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Analysis of dynamics in an eco-epidemiological model with stage structure

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Abstract

This paper is devoted to the study of an eco-epidemiological model with stage structure in the predator and disease in the prey. To begin with, the positivity and boundedness of the solutions are obtained. This shows that the system possesses a bounded absorbing set. Then, by using the LaSalle-Lyapunov invariance principle, limit equation theory, and a geometrical criterion for analyzing the distribution of the eigenvalues, the stability of the boundary equilibria and interior equilibrium are established, respectively. Meanwhile, the existence of Hopf bifurcations is obtained when the delay τ varies in a limitary region. Furthermore, by employing center manifold theory and the normal form method, an algorithm for determining the direction and stability of the Hopf bifurcation is derived. At last, some numerical simulations are carried out for illustrating the analytic results.

Keywords: eco-epidemiological model; time delay; stage structure; stability; Hopf bifurcation

1 Introduction

Ecological models that reveal the amounts of prey and predator have long been and still will be investigated for their universal existence and importance. After the fundamental work of Lotka and Volterra for predator-prey interactions in the middle of 1920s, predator-prey models were studied extensively [1–8]. Some literature considered the stage structure, assuming the immature predator does not consume the prey. Suppose the constant death rate of the immature predator to be d, then the livability is e^{-dt} after t time passed. An epidemiological model is also widely studied. The most frequent types are SI, SIS, SIR, and SIRS. As is well known, the basic reproduction number R_0 makes a significant role in such model. It presents the average number of new susceptible cells acquired from a single infected cell, and determines the persistence of the disease.

The so-called eco-epidemiological model is the combination of infection into ecological model. It contains two types mainly: disease in the predator [2] and disease in the prey [3–5, 9, 10]. When we have disease in the prey, the predator may consume on both the healthy and infected prey [3, 4]. Sometimes the infected ones are weaker or say, their habitats are accessible to the predator (*e.g.* infected fish stay close to the water surface and thus are easy to capture). The literature shows that the predation rate on infected prey may be 31 times higher than on susceptible prey [6]. Thus sometimes it is reasonable to say that the predators consume the infected prey only [5]. The pioneer work for study of eco-epidemiological model is Anderson and May [7] in 1986. After that, Chattopadhyay and Arino [4] used the name 'eco-epidemiological' first. For the detailed evolution of eco-epidemiological model we refer to Bairagi and Chattopadhyay [8].

Usually, an eco-epidemiological model of SI type contains three variables: the susceptible prey $S(t)$, infected prey $I(t)$, and predator $P(t)$. We have the following assumptions:

- Only susceptible prey are capable to reproduce under the logistic law with intrinsic birth rate constant $r > 0$ and carrying capacity $K > 0$, while the infected prey also contribute to the carrying capacity.
- The bilinear incidence with rate ξ make the disease spreads from infected to susceptible prey.
- Suppose the infected prey are vulnerable, thus easier to catch, so the predation on susceptible prey is ignored. The predation on infected prey follows a Holling type II response function.
- The natural death rates of infected prey and predator are μ and d_1, respectively. Assume d_2 to be death rate of predator due to consuming of infected prey, so the total death rate of predator is $d = d_1 + d_2$. Furthermore, assume the predator has no food source other than infected prey, and the toxicity level is taken to be low enough that eating infected prey does more good than harm.

Chattopadhyay and Bairagi [9] have proposed an eco-epidemiological model in the following form:

$$\begin{aligned}
\dot{S} &= rS\left(1 - \frac{S+I}{K}\right) - \xi IS, \\
\dot{I} &= \xi IS - \frac{mIP}{a+I} - \mu I, \\
\dot{P} &= \frac{m\alpha IP}{a+I} - dP.
\end{aligned} \tag{1.1}$$

The local and global stability of the system (1.1) around the biologically feasible equilibria is obtained in [9].

It is realistic and interesting for us to construct the stage-structured eco-epidemiological model and study the combined effects of stage structure and mutual interference by predators. On the meaning of the construction of a stage-structured eco-epidemiological model we refer to Liu and Beretta [11]. Most existing stage-structure models (see [12–15] and the references therein) deal with single species growth, which assumes a constant resource supply [16]. Gourley and Kuang [16] formulated a robust stage-structured predator-prey model with the assumption that stage-structured consumer species growth is a combined result of birth and death processes, both of which are closely linked to the dynamical supply of resource. Enlightened by the modeling methods in [16] and based on the model (1.1), we formulate the robust stage-structured eco-epidemiological model as follows:

$$\begin{aligned}
\dot{S}(t) &= rS(t)\left(1-\frac{S(t)+I(t)}{K}\right)-\xi I(t)S(t),\\
\dot{I}(t) &= \xi I(t)S(t)-\frac{mI(t)P(t)}{a+I(t)}-\mu I(t),\\
\dot{p}(t) &= \frac{m\alpha I(t)P(t)}{a+I(t)}-\frac{m\alpha I(t-\tau)P(t-\tau)}{a+I(t-\tau)}e^{-d_1\tau}-d_1p(t),\\
\dot{P}(t) &= \frac{m\alpha I(t-\tau)P(t-\tau)}{a+I(t-\tau)}e^{-d_1\tau}-dP(t),
\end{aligned}\tag{1.2}$$

where $S(t)$ and $I(t)$ are as mentioned above, $p(t)$ and $P(t)$ represent the immature and mature predator densities, respectively. We assume that the immature predators suffer a mortality rate of d_1 (the through-stage death rate) and take τ units of time to mature; thus $e^{-d_1\tau}$ is the surviving rate of each immature predator to reach maturity.

Notice that the first, second, and fourth equations of system (1.2) are independent of the variable $p(t)$, we see that $(S(t), I(t), P(t))$ satisfy the following system:

$$\begin{aligned}
\dot{S}(t) &= rS(t)\left(1-\frac{S(t)+I(t)}{K}\right)-\xi I(t)S(t),\\
\dot{I}(t) &= \xi I(t)S(t)-\frac{mI(t)P(t)}{a+I(t)}-\mu I(t),\\
\dot{P}(t) &= \frac{m\alpha I(t-\tau)P(t-\tau)}{a+I(t-\tau)}e^{-d_1\tau}-dP(t).
\end{aligned}\tag{1.3}$$

The purpose of the paper is to study the dynamics of (1.3). The rest of this paper is organized as follows: In Section 2, the properties of the solutions such as positivity and boundedness are obtained. In Section 3.1 the stability of the boundary equilibria are specified by using an eigenvalue analysis and the LaSalle-Lyapunov method. The existence and properties of a Hopf bifurcation are investigated in Sections 3.2 and 3.3, respectively. Finally, some simulations are carried out for illustrating the analytic results in Section 4.

2 Positivity and boundedness

In this section, we shall investigate the positivity and boundedness of the solutions of system (1.3) with nonnegative initial conditions. Define $\mathcal{C}=\mathcal{C}([-\tau,0],\mathbb{R})$, then $\mathcal{C}$ is a Banach space under the norm

$$|\varphi| = \sup_{\theta\in[-\tau,0]}\left|\varphi(\theta)\right|.$$

Hence, $\mathbb{R}\times\mathcal{C}\times\mathcal{C}$ can be regarding as a phase space of system (1.3). In the following, we consider system (1.3) with nonnegative initial condition:

$$\varphi_i(\theta)\geq 0 \quad \text{on } -\tau\leq\theta\leq 0\ (i=1,2,3),\tag{2.1}$$

where $\varphi_1(\theta)\equiv \text{const}\in\mathbb{R}$. We have the following conclusion.

Theorem 2.1 *The solutions of system* (1.3) *with initial condition* (2.1) *are nonnegative and uniformly eventually bounded.*

Proof Let $(S(t), I(t), P(t))$ be the solution of (1.3) with initial condition (2.1). Then from the first and second equation in (1.3) we have

$$S(t) = \varphi_1(0)e^{\int_0^t [r(1-\frac{S(\sigma)+I(\sigma)}{K})-\xi I(\sigma)]\,\mathrm{d}\sigma}$$

and

$$I(t) = \varphi_2(0)e^{\int_0^t [\xi S(\sigma)-\frac{mP(\sigma)}{a+I(\sigma)}-\mu]\,\mathrm{d}\sigma},$$

respectively. These show that $S(t) \geq 0$ and $I(t) \geq 0$ for all $t \geq 0$. Particularly, $S(t) > 0$ when $\varphi_1(0) > 0$, and $I(t) > 0$ when $\varphi_2(0) > 0$, for all $t \geq 0$. And $S(t) \equiv 0$ when $\varphi_1(0) = 0$, and $I(t) \equiv 0$ when $\varphi_2(0) = 0$.

Next we show that $P(t) \geq 0$. From the third equation in (1.3) we have

$$\dot{P} = \frac{m\alpha\varphi_2(t-\tau)\varphi_3(t-\tau)}{a+\varphi_2(t-\tau)}e^{-d_1\tau} - dP, \quad \text{for } t \in [0,\tau].$$

Then by φ_2 and φ_3 being both nonnegative, it follows that $\dot{P} \geq -dP$. This implies that

$$P(t) \geq \varphi_3(0)e^{-dt} \geq 0 \quad \text{for } t \in [0,\tau].$$

For $t \in [\tau, 2\tau]$, from the third equation in (1.3) and the discussion above, we have

$$\dot{P} = \frac{m\alpha I(t-\tau)P(t-\tau)}{a+I(t-\tau)}e^{-d_1\tau} - dP \geq -dP.$$

This implies that

$$P(t) \geq P(\tau)e^{-d(t-\tau)} \geq 0 \quad \text{for } t \in [\tau, 2\tau].$$

By mathematical induction, one can obtain $P(t) \geq 0$ for any positive integer n and $t \in [n\tau, (n+1)\tau]$. Hence we have $P(t) \geq 0$ for all $t \geq 0$.

We choose the following function:

$$y(t) = S(t) + I(t) + \frac{e^{d_1\tau}}{\alpha}P(t+\tau),$$

to consider the boundedness of positive solutions. Calculating the derivative of $y(t)$ along the solution of system (1.3), we get

$$\dot{y}(t) = rS\left(1 - \frac{S+I}{K}\right) - \mu I - \frac{de^{d_1\tau}}{\alpha}P(t+\tau).$$

Then there exists a positive constant δ ($\delta \leq \min(\mu, d)$), such that

$$\dot{y} + \delta y \leq (r+\delta)S - \frac{r}{K}S^2.$$

Then we obtain

$$\dot{y} + \delta y \leq c,$$

where $c = \frac{K(r+\delta)^2}{4r}$. Thus $\overline{\lim}_{t\to\infty} y(t) \le \frac{c}{\delta}$. This implies that, for any nonnegative solution $(S(t), I(t), P(t))$, of (1.3), there exists a $T \ge \tau$ such that

$$S(t) + I(t) + \frac{e^{d_1\tau}}{\alpha} P(t+\tau) < c + \varepsilon, \quad t > T,$$

where ε is some positive number. Hence, the nonnegative solutions of system (1.3) is uniformly eventually bounded. □

Remark 2.2 From the proof above, we have $|P_t| < \alpha e^{-d_1\tau}(c+\varepsilon)$ when $t > T + \tau$.

Lemma 2.3 *For system* (1.3) *with initial condition* (2.1), *if* $|\varphi_1 + \varphi_2| < K$, *then*

$$S(t) + I(t) < K \quad \textit{for } t \ge 0.$$

In fact, from the first and second equations in (1.3) we have

$$\frac{d}{dt}(S+I) = rS\left(1 - \frac{S+I}{K}\right) - \frac{mIP}{a+I} - \mu I. \tag{2.2}$$

In the case of $\varphi_2(0) = 0$, by the expression of $I(t)$ we know that $I(t) \equiv 0$. Hence (2.2) becomes

$$\frac{dS}{dt} = rS\left(1 - \frac{S}{K}\right).$$

This implies that $S(t) < K$ when $\varphi_1 < K$, that is, $S(t) + I(t) < K$ for $t \ge 0$.

In the case of $\varphi_2(0) > 0$, by the expression of $I(t)$ we know that $I(t) > 0$ for $t \ge 0$. For a contradiction, we assume that there exists a $t_0 > 0$ such that

$$S(t) + I(t) \le K \quad \text{for } t \in [0, t_0),$$

and $S(t_0) + I(t_0) = K$. Then it follows that

$$\left.\frac{d}{dt}(S+I)\right|_{t=t_0} = -\frac{mI(t_0)P(t_0)}{a + I(t_0)} - \mu I(t_0) < 0.$$

The contradiction implies that the conclusion follows.

Let $\mathbb{R}_+ = [0, \infty)$ and $\mathcal{C}^+ = \mathcal{C}([-\tau, 0], \mathbb{R}_+)$. Define

$$\Gamma = \left\{(\varphi_1, \varphi_2, \varphi_3) \in \mathbb{R}_+ \times \mathcal{C}^+ \times \mathcal{C}^+ : |\varphi_1 + \varphi_2| < K, |\varphi_3| < \left(\frac{c}{\delta} + \varepsilon\right)\alpha e^{-d_1\tau}\right\},$$

where c and δ are in the denotation of the previous proof, ε is arbitrarily small positive number.

By Theorem 2.1 and Lemma 2.3 we know that all solutions eventually enter and remain in the region Γ. This means that, for (1.3), Γ is a bounded absorbing set.

3 Stability and existence of Hopf bifurcation

In this section, we shall investigate the stability of the nonnegative equilibria of system (1.3) and the existence of a Hopf bifurcation.

3.1 Boundary equilibria and their stability

Clearly, system (1.3) always has two nonnegative equilibria given by

$$E_0 : (0,0,0) \quad \text{and} \quad E_1 : (K,0,0).$$

And when

$$R_0 := \frac{K\xi}{\mu} > 1 \tag{3.1}$$

is satisfied, another boundary equilibrium is given by

$$E_2 : (\overline{S},\overline{I},0) = \left(\frac{\mu}{\xi}, \frac{r(K\xi-\mu)}{\xi(r+K\xi)}, 0\right).$$

Moreover, we make the following assumption:

$$m\alpha e^{-d_1\tau} - d > 0 \tag{3.2}$$

throughout this paper, and when

$$R_1 := \frac{K\xi}{\mu} - \frac{ad\xi(K\xi+r)}{r\mu(m\alpha e^{-d_1\tau}-d)} > 1 \tag{3.3}$$

is satisfied, system (1.3) has a unique positive equilibrium given by

$$\begin{aligned} E^* &:= \left(S^*, I^*, P^*\right) \\ &= \left(K - \frac{ad(K\xi+r)}{r(m\alpha e^{-d_1\tau}-d)}, \frac{ad}{m\alpha e^{-d_1\tau}-d}, \frac{1}{m}\left(a+I^*\right)\left(\xi S^*-\mu\right)\right). \end{aligned} \tag{3.4}$$

In fact, (3.3) is equivalent to

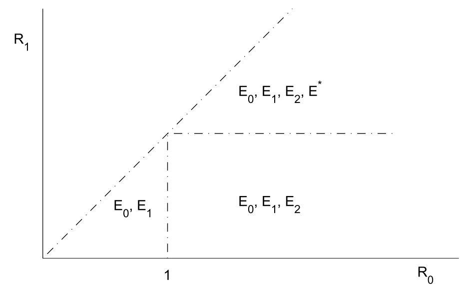
$$K - \frac{ad(K\xi+r)}{r(m\alpha e^{-d_1\tau}-d)} > \frac{\mu}{\xi},$$

hence $S^* > 0$, and $P^* > 0$.

Clearly, $R_0 > R_1$. And R_0 is the basic reproduction number of infection for (1.3) with $\tau = 0$. On the definition of the basic reproduction number of infection, we refer to [17]. In the following, we use the notations introduced in [17]. Then system (1.3) with $\tau = 0$ is rewritten in the following form:

$$\begin{aligned} \dot{I} &= \xi IS - \frac{mIP}{a+I} - \mu I, \\ \dot{S} &= rS\left(1 - \frac{S+I}{K}\right) - \xi IS, \\ \dot{P} &= \frac{m\alpha IP}{a+I} - dP. \end{aligned}$$

Figure 1 Regions of equilibria existence in (R_0, R_1) plane.



Then the infected compartment is I with $m = 1$ and $n = 3$. Meanwhile,

$$\mathscr{F} = \begin{pmatrix} \xi IS \\ 0 \\ 0 \end{pmatrix}$$

and

$$\mathscr{V} = \begin{pmatrix} \frac{mIP}{a+I} + \mu I \\ \xi IS - rS(1 - \frac{S+I}{K}) \\ dP - \frac{m\alpha IP}{a+I} \end{pmatrix}.$$

The equilibrium solution with $I = 0$ is $E_1(0, K, 0)$. Following the description in [17] we have

$$F = \left(\frac{\partial \mathscr{F}_1}{\partial I}\right)\bigg|_{(0,K,0)} = \xi S|_{(0,K,0)} = K\xi,$$

$$V = \left(\frac{\partial \mathscr{V}_1}{\partial I}\right)\bigg|_{(0,K,0)} = \frac{amP}{(a+I)^2} + \mu\bigg|_{(0,K,0)} = \mu.$$

Thus the basic reproduction number of infection is $R_0 = \rho(FV^{-1}) = \frac{K\xi}{\mu}$.

Define

$$\tau^0 = \frac{1}{d_1} \ln \frac{m\alpha}{d + \frac{ad\xi(K\xi+r)}{r(K\xi-\mu)}}. \tag{3.5}$$

Then from the discussion above we know that, under the assumption (3.1), system (1.3) has a positive equilibrium when $0 \leq \tau < \tau^0$.

We can see that the value of R_0 and R_1 are significant to the existence of equilibria, for intuit, we divide the $\frac{1}{8}$ plane ($R_0 > R_1 > 0$) of existence regions for the equilibria into three parts as in Figure 1.

In this figure, the oblique line denotes $R_0 = R_1$. When $0 < R_1 < R_0 < 1$, E_0 and E_1 exist; when $0 < R_1 < 1 < R_0$, E_0, E_1, and E_2 exist; when $1 < R_1 < R_0$, E_0, E_1, E_2, and E^* exist. In the following we study the stability of the nonnegative equilibria.

Theorem 3.1 *For system* (1.3), *the following statements are true.*

(i) E_0 *is always unstable.*

(ii) E_1 *is globally asymptotically stable in* Γ *when* $R_0 < 1$ *and unstable when* $R_0 > 1$.

(iii) E_2 *is asymptotically stable in* Γ *when* $R_1 < 1 < R_0$.

Proof (i) The linearization of (1.3) at the origin E_0 is given by

$$\dot{S} = rS,$$
$$\dot{I} = -\mu I,$$
$$\dot{P} = -dP.$$

Its characteristic equation is

$$(\lambda - r)(\lambda + \mu)(\lambda + d) = 0.$$

Notice that $\lambda_1 = r > 0$, then E_0 is unstable.

(ii) The linearization of (1.3) at the fixed point $E_1 = (K, 0, 0)$ is given by

$$\dot{S} = -rS - (r + K\xi)I,$$
$$\dot{I} = (\xi K - \mu)I,$$
$$\dot{P} = -dP,$$

whose characteristic equation is

$$(\lambda + r)\big(\lambda - (K\xi - \mu)\big)(\lambda + d) = 0.$$

We can see $\lambda_{1,3} < 0$, and

$$\lambda_2 = K\xi - \mu \begin{cases} < 0, & \text{when } R_0 < 1, \\ > 0, & \text{when } R_0 > 1. \end{cases}$$

Hence, E_1 is asymptotically stable when $R_0 < 1$ and unstable when $R_0 > 1$.

We choose a Lyapunov functional $L : \mathbb{R} \times \mathcal{C} \times \mathcal{C} \to \mathbb{R}$ as

$$L(\varphi_1, \varphi_2, \varphi_3) = \varphi_3(0).$$

The derivative of L along the solutions of system (1.3) is

$$\begin{aligned} L'|_{(1)} = I'(t) &= \xi IS - \frac{mIP}{a + I} - \mu I \\ &\leq I(\xi K - \mu) \\ &= \mu I(R_0 - 1). \end{aligned}$$

Therefore, $L'|_{(1)} \leq 0$ for all $S, I, P \geq 0$ when $R_0 < 1$, and $L' = 0$ if and only if $I(t) = 0$. That is,

$$\mathcal{S} = \big\{\varphi \in \overline{\Gamma} : L'(\varphi) = 0\big\} = \big\{(\varphi_1, 0, \varphi_3)\big\}.$$

Define

$$M := \big\{E_0, E_1, (R_+, 0, R_+)\big\}.$$

Then M is the maximal invariant set under (1.3) in $\mathcal{S}$. In fact, substitution $I = 0$ into (1.3) leads to the following initial value problem:

$$\begin{aligned} &\dot{S} = rS\left(1 - \frac{S}{K}\right), \\ &\dot{P} = -dP, \\ &S(t) = \varphi_1(t) > 0, \qquad P(t) = \varphi_3(t) > 0, \quad -\tau \leq t \leq 0. \end{aligned} \tag{3.6}$$

The claim follows.

Clearly,

$$\lim_{t\to\infty} S(t) = K, \qquad \lim_{t\to\infty} P(t) = 0.$$

By Theorem 3.2 in [18], Chapter 5, we know that any solution (S_t, I_t, P_t) of (1.3) with initial value $\varphi \in \bar{\Gamma}$ tends to M as $t \to \infty$. Notice the structure of M, we have

$$\lim_{t\to\infty} I_t = 0.$$

Hence, from the third equation in (1.3) it follows that

$$\lim_{t\to\infty} P_t = 0.$$

Now we consider the first equation in (1.3),

$$\dot{S} = rS\left(1 - \frac{S}{K}\right) - \left(\xi + \frac{r}{K}\right)IS \tag{3.7}$$

and

$$\dot{y} = ry\left(1 - \frac{y}{K}\right). \tag{3.8}$$

Let

$$f(t,S) = rS\left(1 - \frac{S}{K}\right) - \left(\xi + \frac{r}{K}\right)I(t)S \quad \text{and} \quad g(y) = ry\left(1 - \frac{y}{K}\right).$$

Then from $\lim_{t\to\infty} I(t) = 0$ we have

$$f(t,S) \to g(S), \quad t \to \infty, \text{ locally uniformly in } S \in R.$$

We know that $\{K\}$ is an asymptotically stable equilibrium of (3.8). It is well known that for any $S_0 > 0$, the solution S of (3.7) with initial value $S_0 > 0$ is bounded for $t \geq 0$. Denote the ω-limit set of the forward bounded solution of (3.7) as $\omega(0, S_0)$. Then for any $y_0 \in \omega(0, S_0)$, we see that the solution of (3.8) with $y(0) = y_0 > 0$ converges to K as $t \to \infty$. Applying Theorem 1.2 in [19] it follows that $S(t) \to K$ as $t \to \infty$. Thus E_1 is globally attractive in Γ when $R_0 < 1$. Furthermore, combined with the local stability of E_1 it implies that it is globally asymptotically stable in Γ when $R_0 < 1$.

(iii) The linearization of (1.3) at the fixed point $E_2 = (\frac{\mu}{\xi}, \frac{r(K\xi-\mu)}{\xi(r+K\xi)}, 0)$ is given by

$$\begin{aligned}
\dot{S} &= -\frac{r\mu}{K\xi}S - \mu\left(\frac{r}{K\xi}+1\right)I, \\
\dot{I} &= \frac{r(K\xi-\mu)}{r+K\xi}S - \frac{rm(K\xi-\mu)}{a\xi(r+K\xi)+r(K\xi-\mu)}P, \\
\dot{P} &= -dP + \frac{rm\alpha(K\xi-\mu)e^{-d_1\tau}}{a\xi(r+K\xi)+r(K\xi-\mu)}P(t-\tau).
\end{aligned}$$

Its characteristic equation is

$$\left(\lambda^2 + \frac{r\mu}{K\xi}\lambda + \frac{r\mu(K\xi-\mu)}{K\xi}\right)\left(\lambda + d - \frac{rm\alpha(K\xi-\mu)}{a\xi(r+K\xi)+r(K\xi-\mu)}e^{-(\lambda+d_1)\tau}\right) = 0.$$

Obviously, the two roots induced by $\lambda^2 + \frac{r\mu}{K\xi}\lambda + \frac{r\mu(K\xi-\mu)}{K\xi} = 0$ are negative when $R_0 > 1$. Now we will turn to the study of

$$\lambda_3 = \frac{rm\alpha(K\xi-\mu)}{a\xi(r+K\xi)+r(K\xi-\mu)}e^{-(\lambda_3+d_1)\tau} - d. \tag{3.9}$$

Suppose that $\mathrm{Re}(\lambda_3) \geq 0$, compute the real part of (3.9), we get

$$\begin{aligned}
\mathrm{Re}(\lambda_3) &= \frac{rm\alpha(K\xi-\mu)}{a\xi(r+K\xi)+r(K\xi-\mu)}e^{-d_1\tau}e^{-\tau\,\mathrm{Re}(\lambda_3)}\cos\bigl(\tau\,\mathrm{Im}(\lambda_3)\bigr) - d \\
&< \frac{rm\alpha(K\xi-\mu)}{a\xi(r+K\xi)+r(K\xi-\mu)}e^{-d_1\tau} - d \\
&= \frac{r(m\alpha e^{-d_1\tau}-d)(K\xi-\mu) - ad\xi(r+K\xi)}{a\xi(r+K\xi)+r(K\xi-\mu)} \\
&= \frac{r\mu(m\alpha e^{-d_1\tau}-d)}{a\xi(r+K\xi)+r(K\xi-\mu)}(R_1-1) \\
&< 0,
\end{aligned}$$

when $R_1 < 1$. This is a contradiction, hence we have $\mathrm{Re}(\lambda_3) < 0$. This completes the proof. □

3.2 Interior equilibrium and its stability

In this subsection, we always assume $R_1 > 1$, and we will concentrate on the study of the interior equilibrium $E^*(S^*, I^*, P^*)$. Let

$$\tilde{S} = S - S^*, \qquad \tilde{I} = I - I^*, \qquad \tilde{P} = P - P^*. \tag{3.10}$$

Then the interior equilibrium $E^*(S^*, I^*, P^*)$ of system (1.3) is moved to the origin. We remove the superscript for the sake of convenience. Then (1.3) becomes

$$\begin{aligned}
\frac{dS}{dt} &= -\frac{r}{K}S^2 - \left(\xi + \frac{r}{K}\right)SI - \frac{rS^*}{K}S - \left(\xi + \frac{r}{K}\right)S^*I, \\
\frac{dI}{dt} &= \xi SI - \frac{am}{(a+I^*)^2}IP + \frac{m(2a+I^*)P^*}{2(a+I^*)^3}I^2 + \xi I^*S + \frac{mI^*P^*}{(a+I^*)^2}I - \frac{de^{d_1\tau}}{\alpha}P,
\end{aligned} \tag{3.11}$$

$$\begin{aligned}\frac{dP}{dt} &= \frac{am\alpha e^{-d_1\tau}}{(a+I^*)^2}I(t-\tau)P(t-\tau) - \frac{m\alpha(2a+I^*)P^*e^{-d_1\tau}}{2(a+I^*)^3}I^2(t-\tau) - dP \\ &\quad + \frac{am\alpha P^*e^{-d_1\tau}}{(a+I^*)^2}I(t-\tau) + dP(t-\tau).\end{aligned}$$

Obviously, the origin $(0,0,0)$ is an equilibrium of system (3.11). Denote

$$\begin{aligned} B_1(\tau) &= \begin{pmatrix} -\frac{rS^*}{K} & -(\xi+\frac{r}{K})S^* & 0 \\ \xi I^* & \frac{mI^*P^*}{(a+I^*)^2} & -\frac{de^{d_1\tau}}{\alpha} \\ 0 & 0 & -d \end{pmatrix}, \\ B_2(\tau) &= \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & \frac{am\alpha P^*e^{-d_1\tau}}{(a+I^*)^2} & d \end{pmatrix}. \end{aligned} \tag{3.12}$$

So the linearization of (3.11) at the origin is given by

$$\begin{pmatrix} \dot{S} \\ \dot{I} \\ \dot{P} \end{pmatrix} = B_1(\tau)\begin{pmatrix} S \\ I \\ P \end{pmatrix} + B_2(\tau)\begin{pmatrix} S(t-\tau) \\ I(t-\tau) \\ P(t-\tau) \end{pmatrix}.$$

Its characteristic equation is

$$\det\bigl(\lambda I - B_1(\tau) - B_2(\tau)e^{-\lambda\tau}\bigr) = 0,$$

that is,

$$\lambda^3 + a_2\lambda^2 + a_1\lambda + a_0 + \bigl(b_2\lambda^2 + b_1\lambda + b_0\bigr)e^{-\lambda\tau} = 0, \tag{3.13}$$

where

$$\begin{aligned} a_1 &= \frac{rdS^*}{K} - \frac{rmS^*I^*P^*}{K(a+I^*)^2} - \frac{dmI^*P^*}{(a+I^*)^2} + \left(\xi + \frac{r}{K}\right)\xi S^*I^*, \\ a_2 &= \frac{rS^*}{K} - \frac{mI^*P^*}{(a+I^*)^2} + d, \qquad a_0 = \left(\xi + \frac{r}{K}\right)d\xi S^*I^* - \frac{rdmS^*I^*P^*}{K(a+I^*)^2}, \\ b_2 &= -d, b_1 = \frac{dmP^*}{a+I^*} - \frac{drS^*}{K}, \qquad b_0 = \frac{drmS^*P^*}{K(a+I^*)} - \left(\xi + \frac{r}{K}\right)d\xi S^*I^*. \end{aligned}$$

Thus

$$\begin{aligned} a_2 + b_2 &= \left(\frac{r}{K} - \frac{d\xi e^{d_1\tau}}{m\alpha}\right)S^* + \frac{d\mu e^{d_1\tau}}{m\alpha}, \\ a_1 + b_1 &= \frac{armS^*P^*}{K(a+I^*)^2} + \frac{admP^*}{(a+I^*)^2} + S^*\left[\frac{r\mu}{K} + \xi I^*\left(\xi + \frac{r}{K}\right) - \frac{r\xi S^*}{K}\right], \\ a_0 + b_0 &= \frac{adrmS^*P^*}{K(a+I^*)^2} > 0, \end{aligned}$$

$$
\begin{aligned}
&(a_2+b_2)(a_1+b_1)-(a_0+b_0)\\
&\quad=\left(\frac{r}{K}-\frac{d\xi e^{d_1\tau}}{m\alpha}\right)S^*(a_1+b_1)\\
&\qquad+\frac{d\mu e^{d_1\tau}}{m\alpha}\left[\frac{admP^*}{(a+I^*)^2}+S^*\left[\frac{r\mu}{K}+\xi I^*\left(\xi+\frac{r}{K}\right)-\frac{r\xi S^*}{K}\right]\right]\\
&\qquad+\frac{d\mu e^{d_1\tau}}{m\alpha}\cdot\frac{armS^*P^*}{K(a+I^*)^2}-\frac{adrmS^*P^*}{K(a+I^*)^2}.
\end{aligned}
$$

Here a_0, a_1, a_2, b_0, and b_1 depend on the parameter τ, since S^*, I^*, and P^* are continuous functions of τ. When $\tau=0$, equation (3.13) becomes

$$
\lambda^3+\bigl(a_2(0)+b_2(0)\bigr)\lambda^2+\bigl[a_1(0)+b_1(0)\bigr]\lambda+\bigl[a_0(0)+b_0(0)\bigr]=0, \tag{3.14}
$$

where

$$
\begin{aligned}
&a_2(0)+b_2(0)=\left(\frac{r}{K}-\frac{d\xi}{m\alpha}\right)S_0+\frac{d\mu}{m\alpha},\\
&a_1(0)+b_1(0)=\frac{armS_0P_0}{K(a+I_0)^2}+\frac{admP_0}{(a+I_0)^2}+S_0\left[\frac{r\mu}{K}+\xi I_0\left(\xi+\frac{r}{K}\right)-\frac{r\xi S_0}{K}\right],\\
&a_0(0)+b_0(0)=\frac{adrmS_0P_0}{K(a+I_0)^2}>0,\\
&\bigl(a_2(0)+b_2(0)\bigr)\bigl(a_1(0)+b_1(0)\bigr)-\bigl(a_0(0)+b_0(0)\bigr)\\
&\quad=\left(\frac{r}{K}-\frac{d\xi}{m\alpha}\right)S_0(a_1+b_1)\\
&\qquad+\frac{d\mu}{m\alpha}\left[\frac{admP_0}{(a+I_0)^2}+S_0\left[\frac{r\mu}{K}+\xi I_0\left(\xi+\frac{r}{K}\right)-\frac{r\xi S_0}{K}\right]\right]\\
&\qquad+\frac{d\mu}{m\alpha}\cdot\frac{armS_0P_0}{K(a+I_0)^2}-\frac{adrmS_0P_0}{K(a+I_0)^2},
\end{aligned}
$$

and here $S_0=K-\frac{ad(K\xi+r)}{r(m\alpha-d)}$, $I_0=\frac{ad}{m\alpha-d}$, $P_0=\frac{1}{m}(a+I_0)(\xi S_0-\mu)$.

By the Hurwitz criterion, we make the following assumptions on (3.14):

$$
\begin{aligned}
&(\mathrm{H1}):\quad a_2(0)+b_2(0)>0,\\
&(\mathrm{H2}):\quad a_1(0)+b_1(0)>0,\\
&(\mathrm{H3}):\quad \bigl(a_2(0)+b_2(0)\bigr)\bigl(a_1(0)+b_1(0)\bigr)-\bigl(a_0(0)+b_0(0)\bigr)>0,
\end{aligned}
$$

under which we have the following theorem.

Theorem 3.2 *Assume* $R_0>1$ *and* (H1)-(H3) *are satisfied. Then the positive equilibrium* E^* *of* (1.3) *is asymptotically stable when* $\tau=0$.

From the consequence of the distribution of zeros of a transcendental function given by Ruan and Wei [20], we know that as τ varies, the sum of the orders of the roots of (3.13) in the open right half plane can change only if a zero appears on or crosses the imaginary axis.

In order to investigate the purely imaginary roots of (3.13) by using the method introduced by Beretta and Kuang [21], we rewrite equation (3.13) as

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

with

$$P(\lambda,\tau)=\lambda^3+a_2\lambda^2+a_1\lambda+a_0,\qquad Q(\lambda,\tau)=b_2\lambda^2+b_1\lambda+b_0. \tag{3.15}$$

Before applying the geometry criterion in [21] to (3.13), a sequence of conditions on P and Q are required to be verified. This is accomplished by the following proposition.

Proposition 3.3 *Let* $\tau^0=\frac{1}{d_1}\ln\frac{m\alpha}{(1+\frac{K\xi}{r})ad/(K-\frac{\mu}{\xi})+d}$, *and P and Q are defined in* (3.15). *Then the following statements are valid for all* $\tau\in[0,\tau^0)$.

(a) $P(0,\tau)+Q(0,\tau)\neq 0$;
(b) $P(i\omega,\tau)+Q(i\omega,\tau)\neq 0$;
(c) $\overline{\lim}\{|\frac{Q(\lambda,\tau)}{P(\lambda,\tau)}|:|\lambda|\to\infty,\operatorname{Re}\lambda\geq 0\}<1$ *for any* τ;
(d) $F(\omega,\tau):=|P(i\omega,\tau)|^2-|Q(i\omega,\tau)|^2$ *has a finite number of real zeros for each* τ;
(e) *each positive root* $\omega(\tau)$ *of* $F(\omega,\tau)=0$ *is continuous and differentiable in* τ *whenever it exists*.

Proof

(a) $P(0,\tau)+Q(0,\tau)=a_0+b_0>0$, that is, $\lambda=0$ is not a root of (3.13).
(b) By the assumption (H3), we know that (b) is true.
(c) From

$$\lim_{|\lambda|\to\infty}\left|\frac{Q(\lambda,\tau)}{P(\lambda,\tau)}\right|=\lim_{|\lambda|\to\infty}\left|\frac{b_2\lambda^2+b_1\lambda+b_0}{\lambda^3+a_2\lambda^2+a_1\lambda+a_0}\right|=0,$$

we have

$$\overline{\lim_{|\lambda|\to\infty,\operatorname{Re}\lambda\geq 0}}\left|\frac{Q(\lambda,\tau)}{P(\lambda,\tau)}\right|<1.$$

(d) We have

$$\begin{aligned}F(\omega,\tau)&=\left|P(i\omega,\tau)\right|^2-\left|Q(i\omega,\tau)\right|^2\\&=\omega^6+\left(a_2^2-2a_1-b_2^2\right)\omega^4+\left(a_1^2-2a_0a_2-b_1^2+2b_0b_2\right)\omega^2+\left(a_0^2-b_0^2\right).\end{aligned}$$

It is obvious that property (d) is satisfied.

(e) The conclusion is valid because $F(\omega,\tau)$ is a cubic polynomial in ω^2 and the fact that a_i $(i=0,1,2)$ and b_j $(j=0,1)$ are all continuous functions of τ. □

We also mention that

$$\overline{P(-i\omega,\tau)}=P(i\omega,\tau),\qquad\overline{Q(-i\omega,\tau)}=Q(i\omega,\tau).$$

P, Q have real coefficients. This ensures that if $\lambda = i\omega$, for some real ω, is a root of (3.13), then $\lambda = -i\omega$ is a root of (3.13) as well. Let $\lambda = i\omega(\omega > 0)$ be a purely imaginary root of equation (3.13), then

$$-i\omega^3 - a_2\omega^2 + ia_1\omega + a_0 + \left(-b_2\omega^2 + ib_1\omega + b_0\right)(\cos\omega\tau - i\sin\omega\tau) = 0.$$

Separating the real and imaginary parts yields

$$\begin{aligned} \omega^3 - a_1\omega &= \left(b_2\omega^2 - b_0\right)\sin\omega\tau + b_1\omega\cos\omega\tau, \\ a_2\omega^2 - a_0 &= b_1\omega\sin\omega\tau - \left(b_2\omega^2 - b_0\right)\cos\omega\tau. \end{aligned} \tag{3.16}$$

Squaring both sides of (3.16) and summing the two equations, we obtain

$$h\left(\omega^2, \tau\right) = F(\omega, \tau) = \omega^6 + p\omega^4 + q\omega^2 + s = 0, \tag{3.17}$$

where $p = a_2^2 - 2a_1 - b_2^2$, $q = a_1^2 - 2a_0a_2 + 2b_0b_2 - b_1^2$, $s = a_0^2 - b_0^2$.

Set $z = \omega^2$. Then (3.17) becomes

$$h(z, \tau) = z^3 + pz^2 + qz + s. \tag{3.18}$$

Therefore, equation (3.13) has a pair of purely imaginary roots $\pm i\omega(\tau^*)$ when $\tau = \tau^*$ if and only if $\omega(\tau^*)$ is the positive root of (3.17), or equivalently, $z^* = \omega^2(\tau^*)$ is the positive root of (3.18). As follows from (3.16) we get

$$\begin{aligned} \sin\omega\tau &= \frac{b_2\omega^5 + (a_2b_1 - b_0 - a_1b_2)\omega^3 + (a_1b_0 - a_0b_1)\omega}{b_1^2\omega^2 + (b_2\omega^2 - b_0)^2}, \\ \cos\omega\tau &= \frac{(b_1 - a_2b_2)\omega^4 + (a_0b_2 + a_2b_0 - a_1b_1)\omega^2 - a_0b_0}{b_1^2\omega^2 + (b_2\omega^2 - b_0)^2}. \end{aligned} \tag{3.19}$$

By the definitions of $P(\lambda, \tau)$ and $Q(\lambda, \tau)$ as in (3.15), and applying the property (b) in Proposition 3.3, (3.19) can be written as

$$\begin{aligned} \sin\omega\tau &= \operatorname{Im}\left(\frac{P(i\omega, \tau)}{Q(i\omega, \tau)}\right), \\ \cos\omega\tau &= -\operatorname{Re}\left(\frac{P(i\omega, \tau)}{Q(i\omega, \tau)}\right), \end{aligned}$$

which yields

$$\left|P(i\omega, \tau)\right|^2 = \left|Q(i\omega, \tau)\right|^2,$$

that is,

$$F(\omega, \tau) = 0.$$

Define

$$I = \left\{\tau : F(\omega, \tau) = 0 \text{ has positive roots}\right\} \cap [0, \tau^0),$$

and $\tau^1 = \sup_{\tau_i \in I} \tau_i$. Also define $\theta(\tau) \in [0, 2\pi]$ by

$$\sin\theta(\tau) = \frac{b_2\omega^5 + (a_2b_1 - b_0 - a_1b_2)\omega^3 + (a_1b_0 - a_0b_1)\omega}{b_1^2\omega^2 + (b_2\omega^2 - b_0)^2},$$
$$\cos\theta(\tau) = \frac{(b_1 - a_2b_2)\omega^4 + (a_0b_2 + a_2b_0 - a_1b_1)\omega^2 - a_0b_0}{b_1^2\omega^2 + (b_2\omega^2 - b_0)^2}.$$

Then we have $\omega(\tau)\tau = \theta(\tau) + 2n\pi$ obviously. Therefore, $i\omega^*$, $\omega^* = \omega(\tau^*) > 0$, is a purely imaginary root of (3.13) if and only if τ^* is a zero of the function $S_n(\tau)$, which is defined by

$$S_n(\tau) = \tau - \frac{\theta(\tau) + 2n\pi}{\omega(\tau)}, \quad \tau \in I, n \in \mathbb{N}. \tag{3.20}$$

We also know that $\theta(\tau) \neq 0, 2\pi$ on I in terms of (b) in Proposition 3.3, and $S_n(\tau)$ are continuous and differentiable on I from Lemma 2.1 in [21]. The following theorem in [21] can be used to verify the occurrence of Hopf bifurcations when $\tau = \tau^*$.

Theorem 3.4 *Assume that $S_n(\tau) = 0$ has a positive root $\tau^* \in I$ for some $n \in \mathbb{N}$. Then there exists a pair of simple purely imaginary roots $\pm i\omega(\tau^*)$ of (3.13) at $\tau = \tau^*$, and we denote*

$$\begin{aligned}\delta(\tau^*) &= \operatorname{Sign}\left\{\frac{\mathrm{dRe}\lambda(\tau)}{\mathrm{d}\tau}\bigg|_{\lambda = i\omega(\tau^*)}\right\} \\ &= \operatorname{Sign}\left\{\frac{\partial F}{\partial \omega}\big(\omega(\tau^*), \tau^*\big)\right\} \times \operatorname{Sign}\left\{\frac{\mathrm{d}S_n(\tau)}{\mathrm{d}\tau}\bigg|_{\tau = \tau^*}\right\},\end{aligned} \tag{3.21}$$

which determines the direction in which the pair of purely imaginary roots cross the imaginary axis: from left to right if $\delta(\tau^*) > 0$, and from right to left if $\delta(\tau^*) < 0$.

Proposition 3.5 *For $S_n(\tau)$ defined on $[0, \tau^1)$ in (3.20), the following properties hold:*
(i) $S_n(0) < 0$, $\lim_{\tau \to \tau^1} S_n(\tau) = -\infty$;
(ii) $S_n(\tau) > S_{n+1}(\tau)$.

Proof By the definition of $\omega(\tau)$ and $\theta(\tau)$, we know $\omega(\tau) > 0$, $\theta(\tau) \in (0, 2\pi)$.
(i) $S_n(0) = -\frac{\theta(0)+2n\pi}{\omega(0)} < 0$ obviously. When $\tau \to \tau^1$, we have $\omega(\tau) \to 0$ and $\theta(\tau) \to \pi$ by the facts that $\sin\theta(\tau) \to 0$ and $\cos\theta(\tau) \to -1$. Therefore, by (3.20) we get $\lim_{\tau \to \tau^1} S_n(\tau) = -\infty$.
(ii) $S_n(\tau) - S_{n+1}(\tau) = \frac{2\pi}{\omega(\tau)} > 0$ due to the positivity of $\omega(\tau)$. □

Remark 3.6 If $S_0(\tau)$ has no zeros in I, then so does $S_n(\tau)$, from the degression of $S_n(\tau)$ w.r.t. n for all $n \in \mathbb{N}$.

Define the set of possible Hopf bifurcation values by

$$J = \left\{\tau \in \left[0, \tau^1\right) | S_n(\tau) = 0, n \in \mathbb{N}\right\},$$

from the decreasing property of S_n w.r.t. n, we know the set J is finite, so we denote the minimum and maximum element to be $\tau_{\min}$ and $\tau_{\max}$, respectively. Now we state the main results in this section.

Theorem 3.7 *Assume* (H1)-(H3) *are satisfied for system* (1.3). *Then the following conclusions hold*:

(i) *If I is empty or $S_0(\tau)$ has no positive zeros in* $(0, \tau^1)$ *when I is non-empty, which implies set J is empty, then equation* (3.13) *has no pair of purely imaginary roots, thus the positive equilibrium E^* is asymptotically stable for all $\tau \in [0, \tau^0)$.*

(ii) *If $J \neq \emptyset$ and $\delta(\tau^*) \neq 0$ for $\tau^* \in J$, then* (4) *undergoes a Hopf bifurcation at E^* when $\tau = \tau^*$. At this time, E^* is asymptotically stable for $\tau \in [0, \tau_{\min}) \cup (\tau_{\max}, \tau^0)$.*

3.3 Direction and stability of Hopf bifurcation

In the previous section, we can see that a Hopf bifurcation at E^* when τ passes through certain critical values may happen indeed, and sufficient conditions are obtained as well. In this section, we shall study the direction, stability, and the period of the bifurcating periodic solution. The way to do this is the combination of the normal form method and center manifold theory in [22]. Without loss of generality, let τ^* be any critical value such that equation (3.13) has a pair of purely imaginary roots $\pm i\omega^*$, and system (1.3) undergoes a Hopf bifurcation at E^*. Then, by setting $\tau = \tau^* + \mu$, and $\mu = 0$ is the Hopf bifurcation value of (1.3).

After translation (3.10) and time scaling $t \mapsto (t/\tau)$, system (1.3) can be written as

$$\begin{pmatrix} \dot{S}(t) \\ \dot{I}(t) \\ \dot{P}(t) \end{pmatrix} = \tau B_1(\tau) \begin{pmatrix} S(t) \\ I(t) \\ P(t) \end{pmatrix} + \tau B_2(\tau) \begin{pmatrix} S(t-1) \\ I(t-1) \\ P(t-1) \end{pmatrix} + \tau f(S, I, P), \tag{3.22}$$

where $B_1(\tau)$ and $B_2(\tau)$ are defined in (3.12), and

$$f(S, I, P) = \begin{pmatrix} -\frac{r}{K} S^2(t) - (\xi + \frac{r}{K}) S(t) I(t) \\ \xi S(t) I(t) - \frac{am}{(a+I^*)^2} I(t) P(t) + \frac{m(2a+I^*)P^*}{2(a+I^*)^3} I^2(t) \\ \frac{am\alpha e^{-d_1\tau}}{(a+I^*)^2} I(t-1) P(t-1) - \frac{m\alpha(2a+I^*)P^* e^{-d_1\tau}}{2(a+I^*)^3} I^2(t-1) \end{pmatrix}.$$

For $\phi = (\phi_1, \phi_2, \phi_3)^{\mathrm{T}} \in C := C([-1, 0], \mathbb{R}^3)$, define

$$L_\mu(\phi) = \bigl(\tau^* + \mu\bigr) B_1\bigl(\tau^* + \mu\bigr)\phi(0) + \bigl(\tau^* + \mu\bigr) B_2\bigl(\tau^* + \mu\bigr)\phi(-1) \tag{3.23}$$

and

$$G(\mu, \phi) = \bigl(\tau^* + \mu\bigr) \begin{pmatrix} -\frac{r}{K}\phi_1^2(0) - (\xi + \frac{r}{K})\phi_1(0)\phi_2(0) \\ \xi\phi_1(0)\phi_2(0) - \frac{am}{(a+I^*)^2}\phi_2(0)\phi_3(0) + \frac{m(2a+I^*)P^*}{2(a+I^*)^3}\phi_2^2(0) \\ \frac{am\alpha e^{-d_1(\tau^*+\mu)}}{(a+I^*)^2}\phi_2(-1)\phi_3(-1) - \frac{m\alpha(2a+I^*)P^* e^{-d_1(\tau^*+\mu)}}{2(a+I^*)^3}\phi_2^2(-1) \end{pmatrix}.$$

By the Riesz representation theorem, there exists a 3×3 matrix $\eta(\theta, \mu)$, whose components are bounded variation functions for $\theta \in [-1, 0]$, such that

$$L_\mu(\phi) = \int_{-1}^{0} \mathrm{d}\eta(\theta, \mu)\phi(\theta), \quad \text{for } \phi \in C.$$

In fact, $\eta(\theta,\mu)$ can be chosen as

$$\eta(\theta,\mu)=\begin{cases}(\tau^*+\mu)B_1(\tau^*+\mu), & \theta=0,\\ 0, & \theta\in(-1,0),\\ -(\tau^*+\mu)B_2(\tau^*+\mu), & \theta=-1.\end{cases}$$

Define the operators $A(\mu)$ and $R(\mu)$ as

$$A(\mu)\phi(\theta)=\begin{cases}\frac{\mathrm{d}\phi(\theta)}{d\theta}, & \theta\in[-1,0),\\ \int_{-1}^{0}\mathrm{d}\eta(\xi,\mu)\phi(\xi), & \theta=0,\end{cases} \tag{3.24}$$

and

$$R(\mu)\phi(\theta)=\begin{cases}0, & \theta\in[-1,0),\\ G(\mu,\phi), & \theta=0.\end{cases}$$

Then system (3.22) is equivalent to the following operator equation:

$$\dot{X}_t=A(\mu)X_t+R(\mu)X_t,$$

where $X(t)=(S(t),I(t),P(t))^{\mathrm{T}}$ and $X_t(\theta)=X(t+\theta)$ for $\theta\in[-1,0]$.

Let $C^*:=C([0,1],(\mathbb{R}^3)^*)$. For $\psi\in C^*$, define an operator

$$A^*\psi(s)=\begin{cases}-\frac{\mathrm{d}\psi(s)}{\mathrm{d}s}, & s\in(0,1],\\ \int_{-1}^{0}\mathrm{d}\eta(\xi,0)\psi(-\xi), & s=0,\end{cases} \tag{3.25}$$

and a bilinear inner form

$$\langle\psi(s),\phi(\theta)\rangle=\overline{\psi}(0)\phi(0)-\int_{-1}^{0}\int_{\xi=0}^{\theta}\overline{\psi}(\xi-\theta)\,\mathrm{d}\eta(\theta)\phi(\xi)\,\mathrm{d}\xi, \tag{3.26}$$

where $\eta(\theta)=\eta(\theta,0)$. Then $A(0)$ and A^* are adjoint operators.

As shown in Section 3.2, we know that $\pm i\omega^*\tau^*$ are eigenvalues of $A(0)$, thus, they are also eigenvalues of A^*. It can be verified that the vectors

$$q(\theta)=(1,q_1,q_2)^{\mathrm{T}}e^{i\omega^*\tau^*\theta},\quad \theta\in[-1,0],$$

and

$$q^*(s)=\frac{1}{D}\big(1,q_1^*,q_2^*\big)e^{i\omega^*\tau^*s},\quad s\in[0,1],$$

are the eigenvectors of $A(0)$ and A^* corresponding to the eigenvalues $i\omega^*\tau^*$ and $-i\omega^*\tau^*$, respectively, where

$$q_1=-\frac{i\omega^*\tau^*K+rS^*}{(K\xi+r)S^*},\qquad q_2=-\frac{am\alpha P^*e^{-d_1\tau^*}(i\omega^*\tau^*K+rS^*)}{(a+I^*)^2[(i\omega^*\tau^*+d)e^{i\omega^*\tau^*}-d](K\xi+r)S^*}, \tag{3.27}$$

$$q_1^*=\frac{\frac{rS^*}{K}-i\omega^*\tau^*}{\xi I^*},\qquad q_2^*=\frac{de^{d_1\tau^*}(\frac{rS^*}{K}-i\omega^*\tau^*)}{(i\omega^*\tau^*-d+de^{i\omega^*\tau^*})\alpha\xi I^*}, \tag{3.28}$$

and

$$D = 1 + \bar{q}_1^* q_1 + \bar{q}_2^* q_2 + \bar{q}_2^* \tau^* e^{-i\omega^*\tau^*} \left[\frac{am\alpha P^*}{(a+I^*)^2} e^{-d_1\tau^*} q_1 + d q_2 \right].$$

One can find that

$$\langle q^*(s), q(\theta) \rangle = 1.$$

Following the algorithms provided in [22] and using a computation process similar to that in [1, 23, 24], we obtain the following coefficients:

$$\begin{aligned}
g_{20} ={}& \frac{2\tau^*}{D} \left[-\frac{r}{K} - q_1 \left(\xi + \frac{r}{K} \right) + \xi q_1 \overline{q}_1^* - \frac{am}{(a+I^*)^2} q_1 \overline{q}_1^* q_2 + \frac{m(2a+I^*)P^*}{2(a+I^*)^3} q_1^2 \overline{q}_1^* \right. \\
&\left. + \frac{am\alpha e^{-d_1\tau^*}}{(a+I^*)^2} q_1 \overline{q}_2^* q_2 e^{-2i\omega^*\tau^*} - \frac{m\alpha(2a+I^*)P^*}{2(a+I^*)^3} q_1^2 \overline{q}_2^* e^{-d_1\tau^*} e^{-2i\omega^*\tau^*} \right], \\
g_{11} ={}& \frac{\tau^*}{D} \left[-\frac{2r}{K} - \left(\xi + \frac{r}{K} \right)(q_1 + \overline{q}_1) + \xi (q_1 + \overline{q}_1) \overline{q}_1^* - \frac{m\alpha(2a+I^*)P^*}{(a+I^*)^3} e^{-d_1\tau^*} q_1 \overline{q}_1 \overline{q}_2^* \right. \\
&\left. - \frac{am}{(a+I^*)^2} (q_1 \overline{q}_2 + \overline{q}_1 q_2) \overline{q}_1^* + \frac{m(2a+I^*)P^*}{(a+I^*)^3} q_1 \overline{q}_1 \overline{q}_1^* + \frac{am\alpha e^{-d_1\tau^*}}{(a+I^*)^2} (q_1 \overline{q}_2 + \overline{q}_1 q_2) \overline{q}_2^* \right], \\
g_{02} ={}& \frac{2\tau^*}{D} \left[-\frac{r}{K} - \overline{q}_1 \left(\xi + \frac{r}{K} \right) + \xi \overline{q}_1 \overline{q}_1^* - \frac{am}{(a+I^*)^2} \overline{q}_1 \overline{q}_2 \overline{q}_1^* + \frac{m(2a+I^*)P^*}{2(a+I^*)^3} \overline{q}_1^2 \overline{q}_1^* \right. \\
&\left. + \frac{am\alpha e^{-d_1\tau^*}}{(a+I^*)^2} \overline{q}_1 \overline{q}_2 \overline{q}_2^* e^{2i\omega^*\tau^*} - \frac{m\alpha(2a+I^*)P^*}{2(a+I^*)^3} \overline{q}_1^2 \overline{q}_2^* e^{-d_1\tau^*} e^{2i\omega^*\tau^*} \right], \\
g_{21} ={}& \frac{2\tau^*}{D} \left\{ -\frac{r}{K} \left[2W_{11}^{(1)}(0) + W_{20}^{(1)}(0) \right] + \left[\xi \overline{q}_1^* - \xi - \frac{r}{K} \right] \right. \\
&\times \left[W_{11}^{(2)}(0) + \frac{W_{20}^{(2)}(0)}{2} + \overline{q}_1 \frac{W_{20}^{(1)}(0)}{2} + q_1 W_{11}^{(1)}(0) \right] \\
&- \frac{am}{(a+I^*)^2} \overline{q}_1^* \left[q_1 W_{11}^{(3)}(0) + \overline{q}_1 \frac{W_{20}^{(3)}(0)}{2} + \overline{q}_2 \frac{W_{20}^{(2)}(0)}{2} + q_2 W_{11}^{(2)}(0) \right] \\
&+ \frac{m(2a+I^*)P^*}{2(a+I^*)^3} \overline{q}_1^* \left[2q_1 W_{11}^{(2)}(0) + \overline{q}_1 W_{20}^{(2)}(0) \right] + \frac{am\alpha e^{-d_1\tau^*}}{(a+I^*)^2} \overline{q}_2^* \left[q_1 W_{11}^{(3)}(-1) e^{-i\omega^*\tau^*} \right. \\
&\left. + \overline{q}_1 \frac{W_{20}^{(3)}(-1)}{2} e^{i\omega^*\tau^*} + \overline{q}_2 \frac{W_{20}^{(2)}(-1)}{2} e^{i\omega^*\tau^*} + q_2 W_{11}^{(2)}(-1) e^{-i\omega^*\tau^*} \right] \\
&\left. - \frac{m\alpha(2a+I^*)P^*}{2(a+I^*)^3} \overline{q}_2^* e^{-d_1\tau^*} \left[2q_1 W_{11}^{(2)}(-1) e^{-i\omega^*\tau^*} + \overline{q}_1 W_{20}^{(2)}(-1) e^{i\omega^*\tau^*} \right] \right\},
\end{aligned}$$

where

$$\begin{aligned}
W_{20}(\theta) &= \frac{ig_{20}}{\omega^*\tau^*} q(0) e^{i\omega^*\tau^*\theta} + \frac{i\overline{g}_{02}}{3\omega^*\tau^*} \overline{q}(0) e^{-i\omega^*\tau^*\theta} + F_1 e^{2i\omega^*\tau^*\theta}, \\
W_{11}(\theta) &= -\frac{ig_{11}}{\omega^*\tau^*} q(0) e^{i\omega^*\tau^*\theta} + \frac{i\overline{g}_{11}}{\omega^*\tau^*} \overline{q}(0) e^{-i\omega^*\tau^*\theta} + F_2,
\end{aligned}$$

and

$$F_1 = 2\begin{pmatrix} 2i\omega^* + \frac{rS^*}{K} & (\xi + \frac{r}{K})S^* & 0 \\ -\xi I^* & 2i\omega^* - \frac{mI^*P^*}{(a+I^*)^2} & \frac{de^{d_1\tau^*}}{\alpha} \\ 0 & -\frac{am\alpha P^*e^{-d_1\tau^*}}{(a+I^*)^2}e^{-2i\omega^*\tau^*} & 2i\omega^* + d - de^{-2i\omega^*\tau^*} \end{pmatrix}^{-1}$$
$$\times \begin{pmatrix} -\frac{r}{K} - (\xi + \frac{r}{K})q_1 \\ \xi q_1 - \frac{am}{(a+I^*)^2}q_1q_2 + \frac{m(2a+I^*)P^*}{2(a+I^*)^2}q_1^2 \\ \frac{am\alpha}{(a+I^*)^2}q_1q_2e^{-2i\omega^*\tau^*-d_1\tau^*} - \frac{(2a+I^*)P^*}{2(a+I^*)^3}q_1^2e^{-2i\omega^*\tau^*-d_1\tau^*} \end{pmatrix},$$

$$F_2 = \begin{pmatrix} \frac{rS^*}{K} & (\xi + \frac{r}{K})S^* & 0 \\ -\xi I^* & -\frac{mI^*P^*}{(a+I^*)^2} & \frac{de^{d_1\tau^*}}{\alpha} \\ 0 & -\frac{am\alpha P^*e^{-d_1\tau^*}}{(a+I^*)^2} & 0 \end{pmatrix}^{-1}$$
$$\times \begin{pmatrix} -\frac{2r}{K} - (\xi + \frac{r}{K})(q_1 + \overline{q}_1) \\ \xi(q_1 + \overline{q}_1) - \frac{am}{(a+I^*)^2}(q_1\overline{q}_2 + \overline{q}_1q_2) + \frac{m(2a+I^*)P^*}{(a+I^*)^2}q_1\overline{q}_1 \\ \frac{am\alpha e^{-d_1\tau^*}}{(a+I^*)^2}(q_1\overline{q}_2 + \overline{q}_1q_2) - \frac{(2a+I^*)P^*e^{-d_1\tau^*}}{(a+I^*)^3}q_1\overline{q}_1 \end{pmatrix}.$$

So far, $g_{20}, g_{11}, g_{02}, g_{21}$ can be calculated exactly. Then we can compute the following quantities:

$$\begin{aligned} c_1(0) &= \frac{i}{2\omega^*\tau^*}\left(g_{11}g_{20} - 2|g_{11}|^2 - \frac{|g_{02}|^2}{3}\right) + \frac{g_{21}}{2}, \\ \mu_2 &= -\frac{\operatorname{Re}(c_1(0))}{\operatorname{Re}(\lambda'(\tau^*))}, \\ \beta_2 &= 2\operatorname{Re}\bigl(c_1(0)\bigr), \\ T_2 &= -\frac{\operatorname{Im}(c_1(0)) + \mu_2\operatorname{Im}(\lambda'(\tau^*))}{\omega^*\tau^*}, \end{aligned} \tag{3.29}$$

which determine the properties of bifurcating periodic solutions. From the discussion in Sections 3.2 and 3.3, we have the following results immediately.

Assume that the conditions in (ii) of Theorem 3.7 hold. Then μ_2, β_2, T_2 determine the direction, stability, and period of the corresponding Hopf bifurcation, respectively:

(i) The direction of the Hopf bifurcation of the system (1.3) at the E^* when $\tau = \tau^*$ is backward (forward) if $\mu_2 < 0$ ($\mu_2 > 0$), that is, there exists a bifurcating periodic solution for $\tau < \tau^*$ ($\tau > \tau^*$) in a sufficiently small τ^*-neighborhood;

(ii) The bifurcating periodic solution on the center manifold is unstable (stable) if $\beta_2 > 0$ ($\beta_2 < 0$); Particularly, the stability of the bifurcating periodic solutions of (1.3) is the same as that of bifurcating periodic solutions on the center manifold when $\tau^* = \tau_{\min}$ and $\tau^* = \tau_{\max}$.

(iii) The period of the bifurcating periodic solution decreases (increases) if $T_2 < 0$ ($T_2 > 0$).

4 Numerical simulations

Under the guidance of Section 3.2, we choose a set of parameters which satisfy conditions (H1)-(H3):

$$\begin{aligned} &r = 7, \quad K = 27, \quad \xi = 0.2, \quad m = 2.3, \quad a = 15, \\ &\mu = 0.85, \quad \alpha = 0.42, \quad d = 0.09, \quad d1 = 0.02. \end{aligned} \tag{4.1}$$

By direct calculation, we have $\tau^0 \approx 79.978$ and $\tau^1 \approx 48.84$. The intersections of S_n with τ-axis imply four Hopf bifurcation points (see Figure 2), denoted by

$$\tau_1 \approx 0.58, \qquad \tau_2 \approx 13.06, \qquad \tau_3 \approx 39.59, \quad \text{and} \quad \tau_4 \approx 47.64.$$

From Theorem 3.7, we know that the positive fixed point E^* is asymptotically stable when $\tau \in [0, \tau_1) \cup (\tau_4, \tau^0)$ (see Figures 3 and 4) and unstable when $\tau \in (\tau_1, \tau_4)$ (see Figure 5).

From the formula (3.21) and the algorithm derived in Section 3, we calculate some important quantities as in Table 1.

It shows us that for system (1.3) with the data (4.1):

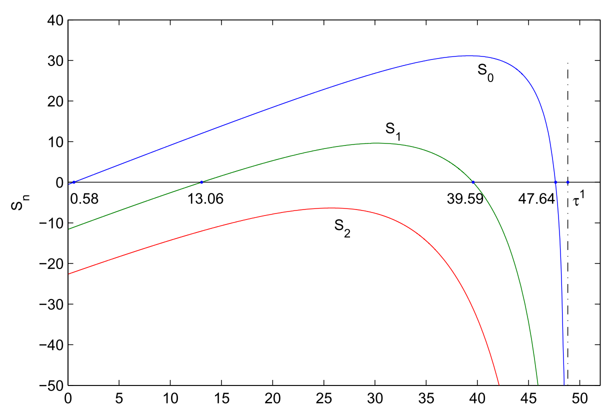


Figure 2 Graphs of $S_n(\tau)$ on $[0, \tau^1)$ with parameters given in (4.1).

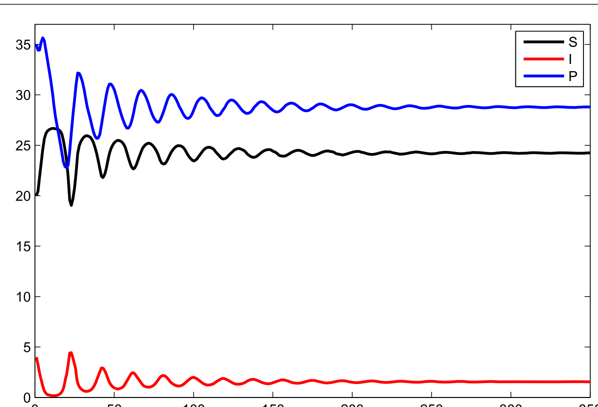


Figure 3 $E^* \approx (24.25, 1.55, 28.78)$ is asymptotically stable when $\tau \in [0, \tau_1)$, where $\tau = 0.4 < \tau_1 \approx 0.58$, and the initial condition is (20, 4, 35).

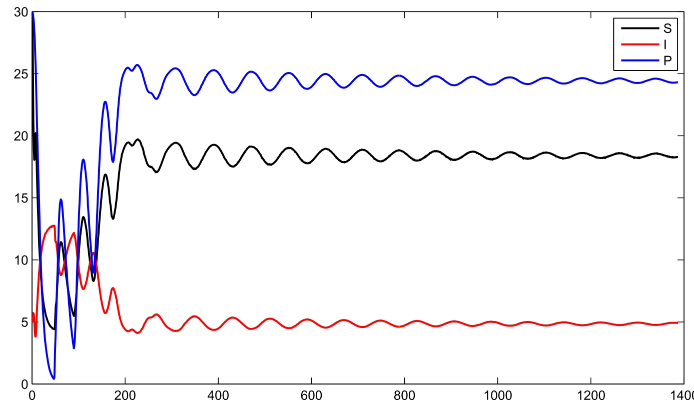


Figure 4 $E^* \approx (18.41, 4.85, 24.44)$ **is asymptotically stable when** $\tau \in (\tau_4, \tau^0)$**, where** $47.64 \approx \tau_4 < \tau = 48.2 < \tau^0 \approx 79.978$**, and the initial condition is (30, 5, 30).**

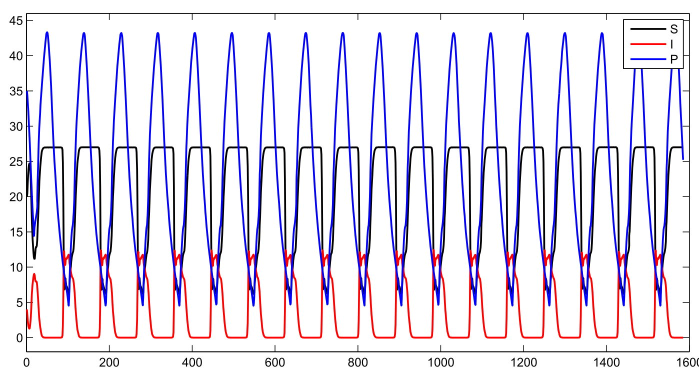


Figure 5 $E^* \approx (23.59, 1.93, 28.46)$ **is unstable, and sustained oscillation occurs when** $\tau \in (\tau_1, \tau_4)$**, where** $0.58 \approx \tau_1 < \tau = 10 < \tau_4 \approx 47.64$ **and the initial condition is (20, 4, 35).**

Table 1 List of quantities under (4.1)

	$\frac{\partial F}{\partial \omega}$	δ	$\mathrm{Re}(c_1(0))$	μ_2	β_2
$\tau_1 \approx 0.58$	$25.2805 > 0$	> 0	$-0.8258 < 0$	> 0	< 0
$\tau_2 \approx 13.06$	$18.7185 > 0$	> 0	$-0.0921 < 0$	> 0	< 0
$\tau_3 \approx 39.59$	$6.1430 > 0$	< 0	$-0.0230 < 0$	< 0	< 0
$\tau_4 \approx 47.64$	$2.4689 > 0$	< 0	$-0.0093 < 0$	< 0	< 0

1. The direction of the Hopf bifurcation at the E^* is forward when $\tau = \tau_1$ and $\tau = \tau_2$, and backward when $\tau = \tau_3$ and $\tau = \tau_4$, respectively.
2. All the bifurcating periodic solutions on the center manifold are stable. Particularly, the bifurcating periodic solutions are stable from τ_1 and τ_4, respectively.

From Figure 5 one can see that there maybe exist global Hopf branches even though we have no proof of this theoretically. In the following we carry out a numerical simulation to show this. A bifurcation diagram starting from $\tau = 0.58$ and $\tau = 13.06$ (see Figure 6) is constructed to show the global continuation of a periodic solution using DDE-BIFTOOL developed by Engelborghs *et al.* [25, 26]. In Figure 6, we can see the periodic solution starting from $\tau_2 \approx 13.06$ does not stop until it connected with $\tau_3 \approx 39.59$. The periodic

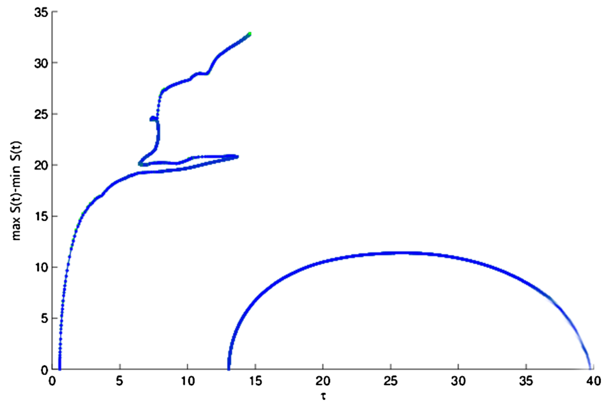


Figure 6 Hopf bifurcaton branches starting from $\tau_1 \approx 0.58$, $\tau_2 \approx 13.06$ and $\tau_3 \approx 39.59$ on the (τ, d) plane, where $d = \max S(t) - \min S(t)$.

solution starting from $\tau_1 \approx 0.58$ also goes on a long way, and the strange behavior from $\tau \approx 6.7$ in the first branch needs to be studied.

Competing interests
The authors declare that they have no competing interests.

Authors' contributions
All authors contributed equally to the writing of this paper. All authors read and approved the final manuscript.

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