, $d_1 = 0.5$, $d_2 = 0.9$, $p = 1$, $k = 1$, $a_1 = 0.2$, $a_2 = 0.7$. It follows that the conditions of Theorem 4.1 are satisfied. Therefore, at $\tau_{20} \approx 0.5307$, Hopf bifurcation occurs. Figures 1–3 display a Hopf bifurcation of stable periodic solutions when $\tau_2 = 0.9500$.

4.2. Case 2. $\tau_2 = 0$. The subsystem of system (1) with $\tau_2 = 0$ becomes

$$(19) \quad \begin{aligned} \dot{x}_m(t) &= be^{-d_1\tau_1}x_m(t - \tau_1) - a_1x_m^2(t) - px_m(t)y(t), \\ \dot{y}(t) &= kpx_m(t)y(t) - d_2y(t) - a_2y^2(t). \end{aligned}$$

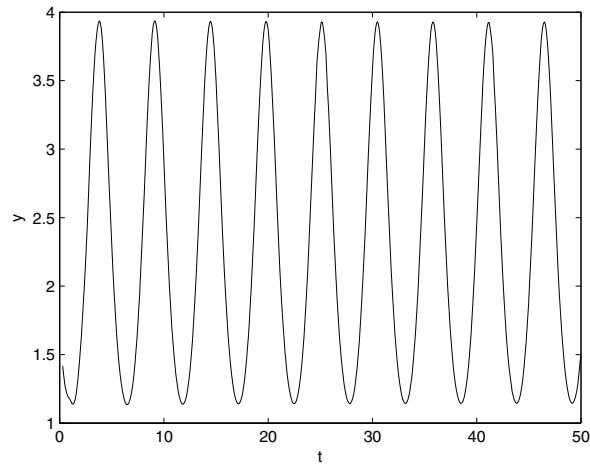


FIGURE 2. y as a function of t for system (13) with $\tau_2 = 0.9500 > \tau_{20}$, indicating that a Hopf bifurcation of stable periodic solutions from E^* occurs.

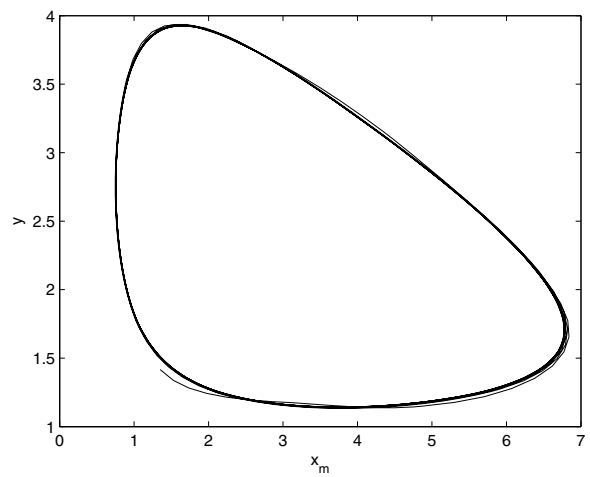


FIGURE 3. The periodic solutions for system (13) with $\tau_2 = 0.9500 > \tau_{20}$.

When condition (H1), $bkpe^{-d_1\tau_1} > a_1d_2$, holds, system (19) has a unique positive equilibrium $E^*(x_m^*, y^*)$, where

$$x_m^* = \frac{a_2be^{-d_1\tau_1} + d_2p}{a_1a_2 + kp^2}, \quad y^* = \frac{bkpe^{-d_1\tau_1} - a_1d_2}{a_1a_2 + kp^2}.$$

The characteristic equation of the equilibrium E^* is

$$(20) \quad D(\lambda, \tau_1) := \lambda^2 + a(\tau_1)\lambda + b_0(\tau_1)\lambda e^{-\lambda\tau_1} + c(\tau_1) + d(\tau_1)e^{-\lambda\tau_1} = 0.$$

Denote

$$(21) \quad P(\lambda, \tau_1) := \lambda^2 + a(\tau_1)\lambda + c(\tau_1), \quad Q(\lambda, \tau_1) = b_0(\tau_1)\lambda + d(\tau_1),$$

where

$$(22) \quad \begin{aligned} a(\tau_1) &= a_1x_m^* + a_2y^* + be^{-d_1\tau_1} > 0, & b_0(\tau_1) &= -be^{-d_1\tau_1} < 0, \\ c(\tau_1) &= y^*(2a_2be^{-d_1\tau_1} + d_2p) > 0, & d(\tau_1) &= -a_2be^{-d_1\tau_1}y^* < 0. \end{aligned}$$

Clearly, $c(\tau_1) + d(\tau_1) = y^*(a_2be^{-d_1\tau_1} + d_2p) > 0$, which implies $\lambda = 0$ can never be a root of equation (20). When $\tau_1 = 0$, equation (20) reduces to

$$(23) \quad \lambda^2 + (a + b_0)\lambda + c + d = 0,$$

where

$$a + b_0 = a_1x_m^* + a_2y^* > 0.$$

This shows that equation (23) has roots with negative real parts, implying that E^* is locally asymptotically stable when $\tau_1 = 0$.

Theorem 4.2. *There is no purely imaginary root for characteristic equation (20) at positive equilibrium E^* . That is, varying τ_1 does not affect the stability of system (19).*

Proof. Let $\lambda = i\omega$. In equation (21), we have

$$F(\omega, \tau_1) = |P(i\omega, \tau_1)|^2 - |Q(i\omega, \tau_1)|^2 = (c - \omega^2)^2 + \omega^2a^2 - (\omega^2b_0^2 + d^2).$$

Hence, $F(\omega, \tau_1) = 0$ implies

$$(24) \quad \omega^4 - \omega^2(b_0^2 + 2c - a^2) + (c^2 - d^2) = 0,$$

and its roots are given by

$$\omega_+^2 = \frac{1}{2}\{(b_0^2 + 2c - a^2) + \Delta^{1/2}\}, \quad \omega_-^2 = \frac{1}{2}\{(b_0^2 + 2c - a^2) - \Delta^{1/2}\},$$

where

$$\begin{aligned} \Delta &= (b_0^2 + 2c - a^2)^2 - 4(c^2 - d^2), \\ c^2 - d^2 &= (y^*)^2(a_2be^{-d_1\tau_1} + d_2p)(3a_2be^{-d_1\tau_1} + d_2p) > 0. \end{aligned}$$

To ensure that equation (24) has at least one positive root, the following conditions must be satisfied:

$$(25) \quad b_0^2 + 2c - a^2 > 0, \quad \Delta \geq 0.$$

First, we assume that $b_0^2 + 2c - a^2 > 0$ holds. By (22), we can get $a^2 - b_0^2 > 0$. So,

$$(26) \quad 0 < a^2 - b_0^2 < 2c.$$

By (22) and (26), we get

$$\begin{aligned} \Delta &= (b_0^2 + 2c - a^2)^2 - 4(c^2 - d^2) \\ &= (b_0^2 + 4c - a^2)(b_0^2 - a^2) + 4d^2 \\ &= (a^2 - b_0^2)^2 - 4c(a^2 - b_0^2) + 4d^2 \\ &< 2c(a^2 - b_0^2) - 4c(a^2 - b_0^2) + 4d^2 \\ &= 4d^2 - 2c(a^2 - b_0^2) \\ &= 4(a_2be^{-d_1\tau_1}y^*)^2 - 2y^*(2a_2be^{-d_1\tau_1} + d_2p)(a_1x_m^* + a_2y^* + 2be^{-d_1\tau_1}) \\ &\quad (a_1x_m^* + a_2y^*) \\ &= -4a_2be^{-d_1\tau_1}y^*[(a_1x_m^* + a_2y^*)^2 + be^{-d_1\tau_1}(2a_1x_m^* + a_2y^*)] \\ &\quad - 2d_2py^*(a_1x_m^* + a_2y^* + 2be^{-d_1\tau_1})(a_1x_m^* + a_2y^*) \\ &< 0, \end{aligned}$$

contradicting (25).

Clearly, equation (24) has no positive roots. So, there is no purely imaginary root for characteristic equation (20) at the positive equilibrium E^* . This completes the proof of Theorem 4.2. \square

5. Discussion. In this paper, we studied a predator-prey system with stage-structured prey population. The model involves two time delays: gestation and maturation. Using an iteration technique and a comparison argument, we established sufficient conditions for the global asymptotical stability of the positive equilibrium and the boundary equilibrium. These conditions require the product of intra-specific coefficients to be greater than the product of inter-specific coefficients and are relevant only to the intra-specific competition rates of the mature prey and predator, the capturing rate, and the effective consumption rate. We also discussed special cases where one of the delays is ignored. In particular, we obtained sufficient conditions for the occurrence of a Hopf bifurcation of stable periodic solutions when the maturation delay is zero, and we also showed that varying the maturation delay does not affect stability of the positive equilibrium.

The sufficient conditions provided in [8, 9] for global stability of the positive steady state depend upon time delay. In [13], Xu gave a numerical simulation to show the existence of Hopf bifurcation as gestation delay varies. However, the sufficient conditions obtained in this paper do not depend upon the two time delays. Furthermore, the sufficient conditions shown in Theorem 4.1 indicate that a Hopf bifurcation occurs as gestation delay increases, and this result is confirmed by numerical investigation (see Figure 2 in more detail). Our results also show that the maturation delay does not affect the stability of the positive equilibrium, which is consistent with the results obtained in [7].

It remains a challenging but interesting problem whether the local Hopf bifurcation can be continued for all large gestation delays.

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