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Ratio-dependent predator–prey model of interacting population with delay effect

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Abstract A system of delay differential equation is proposed to account the effect of delay in the predator–prey model of interacting population. In this article, the modified ratio-dependent Bazykin model with delay in predator equation has been considered. The essential mathematical features of the proposed model are analyzed with the help of equilibria, local and global stability analysis, and bifurcation theory. The parametric space under which the system enters into a Hopf-bifurcation has been investigated. Global stability results are obtained by constructing suitable Lyapunov functions. We derive the explicit formulae for determining the stability, direction, and other properties of bifurcating periodic solutions by using normal form and central manifold theory. Using the global Hopf-bifurcation result of Wu (Trans. Am. Math. Soc., 350:4799–4838, 1998) for functional differential equations, the global existence of periodic solutions has been established. Our analytical findings are supported by numerical experiments. Biological implication of the analytical findings are discussed in the conclusion section.

Keywords Population model · Delay · Local stability · Global stability · Hopf-bifurcation · Permanence · Numerical simulation

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1 Introduction

Ecological models have received much attention from scientists. Relevant references in this context are also vast and we mention a few here (cf. Anderson and May [2–5], Bailey [6], and Diekman et al. [7]). It is well understood that many of the processes both natural and man-made in biology and medicine involve time delays. Time delay occurs often in almost every situation, ignoring them, therefore, is not realistic. Kuang [8] mentioned that an animal must take time delays to digest their food before their further activities take place. Hence, models of species dynamics without delays is an approximation. It is more realistic to assume that the reproduction of predator after predating the prey will not be instantaneous, but mediated through some time lag which is required for gestation of the predator. In ecological science, the food chain is constructed by food and feeding relationships between the organisms. After predation, some amounts of energy in the form of biomass of prey assimilate into the predator's energy also in the form of biomass. But this bio-physiological process is not simple; the conversion of prey energy to predator energy is not instantaneous, and several processes are involved in this mechanism. First, the portion of prey biomass enters into the digestive system of predator. Digestion is a complicated process and time consuming; several enzymes are secreted in the digestive system which act one by one and different components of prey food such as carbohydrate, protein, and fat are digested and transformed into monosaccharide, amino acids, fatty acids, and glycerol. After digestion, the next process is absorption; the digested foods are absorbed in the digestive system of the predator through different pathways and enter into the body. After entering into the predator's body, the absorbed prey food finally is assimilated into the predator's protoplasm, i.e., transformed into the predator's energy in the form of biomass. The whole transformation process requires time. Detailed arguments on the importance of time delays in realistic models can be found in the classical books of Kuang [8], Gopalsamy [9], MacDonald [10], and May [11]. So, inclusion of time delay will certainly make the predator–prey model one step closer to real situation.

After the pioneering works of Lotka and Volterra, a large volume of work has been carried out on the predator–prey model. The most crucial element in these models is the "functional response"—the expression that describes the rate at which the number of prey is consumed by a predator. Modifications were limited to replacing the Malthusian growth function, the predator per capita consumption of prey functions such as Holling type I, II, III functional responses, or density dependent mortality rates. These functional responses depend only on the prey volume x, but soon it became clear that the predator volume y can influence this function by direct interference while searching or by pseudo interference (cf. Curds and Cockburn [12], Hassell and Varley [13], and Salt [14]). A simple way of incorporating predator dependence in the functional response was proposed by Arditi and Ginzburg [15], who considered this response function as a function of the ratio x/y. In recent times, there are growing explicit biological and physiological evidences that in many situations, when a predator has to search for food, a more suitable general predator–prey theory should be based on the so-called ratio-dependent theory as in Arditi and Berryman [16], Arditi and Saiah [17], Akcakaya et al. [18], Cosner et al. [19], and Gutierrez [20], which may roughly be stated as the per capita predator growth rate should be a function of predator–prey abundance. A recent finding of Jost et al. [21] shows that prey-dependent and ratio-dependent models can fit well with the time series generated by each other. Interestingly, it has been investigated that the ratio-dependent predator–prey models are more appropriate for predator–prey interactions when the predator involves serious hunting processes, like animals searching for animals, etc. (cf. Kuang [22]). It is justified through some basic but different principles that ratio dependent models are more appropriate for modeling predator–prey interactions (cf. Thieme [23] and Cosner et al. [19]). Moreover, the ratio-dependent model is more flexible and versatile as evident from the findings of Hsu et al. [24] and Cosner [25]. Keeping these in mind, an attempt is made in the present investigation to study the effect of delay as well as self-interaction on a ratio-dependent predator–prey model.

2 Basic assumptions and our mathematical model

The ratio-dependent model due to Kuang and Beretta [26] is as follows:

$$\frac{dx}{dt} = ax - \frac{bxy}{Ay + x}, \tag{2.1a}$$

$$\frac{dy}{dt} = -cy + \frac{dxy}{Ay + x}, \tag{2.1b}$$

$$x(0) = x_0 > 0, \quad y(0) = y_0 > 0,$$

where a, b, c, d, A are positive constants with their usual ecological meanings.

The classical Bazykin's model (Sect. 3.5.2 of Bazykin [27]) can be written as

$$\frac{dx}{dt} = ax - \frac{bxy}{1 + Ax} - ex^2, \tag{2.2a}$$

$$\frac{dy}{dt} = -cy + \frac{dxy}{1 + Ax} - hy^2, \tag{2.2b}$$

$$x(0) = x_0 > 0, \quad y(0) = y_0 > 0.$$

The system (2.2a)–(2.2b) is studied extensively by Alekseev [28], Bazykin [29, 30]. and Bazykin et al. [31].

Observing the importance of the ratio-dependent predator–prey model, we are influenced to modify the classical Bazykin's model by taking into account the ratio-dependent terms when a predator experiences serious hunting process, and thus the system (2.2a)–(2.2b) takes the following form:

$$\frac{dx}{dt} = ax - \frac{bxy}{y + Ax} - ex^2, \tag{2.3a}$$

$$\frac{dy}{dt} = -cy + \frac{dxy}{y + Ax} - hy^2, \tag{2.3b}$$

$$x(0) = x_0 > 0, \quad y(0) = y_0 > 0,$$

where $\frac{d}{b} \in (0, 1)$ is the conversion factor which represents the rate of conversion of the consumed prey into predator.

As the reproduction of the predator population after predating the prey will not be instantaneous, but mediated by some constant time lag $\tilde{\tau} > 0$ for gestation of predator (cf. Wang and Chen [32] and Zhao et al. [33]), we incorporate time delay in the predator equation into the system (2.3a)–(2.3b). With the above assumptions, our model takes the final form as

$$\frac{dx}{dt} = ax - \frac{bxy}{y + Ax} - ex^2, \tag{2.4a}$$

$$\frac{dy}{dt} = -cy + \frac{dx(t - \tilde{\tau})y(t - \tilde{\tau})}{y(t - \tilde{\tau}) + Ax(t - \tilde{\tau})} - hy^2, \tag{2.4b}$$

where $\tilde{\tau}$ represents the time lag required for gestation of predator which is based on the assumption that the rate of change of predator depends on the number of prey and of predators present at some previous time.

Introducing the nondimensional variables $u' = \frac{ex}{a}$, $v' = \frac{bey}{ad}$, and $t' = at$, the system (2.4a)–(2.4b) reduces to the following nondimensional form as (after dropping $'$):

$$\frac{du}{dt} = u - \frac{\epsilon uv}{\alpha u + v} - u^2 = F_1(u, v), \tag{2.5a}$$

$$\frac{dv}{dt} = -\gamma v + \frac{\epsilon u(t - \tau)v(t - \tau)}{\alpha u(t - \tau) + v(t - \tau)} - \delta v^2 = F_2(u, v), \tag{2.5b}$$

with initial conditions

$$u(\theta) = \phi(\theta) \geq 0, \quad v(\theta) = \psi(\theta) \geq 0,$$

$$\theta \in [-\tau, 0), \quad \phi(0) > 0, \quad \psi(0) > 0,$$

where $\epsilon = \frac{b}{d}$, $\alpha = \frac{Ab}{d}$, $\gamma = \frac{c}{a}$, $\delta = \frac{hd}{be}$, $\tau = a\tilde{\tau}$. Here, $\phi(\theta)$, $\psi(\theta)$ are continuous functions in the interval $[-\tau, 0)$. For ecological reasons, we consider the model (2.5a)–(2.5b) only in $\mathrm{Int}(\mathbf{R}_+^2) = \{(u, v); u > 0, v > 0\}$.

We discuss the dynamics of the system (2.5a)–(2.5b) with $\tau > 0$ in Sects. 5–8. Simulation results are reported in Sect. 9, while a final discussion and interpretations of our results in terms of ecology are given in Sect. 10.

3 Equilibria of the delayed system (2.5a)–(2.5b)

The system (2.5a)–(2.5b) has three positive steady states, namely (i) $E^0(0,0)$, the trivial equilibrium, (ii) $E^1(1,0)$, the axial equilibrium, and (iii) $E^*(u^*, v^*)$, the interior equilibrium, where u^*, v^* can be obtained from the following system of algebraic equations:

$$1 - u^* - \frac{\epsilon v^*}{\alpha u^* + v^*} = 0, \tag{3.1a}$$

$$-\gamma - \delta v^* + \frac{\epsilon u^*}{\alpha u^* + v^*} = 0. \tag{3.1b}$$

Substituting the value of $v^* = \frac{\alpha u^*(1-u^*)}{(u^*-1+\epsilon)}$ from (3.1a) into (3.1b), we have the quadratic equation in u^* given by

$$\begin{aligned}&(\delta\alpha^2 + 1)u^{*2} - (\gamma\alpha + 2(1 - \epsilon) + \delta\alpha^2)u^* \\ &\quad + \gamma\alpha(1 - \epsilon) + (1 - \epsilon)^2 = 0.\end{aligned} \tag{3.2}$$

The roots of the above quadratic are given by $u_\pm^* = \frac{\gamma\alpha+2(1-\epsilon)+\delta\alpha^2\pm\sqrt{\Delta_1}}{2(\delta\alpha^2+1)}$, where

$$\begin{aligned}\Delta_1 &= (\gamma\alpha + 2(1 - \epsilon) + \delta\alpha^2)^2 \\ &\quad - 4(\delta\alpha^2 + 1)(\gamma\alpha(1 - \epsilon) + (1 - \epsilon)^2).\end{aligned}$$

If we consider the conditions (i) $(\gamma\alpha + 2(1 - \epsilon) + \delta\alpha^2) > 0$ and (ii) $\gamma\alpha(1 - \epsilon) + (1 - \epsilon)^2 < 0$, then it is clear from Descarte's rule of sign that the above quadratic equation (3.2) possesses a unique positive root $u_+^* = \frac{\gamma\alpha+2(1-\epsilon)+\delta\alpha^2+\sqrt{\Delta_1}}{2(\delta\alpha^2+1)}$. Using this value of u_+^*, we certainly have $v_+^* = \frac{\alpha u_+^*(1-u_+^*)}{(u_+^*-1+\epsilon)}$.

4 Local stability of the delayed ($\tau > 0$) system (2.5a)–(2.5b) around E^0 and E^1

It is clear that the delayed system is unconditionally unstable around $E^0(0,0)$ due to the existence of the positive eigenvalue. Now we direct our attention to discuss the stability of the system around the axial equilibrium E^1.

The variational matrix of the system (2.5a)–(2.5b) at E^1 takes the form as

$$J^1 = \begin{bmatrix} -1 & -\frac{\epsilon}{\alpha} \\ 0 & -\gamma + \frac{\epsilon}{\alpha} e^{-\tau\lambda} \end{bmatrix}.$$

Then the characteristic equation of the system at E^1 is of the form

$$(\lambda + 1)\left(\lambda + \gamma - \frac{\epsilon}{\alpha} e^{-\tau\lambda}\right) = 0.$$

Here, $\lambda = -1$ is a negative eigenvalue, we now consider the equation

$$\lambda = -\gamma + \frac{\epsilon}{\alpha} e^{-\tau\lambda}. \tag{4.1}$$

If $\tau = 0$ and $\gamma\alpha > \epsilon$, the equilibrium E^1 is locally asymptotically stable.

Again by substituting $\lambda = i\vartheta$ in (4.1) and equating real and imaginary parts, we obtain

$$\vartheta\alpha = -\epsilon \sin\vartheta\tau,$$
$$\gamma\alpha = +\epsilon\cos\vartheta\tau.$$

Eliminating τ, we have

$$\vartheta^2 = \frac{\epsilon^2}{\alpha^2} - \gamma^2. \tag{4.2}$$

We know that (4.2) has a positive root ϑ_+ if $\epsilon > \gamma\alpha$. Therefore, there is a positive constant τ_+ such that for $\tau > \tau_+$, E^1 becomes unstable.

5 Dynamics of the delayed system around the interior equilibrium E^*

Using Taylor expansion about the interior equilibrium $E^* \equiv (u^*, v^*)$, the system (2.5a)–(2.5b) reduces to

$$\frac{du_1}{dt} = J_{11}u_1(t) + J_{12}v_1(t) + \sum_{\substack{i+j\ge 2\\ i,j\ge 0}} a_{ij} u_1^i(t) v_1^j(t), \tag{5.1a}$$

$$\frac{dv_1}{dt} = J_{21}u_1(t-\tau) - J_{12}v_1(t-\tau) - \left(\gamma + 2\delta v^*\right)v_1(t) + \sum_{\substack{i+j+k\ge 2\\ i,j,k\ge 0}} b_{ijk} u_1^i(t-\tau) v_1^j(t-\tau) v_1^k(t), \tag{5.1b}$$

where

$$u_1 = u - u^*, \qquad v_1 = v - v^*,$$

$$J_{11} = \frac{\partial F_1}{\partial u_1}\bigg|_{E^*} = \frac{\alpha\epsilon u^* v^*}{(\alpha u^* + v^*)^2} - u^*,$$

$$J_{12} = \frac{\partial F_1}{\partial v_1}\bigg|_{E^*} = -\frac{\alpha\epsilon u^{*2}}{(\alpha u^* + v^*)^2},$$

$$J_{21} = \frac{\partial F_2}{\partial u_1}\bigg|_{E^*} = \frac{\epsilon v^{*2}}{(\alpha u^* + v^*)^2},$$

$$a_{ij} = \frac{1}{i!j!} \frac{\partial^{i+j}(F_1)}{\partial u_1^i \partial v_1^j}\bigg|_{E^*} \quad \text{and}$$

$$b_{ijk} = \frac{1}{i!j!k!} \frac{\partial^{i+j+k}(F_2)}{\partial u_1^i(t-\tau)\partial v_1^j(t-\tau)\partial v_1^k}\bigg|_{E^*}.$$

Considering only the linear expansion of the system (2.5a)–(2.5b) about the interior equilibrium E^*, we have

$$\frac{du_1}{dt} = J_{11}u_1(t) + J_{12}v_1(t), \tag{5.2a}$$

$$\frac{dv_1}{dt} = J_{21}u_1(t-\tau) - J_{12}v_1(t-\tau) - \left(\gamma + 2\delta v^*\right)v_1(t). \tag{5.2b}$$

The Jacobian matrix of the system (2.5a)–(2.5b) with discrete delay ($\tau > 0$) at E^* is given by

$$J^* = \begin{bmatrix} \frac{\alpha\epsilon u^* v^*}{(\alpha u^*+v^*)^2} - u^* & -\frac{\alpha\epsilon u^{*2}}{(\alpha u^*+v^*)^2} \\ \frac{\epsilon v^{*2}}{(\alpha u^*+v^*)^2} e^{-\tau\lambda} & -\gamma - 2\delta v^* + \frac{\alpha\epsilon u^{*2}}{(\alpha u^*+v^*)^2} e^{-\tau\lambda} \end{bmatrix}$$

and its corresponding characteristic equation is

$$\begin{vmatrix} \frac{\alpha\epsilon u^* v^*}{(\alpha u^*+v^*)^2} - u^* - \lambda & -\frac{\alpha\epsilon u^{*2}}{(\alpha u^*+v^*)^2} \\ \frac{\epsilon v^{*2}}{(\alpha u^*+v^*)^2} e^{-\tau\lambda} & -\gamma - 2\delta v^* + \frac{\alpha\epsilon u^{*2}}{(\alpha u^*+v^*)^2} e^{-\tau\lambda} - \lambda \end{vmatrix} = 0,$$

or equivalently,

$$\begin{vmatrix} J_{11} - \lambda & J_{12} \\ J_{21}e^{-\tau\lambda} & -(\gamma + 2\delta v^* + J_{12}e^{-\tau\lambda} + \lambda) \end{vmatrix} = 0.$$

Hence, under the above assumption, the characteristic equation around the interior equilibrium $E^* \equiv (u^*, v^*)$ with positive delay takes the following transcendental equation as

$$\lambda^2 + (\gamma + 2\delta v^* - J_{11})\lambda - J_{11}(\gamma + 2\delta v^*) = J_{12}(J_{11} + J_{21} - \lambda)e^{-\lambda\tau}. \tag{5.3}$$

It is well known that the sign of the real parts of the solutions of (5.3) characterize the stability behavior of E^*. Therefore, by substituting $\lambda = \xi + i\eta$ in (5.3), we obtain real and imaginary parts respectively as

$$\xi^2 - \eta^2 + (\gamma + 2\delta v^* - J_{11})\xi - J_{11}(\gamma + 2\delta v^*) = J_{12}e^{-\xi\tau}\big((J_{11} + J_{21} - \xi)\cos\tau\eta - \eta\sin\tau\eta\big) \tag{5.4}$$

and

$$2\xi\eta + (\gamma + 2\delta v^* - J_{11})\eta = -J_{12}e^{-\xi\tau}\big((J_{11} + J_{21} - \xi)\sin\tau\eta + \eta\cos\tau\eta\big). \tag{5.5}$$

A necessary condition for the change of stability of the equilibrium E^* is that the characteristic equation (5.3) should have purely imaginary roots. Hence, to obtain stability criterion, we take $\xi = 0$ in (5.4) and (5.5). Therefore, the above two equations reduce to

$$-\eta^2 - J_{11}(\gamma + 2\delta v^*) = J_{12}\big((J_{11} + J_{21})\cos\tau\eta - \eta\sin\tau\eta\big), \tag{5.6}$$

$$(\gamma + 2\delta v^* - J_{11})\eta = -J_{12}\big(\eta\cos\tau\eta + (J_{11} + J_{21})\sin\tau\eta\big). \tag{5.7}$$

Eliminating τ from (5.6) and (5.7), we get a biquadratic equation in τ as

$$\eta^4 + \big(2J_{11}(\gamma + 2\delta v^*) - J_{12}^2 + (\gamma + 2\delta v^* - J_{11})^2\big)\eta^2 + J_{11}^2(\gamma + 2\delta v^*)^2 - J_{12}^2(J_{11} + J_{21})^2 = 0. \tag{5.8}$$

Substituting $\eta^2 = \sigma$ in the above equation, we have a quadratic equation in σ of the form

$$\sigma^2 + \big(2J_{11}(\gamma + 2\delta v^*) - J_{12}^2 + (\gamma + 2\delta v^* - J_{11})^2\big)\sigma + J_{11}^2(\gamma + 2\delta v^*)^2 - J_{12}^2(J_{11} + J_{21})^2 = 0, \tag{5.9}$$

which on simplification gives

$$\sigma^2 + \big(J_{11}^2 - J_{12}^2 + (\gamma + 2\delta v^*)^2\big)\sigma + J_{11}^2(\gamma + 2\delta v^*)^2 - J_{12}^2(J_{11} + J_{21})^2 = 0. \tag{5.10}$$

Hence, the constant term of the quadratic equation (5.10) is negative if $|J_{11}(\gamma + 2\delta v^*)| < |J_{12}(J_{11} + J_{21})|$, that is, if $-J_{11}(\gamma + 2\delta v^*) < J_{12}(J_{11} + J_{21})$.

Therefore, by the Descartes rule of sign, the quadratic equation (5.10) always has a unique positive root irrespective of the sign of the coefficient of σ. The stability criteria of system (2.5a)–(2.5b) for $\tau = 0$ will not necessarily ensure the stability of the same system with positive delay $\tau > 0$. In the following theorem, we give a criterion for switching the stability behavior of E^*.

Theorem 5.1 *Let E^* exists and locally asymptotically stable for the system (2.5a)–(2.5b) with $\tau = 0$. Also let $\sigma^* = \eta^{*2}$ be a positive root of (5.10), then there exists a $\tau = \tau^*$ such that E^* is locally asymptotically stable for $\tau \in (0, \tau^*]$ and unstable for $\tau > \tau^*$. Furthermore, the system undergoes Hopf-bifurcation at E^* when $\tau = \tau^*$, provided $(Z(\eta)X(\eta) - Y(\eta)W(\eta)) > 0$.*

Proof Since η^* is a solution of (5.8), therefore, the characteristic equation (5.3) has a pair of purely imaginary roots of the form $\pm i\eta^*$. From (5.6) and (5.7), we have

$$\tau_n^* = \frac{1}{\eta^*}\arccos\left[\frac{-\eta^{*2}(\gamma + 2\delta v^* + J_{21})}{J_{12}((J_{11} + J_{21})^2 + \eta^{*2})} - \frac{J_{11}(J_{11} + J_{21})(\gamma + 2\delta v^*)}{J_{12}((J_{11} + J_{21})^2 + \eta^{*2})}\right] + \frac{2\pi n}{\eta^*}, \tag{5.11}$$

where $n = 0, 1, 2, \ldots$.

For $\tau = 0$, E^* is locally asymptotically stable. Hence, by Butler's lemma (cf. Freedman and Hari Rao [34]), E^* remains stable for $\tau < \tau^*$, where $\tau^* = \tau_n^*$ as $n = 0$. The theorem will be proved if we can show that

$$\frac{d}{d\tau}\big(\mathrm{Re}(\lambda(\tau))\big)\big|_{\tau=\tau^*} > 0. \tag{5.12}$$

Differentiating equations (5.4) and (5.5) with respect to τ and then letting $\xi = 0$, we obtain

$$X(\eta)\frac{d\xi}{d\tau} + Y(\eta)\frac{d\eta}{d\tau} = Z(\eta), \tag{5.13}$$

$$-Y(\eta)\frac{d\xi}{d\tau} + X(\eta)\frac{d\eta}{d\tau} = W(\eta), \tag{5.14}$$

where

$$
\begin{aligned}
X(\eta) &= \big(\gamma + 2\delta v^* - J_{11}\big) + \big(\tau(J_{11} + J_{21})\cos\tau\eta \\
&\quad - \tau\eta\sin\tau\eta + \cos\tau\eta\big)J_{12}, \\
Y(\eta) &= \big(\tau(J_{11} + J_{21})\sin\tau\eta \\
&\quad + \tau\eta\cos\tau\eta + \sin\tau\eta\big)J_{12} - 2\eta, \\
Z(\eta) &= -J_{12}\big(\eta(J_{11} + J_{21})\sin\tau\eta + \eta^2\cos\tau\eta\big), \\
W(\eta) &= J_{12}\big(\eta^2\sin\tau\eta - \eta(J_{11} + J_{21})\cos\tau\eta\big).
\end{aligned}
$$

Solving the system of (5.13)–(5.14) for $\frac{d\xi}{d\tau}$ and $\frac{d\eta}{d\tau}$, we have

$$
\frac{d\xi}{d\tau}\bigg|_{\tau=\tau^*,\eta=\eta^*} = \frac{Z(\eta)X(\eta) - Y(\eta)W(\eta)}{X^2(\eta) + Y^2(\eta)}\bigg|_{\tau=\tau^*,\eta=\eta^*},
$$

or equivalently

$$
\frac{d}{d\tau}\big(\mathrm{Re}\big(\lambda(\tau)\big)\big)\big|_{\tau=\tau^*,\eta=\eta^*} > 0 \quad \text{if } \big\{Z(\eta)X(\eta) - Y(\eta)W(\eta)\big\} > 0.
$$

Therefore, the transversality condition is satisfied and Hopf-bifurcation occurs at $\tau = \tau^*$. Hence, the proof. □

6 Global stability with nonzero time lag around E^*

6.1 Boundedness of the system with $\tau > 0$

Proposition 6.1 *All the solution of the system* (2.5a)–(2.5b) *are uniformly bounded with an ultimate bound.*

Proof Define a function $W(t) = u(t - \tau) + v(t)$, which on differentiation with respect to time gives (by making use of (2.5a)–(2.5b))

$$
\begin{aligned}
\dot{W} &= \dot{u}(t - \tau) + \dot{v}(t) \\
&= u(t - \tau)\big(1 - u(t - \tau)\big) - \frac{\epsilon u(t - \tau)v(t - \tau)}{\alpha u(t - \tau) + v(t - \tau)} \\
&\quad - \gamma v + \frac{\epsilon u(t - \tau)v(t - \tau)}{\alpha u(t - \tau) + v(t - \tau)} - \delta v^2 \\
&= -\big(u(t - \tau) + v(t)\big) + u(t - \tau)\big(2 - u(t - \tau)\big) \\
&\quad + \delta v\left(\frac{(1 - \gamma)}{\delta} - v\right) \\
&\le -W + \left(1 + \frac{(1 - \gamma)^2}{4\delta}\right),
\end{aligned} \tag{6.1}
$$

which yields

$$
\limsup_{t\to\infty} W(t) \le 1 + \frac{(1 - \gamma)^2}{4\delta} \equiv \mathcal{L}. \tag{6.2}
$$

Thus, there exists a positive constant $\mathcal{L} > 0$ such that $W(t) < \mathcal{L}$ for all large t. □

Theorem 6.2 *Consider the equation $\dot{x}(t) = ax(t - \tau) - bx(t) - cx^2(t)$, where $a, b, c, \tau > 0$ for $-\tau < t < 0$. Then* (i) *if $a > b$, $\lim_{t\to+\infty} x(t) = \frac{a-b}{c}$ and* (ii) *if $a < b$, $\lim_{t\to+\infty} x(t) = 0$.*

Proof See Lemma 3.1 in Song and Chen [35]. □

Lemma 1 *For any positive solution $w(t) = (u(t), v(t))$ of the system* (2.5a)–(2.5b), *there exists a $T > 0$ such that* (i) *$m_1 < u(t) < 1$ and* (ii) *$m_2 < v(t) < M_2$ for $t > T = \max(T_1, T_2)$, where $m_1 = (1 - \epsilon)$, $M_2 = \frac{(\epsilon-\gamma\alpha)}{\alpha\delta}$ and $m_2 = \frac{1}{\delta}(-\gamma + \frac{\epsilon m_1}{\alpha+M_2})$.*

Proof From the first equation of the model (2.5a)–(2.5b), we have

$$
\frac{du}{dt} \le u(1 - u).
$$

By using standard argument, we have

$$
\limsup_{t\to+\infty} u(t) < 1.
$$

We also write (2.5a) as

$$
\frac{du}{dt} \ge u\big((1 - \epsilon) - u\big),
$$

which shows that $\liminf_{t\to+\infty} u(t) > 1 - \epsilon = m_1$ where $1 > \epsilon$.

Again from (2.5b), we obtain

$$
\frac{dv}{dt} \le \frac{\epsilon}{\alpha}v(t - \tau) - \gamma v - \delta v^2.
$$

By Theorem 6.2, we have $\lim_{t\to+\infty} v(t) \le \frac{\epsilon-\gamma\alpha}{\alpha\delta}$. Therefore, there exists a $t > T_1$ such that $v(t) \le \frac{(\epsilon-\gamma\alpha)}{\alpha\delta} = M_2$.

Equation (2.5b) can be written as

$$
\frac{dv}{dt} \ge \frac{\epsilon m_1}{\alpha + M_2}v(t - \tau) - \gamma v - \delta v^2.
$$

Hence, by using the similar argument, we have $\lim_{t\to+\infty} v(t) \ge \frac{1}{\delta}(-\gamma + \frac{\epsilon m_1}{\alpha+M_2})$. Therefore, there exists a $t > T_2$ such that $v(t) \ge \frac{1}{\delta}(-\gamma + \frac{\epsilon m_1}{\alpha+M_2}) = m_2$. Hence, the proof. □

6.2 Global stability of the system with discrete delay $\tau > 0$ around E^1

Theorem 6.3 *If* $\epsilon < \frac{\gamma\alpha}{1+\gamma\alpha}$, *then the equilibrium* $E^1(1,0)$ *of the system (2.5a)–(2.5b) is globally asymptotically stable.*

Proof Let $(u(t), v(t))$ be any positive solution of the system (2.5a)–(2.5b). Define

$$V_{01}(t) = u(t) - 1 - \ln u(t) + v(t). \tag{6.3}$$

Calculating the time derivative of V_{01}, we have by making use of (2.5a)–(2.5b)

$$\begin{aligned}\dot V_{01} &= (u-1)\left(-(u-1) - \frac{\epsilon v}{\alpha u + v}\right) - \gamma v \\ &\quad + \frac{\epsilon u(t-\tau)v(t-\tau)}{\alpha u(t-\tau) + v(t-\tau)} - \delta v^2 \\ &= -(u-1)^2 - \delta v^2 + \frac{\epsilon v}{\alpha u + v} - \gamma v - \frac{\epsilon u v}{\alpha u + v} \\ &\quad + \frac{\epsilon u(t-\tau)v(t-\tau)}{\alpha u(t-\tau) + v(t-\tau)}. \end{aligned} \tag{6.4}$$

Let us consider the Lyapunov function due to the structure of (6.4) as follows:

$$V_{02}(t) = V_{01}(t) + \epsilon \int_{t-\tau}^{t} \frac{u(s)v(s)}{\alpha u(s) + v(s)}\, ds. \tag{6.5}$$

Taking the positive derivative on both sides of (6.5) and using (6.4), we have

$$\begin{aligned}\dot V_{02} &= \dot V_{01} + \frac{\epsilon u v}{\alpha u + v} - \frac{\epsilon u(t-\tau)v(t-\tau)}{\alpha u(t-\tau) + v(t-\tau)} \\ &= -(u-1)^2 - \delta v^2 + \frac{\epsilon v}{\alpha u + v} - \gamma v \qquad (6.6)\\ &\le -(u-1)^2 - \delta(v-0)^2 + \left(\frac{\epsilon}{\alpha m_1} - \gamma\right) v, \\ &\text{where } m_1 = 1 - \epsilon. \qquad (6.7)\end{aligned}$$

If $\epsilon \le \gamma\alpha m_1$, i.e., $\epsilon \le \frac{\gamma\alpha}{1+\gamma\alpha}$, then from (6.7) we have $\dot V_{02} < 0$. Therefore, the solutions ultimately go to $\mathcal{M}$, the largest invariant subset of $\dot V_{02} = 0$ (cf. Hale [36]). It is clear from (6.6) that $\dot V_{02} = 0$ iff $u(t) = 1, v(t) = 0$. Accordingly, the global asymptotic stability of E_1 follows from LaSalle's invariance principle. Hence, the proof is completed. □

6.3 Global stability of the system with discrete delay $\tau > 0$ around E^*

Theorem 6.4 *If*

$$\begin{aligned}\min\Bigg\{&1 - \frac{\epsilon}{m_1} - \frac{\epsilon v^*}{\alpha m_2 u^*}\left(1 + \frac{\epsilon M_2 \tau}{\alpha m_2}\right), \\ &\left(1 - \frac{\tau\epsilon M_2}{\alpha m_2}\right)\left(\delta + \frac{\epsilon u^*}{M_2(\alpha u^* + v^*)}\right) \\ &\quad - \frac{\epsilon}{\alpha}\left(\frac{1}{m_1} + \frac{1}{m_2} + \frac{\epsilon M_2 \tau}{\alpha m_2^2}\right)\Bigg\} > 0,\end{aligned}$$

then the interior equilibrium E^* *of the system (2.5a)–(2.5b) is globally asymptotically stable.*

Proof To prove the global stability of the system (2.5a)–(2.5b) around E^*, we need the help of Lemma 1. Let $D = \{(u,v) : m_1 < u(t) \le 1; m_2 < v(t) < M_2\}$, then D is a compact bounded region in $\mathbf{R}_+^2$ which has positive distance from the coordinate axes. Then there exists a T^* such that for all $t > T^* = T + \tau$, every positive solution of the system (2.5a)–(2.5b) with $\tau > 0$, eventually enters and remains in the region D.

We now derive sufficient condition which guarantees that the positive interior equilibrium $E^*(u^*, v^*)$ of the system (2.5a)–(2.5b) is globally asymptotically stable. The strategy used in this proof is to construct a suitable Lyapunov functional. For mathematical convenience, the following transformations of variables have been made use of:

$$u(t) = u^* e^{X(t)}, \qquad v(t) = v^* e^{Y(t)}. \tag{6.8}$$

These coordinate transformations reduce the positive equilibrium E^* into the trivial equilibrium $X(t) = Y(t) = 0$ for all $t > 0$. Due to the variable change (6.8), the system (2.5a)–(2.5b) changes to the following set of autonomous nonlinear differential equations:

$$\begin{aligned}\frac{dX}{dt} &= -u^*\left(e^{X(t)} - 1\right) - \frac{\epsilon\alpha u^* v^* (e^{Y(t)} - 1)}{(\alpha u + v)(\alpha u^* + v^*)} \\ &\quad + \frac{\epsilon\alpha u^* v^* (e^{X(t)} - 1)}{(\alpha u + v)(\alpha u^* + v^*)},\end{aligned} \tag{6.9a}$$

$$\begin{aligned}\frac{dY}{dt} &= -\left(\delta + \frac{\epsilon u^*}{v(\alpha u^* + v^*)}\right) v^*\left(e^{Y(t)} - 1\right) \\ &\quad + \frac{\epsilon u^* v^* v(t-\tau)(e^{X(t-\tau)} - 1)}{(\alpha u(t-\tau) + v(t-\tau)) v(\alpha u^* + v^*)} \\ &\quad + \frac{\epsilon u^* v^* \alpha u(t-\tau)(e^{Y(t-\tau)} - 1)}{(\alpha u(t-\tau) + v(t-\tau)) v(\alpha u^* + v^*)}.\end{aligned} \tag{6.9b}$$

Let $V_1 = |X(t)|$. Computing the upper right derivative of $V_1(t)$ along with the solution of (2.5a)–(2.5b), one can easily obtain

$$D^+V_1(t) \le -u^*|e^{X(t)}-1| - \frac{\epsilon\alpha u^* v^* |e^{Y(t)}-1|}{(\alpha u+v)(\alpha u^*+v^*)} + \frac{\epsilon\alpha u^* v^* |e^{X(t)}-1|}{(\alpha u+v)(\alpha u^*+v^*)} \le -u^*|e^{X(t)}-1| + \frac{\epsilon v^*}{\alpha m_1}|e^{Y(t)}-1| + \frac{\epsilon u^*}{m_1}|e^{X(t)}-1| = -u^*\left(1-\frac{\epsilon}{m_1}\right)|e^{X(t)}-1| + \frac{\epsilon}{\alpha m_1}v^*|e^{Y(t)}-1|. \tag{6.10}$$

Now, (6.9b) can be rewritten as

$$\begin{aligned}\frac{dY}{dt} = &-\left(\delta+\frac{\epsilon u^*}{v(\alpha u^*+v^*)}\right)v^*(e^{Y(t)}-1) + \frac{\epsilon u^* v^* v(t-\tau)(e^{X(t-\tau)}-1)}{(\alpha u(t-\tau)+v(t-\tau))v(\alpha u^*+v^*)} \\ &+ \frac{\epsilon u^* v^* \alpha u(t-\tau)(e^{Y(t)}-1)}{(\alpha u(t-\tau)+v(t-\tau))v(\alpha u^*+v^*)} - \frac{\epsilon\alpha u^* v^* u(t-\tau)}{(\alpha u^*+v^*)v(\alpha u(t-\tau)+v(t-\tau))} \\ &\times \int_{t-\tau}^{t} e^{Y(s)}\left[-\left(\delta+\frac{u^*}{v(\alpha u^*+v^*)}\right) \times v^*(e^{Y(s)}-1) + \frac{\epsilon u^* v^* v(s-\tau)}{v(\alpha u^*+v^*)} \times \frac{(e^{X(s-\tau)}-1)}{(\alpha u(s-\tau)+v(s-\tau))} \right. \\ &\left. + \frac{\epsilon u^* v^* \alpha u(s-\tau)(e^{Y(s-\tau)}-1)}{(\alpha u(s-\tau)+v(s-\tau))v(s)(\alpha u^*+v^*)}\right] ds.\end{aligned} \tag{6.11}$$

In the above equation we use the following relation:

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

Let $V_2(t) = |Y(t)|$. Computing the upper right derivative of $V_2(t)$ along with the solution of (2.5a)–(2.5b), we have from (6.11)

$$\begin{aligned}D^+V_2 \le &-\left(\delta+\frac{\epsilon u^*}{M_2(\alpha u^*+v^*)}\right)v^*|e^{Y(t)}-1| + \frac{\epsilon v^*|e^{X(t-\tau)}-1|}{\alpha m_2} + \frac{\epsilon v^*|e^{Y(t)}-1|}{\alpha m_2} \\ &+ \frac{\epsilon v^*}{\alpha m_2}\int_{t-\tau}^{t} e^{Y(s)}\left[\left(\delta+\frac{u^*}{M_2(\alpha u^*+v^*)}\right) \times v^*|e^{Y(s)}-1| + \frac{\epsilon v^*|e^{X(s-\tau)}-1|}{\alpha m_2} + \frac{\epsilon v^*|e^{Y(s-\tau)}-1|}{\alpha m_2}\right] ds.\end{aligned} \tag{6.12}$$

We find that there exists a $T>0$, such that $v^* e^{Y(t)} < M_2$ for all $t>T$, and for $t>T+\tau$, we have

$$\begin{aligned}D^+V_2 \le &-\left(\delta+\frac{\epsilon u^*}{M_2(\alpha u^*+v^*)}\right)v^*|e^{Y(t)}-1| + \frac{\epsilon v^*|e^{X(t-\tau)}-1|}{\alpha m_2} + \frac{\epsilon v^*|e^{Y(t)}-1|}{\alpha m_2} \\ &+ \frac{\epsilon M_2}{\alpha m_2}\int_{t-\tau}^{t}\left[\left(\delta+\frac{u^*}{M_2(\alpha u^*+v^*)}\right) \times v^*|e^{Y(s)}-1| + \frac{\epsilon v^*|e^{X(s-\tau)}-1|}{\alpha m_2} + \frac{\epsilon v^*|e^{Y(s-\tau)}-1|}{\alpha m_2}\right] ds.\end{aligned} \tag{6.13}$$

Again due to the structure of (6.13), we consider the following functional:

$$\begin{aligned}V_{22}(t) = V_2(t) &+ \frac{\epsilon M_2}{\alpha m_2}\int_{t-\tau}^{t}\int_{v}^{t}\left[\left(\delta+\frac{\epsilon u^*}{M_2(\alpha u^*+v^*)}\right) \times v^*|e^{Y(s)}-1| + \frac{\epsilon v^*|e^{X(s-\tau)}-1|}{\alpha m_2} + \frac{\epsilon v^*|e^{Y(s-\tau)}-1|}{\alpha m_2}\right] ds\,dv \\ &+ \frac{\epsilon^2 M_2 v^*\tau}{\alpha^2 m_2^2}\int_{t-\tau}^{t}|e^{X(s)}-1|\,ds + \frac{\epsilon^2 M_2 v^*\tau}{\alpha^2 m_2^2}\int_{t-\tau}^{t}|e^{Y(s)}-1|\,ds + \frac{\epsilon v^*}{\alpha m_2}\int_{t-\tau}^{t}|e^{X(s)}-1|\,ds,\end{aligned} \tag{6.14}$$

whose upper right derivative along the solution of the system (2.5a)–(2.5b) is given by

$$\begin{aligned}
D^+V_{22} &= D^+V_2 + \frac{\epsilon M_2\tau}{\alpha m_2}\Bigg[\left(\delta + \frac{\epsilon u^*}{M_2(\alpha u^*+v^*)}\right) \\
&\quad \times v^*\left|e^{Y(t)}-1\right| + \frac{\epsilon v^*|e^{X(t-\tau)}-1|}{\alpha m_2} \\
&\quad + \frac{\epsilon v^*|e^{Y(t-\tau)}-1|}{\alpha m_2}\Bigg] \\
&\quad - \frac{\epsilon M_2}{\alpha m_2}\int_{t-\tau}^{t}\Bigg[\left(\delta + \frac{\epsilon u^*}{M_2(\alpha u^*+v^*)}\right) \\
&\quad \times v^*\left|e^{Y(s)}-1\right| + \frac{\epsilon v^*}{\alpha m_2}\left|e^{X(s-\tau)}-1\right| \\
&\quad + \frac{\epsilon v^*|e^{Y(s-\tau)}-1|}{\alpha m_2}\Bigg]ds \\
&\quad + \frac{\epsilon^2 M_2 v^*\tau}{\alpha^2 m_2^2}\left[\left|e^{X(t)}-1\right| + \left|e^{Y(t)}-1\right|\right] \\
&\quad - \frac{\epsilon^2 M_2 v^*\tau}{\alpha^2 m_2^2}\left[\left|e^{X(t-\tau)}-1\right| + \left|e^{Y(t-\tau)}-1\right|\right] \\
&\quad + \frac{\epsilon v^*}{\alpha m_2}\left[\left|e^{X(t)}-1\right| - \left|e^{X(t-\tau)}-1\right|\right] \\
&\le -\left(1-\frac{\tau\epsilon M_2}{\alpha m_2}\right)\left(\delta + \frac{\epsilon u^*}{M_2(\alpha u^*+v^*)}\right) \\
&\quad \times v^*\left|e^{Y(t)}-1\right| + \frac{\epsilon v^*|e^{Y(t)}-1|}{\alpha m_2} \\
&\quad + \frac{\epsilon v^*}{\alpha m_2}\left|e^{X(t)}-1\right| \\
&\quad + \frac{\epsilon^2 M_2 v^*\tau}{\alpha^2 m_2^2}\left[\left|e^{X(t)}-1\right| + \left|e^{Y(t)}-1\right|\right] \\
&= \frac{\epsilon v^*}{\alpha m_2}\left(1+\frac{\epsilon M_2\tau}{\alpha m_2}\right)\left|e^{X(t)}-1\right| \\
&\quad - v^*\Bigg[\left(1-\frac{\tau\epsilon M_2}{\alpha m_2}\right)\left(\delta + \frac{\epsilon u^*}{M_2(\alpha u^*+v^*)}\right) \\
&\quad - \frac{\epsilon}{\alpha m_2}\left(1+\frac{\epsilon M_2\tau}{\alpha m_2}\right)\Bigg]\left|e^{Y(t)}-1\right|. \qquad (6.15)
\end{aligned}$$

Let us define a Lyapunov functional $V(t)$ as

$$V(t) = V_1(t) + V_{22}(t) > \left|X(t)\right| + \left|Y(t)\right|.$$

Computing the upper right derivative of $V(t)$ along with the solution of (2.5a)–(2.5b), and by using (6.10) and (6.15), we have

$$\begin{aligned}
D^+V(t) &= D^+V_1(t) + D^+V_{22}(t) \\
&\le -u^*\left(1-\frac{\epsilon}{m_1}\right)\left|e^{X(t)}-1\right| \\
&\quad + \frac{\epsilon}{\alpha m_1}v^*\left|e^{Y(t)}-1\right| \\
&\quad + \frac{\epsilon v^*}{\alpha m_2}\left(1+\frac{\epsilon M_2\tau}{\alpha m_2}\right)\left|e^{X(t)}-1\right| \\
&\quad - v^*\Bigg[\left(1-\frac{\tau\epsilon M_2}{\alpha m_2}\right)\left(\delta+\frac{\epsilon u^*}{M_2(\alpha u^*+v^*)}\right) \\
&\quad - \frac{\epsilon}{\alpha m_2}\left(1+\frac{\epsilon M_2\tau}{\alpha m_2}\right)\Bigg]\left|e^{Y(t)}-1\right| \\
&\le -p_1u^*\left|e^{X(t)}-1\right| - p_2v^*\left|e^{Y(t)}-1\right|,
\end{aligned}$$

where

$$\begin{aligned}
p_1 &= 1 - \frac{\epsilon}{m_1} - \frac{\epsilon v^*}{\alpha m_2 u^*}\left(1+\frac{\epsilon M_2\tau}{\alpha m_2}\right) > 0, \\
p_2 &= \left(1-\frac{\tau\epsilon M_2}{\alpha m_2}\right)\left(\delta + \frac{\epsilon u^*}{M_2(\alpha u^*+v^*)}\right) \\
&\quad - \frac{\epsilon}{\alpha}\left(\frac{1}{m_1}+\frac{1}{m_2}+\frac{\epsilon M_2\tau}{\alpha m_2^2}\right) > 0.
\end{aligned}$$

Since the model system (2.5a)–(2.5b) is permanent, therefore, for all $t > T^*$, we have

$$u^*e^{X(t)} = u(t) \ge m_1, \qquad v^*e^{Y(t)} = v(t) \ge m_2.$$

Using the mean value theorem, we have

$$\begin{aligned}
u^*\left|e^{X(t)}-1\right| &= u^*e^{\theta_1(t)}\left|X(t)\right| > m_1\left|X(t)\right|, \\
v^*\left|e^{Y(t)}-1\right| &= v^*e^{\theta_2(t)}\left|Y(t)\right| > m_2\left|Y(t)\right|,
\end{aligned}$$

where $u^*e^{\theta_1(t)}$ lies between u^* and $u(t)$, and $v^*e^{\theta_2(t)}$ lies between v^* and $v(t)$. Therefore,

$$\begin{aligned}
D^+V(t) &\le -p_1m_1\left|X(t)\right| - p_2m_2\left|Y(t)\right| \\
&\le -\kappa\left(\left|X(t)\right| + \left|Y(t)\right|\right), \quad \text{where} \\
\kappa &= \min\{p_1m_1, p_2m_2\}. \qquad (6.16)
\end{aligned}$$

Noting that $V(t) \ge |X(t)| + |Y(t)|$.

Hence, by applying global stability theorem and (6.16), we can conclude that the zero solution of the reduced system (6.9a)–(6.9b) is globally asymptotically stable. Therefore, the positive equilibrium of the original system (2.5a)–(2.5b) is globally asymptotically stable. □

7 Direction and stability of Hopf bifurcation

In this section, our attention is focused on investigation of the direction, stability, and period of the periodic solution bifurcating from a stable equilibrium $E^*(u^*, v^*)$. Following the ideas of Hassard et al. [37], we derive the explicit formulae for determining the Hopf bifurcation at the critical value of τ_j by using normal form and central manifold theory. Without loss of generality, we denote any one of the critical values τ_j^*, $j = 0, 1, 2, 3, \dots$ by τ^*, at which (5.8) has a pair of purely imaginary roots $\pm i\eta^*$ and the system (2.5a)–(2.5b) undergoes a Hopf bifurcation at E^*. Let $u_1(t) = u(t) - u^*$, $v_1(t) = v(t) - v^*$, $\mu = \tau - \tau^*$ and $t \to \frac{t}{\tau}$, where $\mu \in \mathbf{R}$, then $\mu = 0$ is a Hopf bifurcation value of the system (2.5a)–(2.5b). Now the system (2.5a)–(2.5b) can be written as

$$\frac{du_1}{dt} = J_{11}u_1(t) + J_{12}v_1(t), \tag{7.1a}$$

$$\frac{dv_1}{dt} = J_{21}u_1(t-\tau) - J_{12}v_1(t-\tau) - \left(\gamma + 2\delta v^*\right)v_1(t), \tag{7.1b}$$

where $J_{11} = \frac{\alpha\epsilon u^* v^*}{(\alpha u^*+v^*)^2} - u^*$; $J_{12} = -\frac{\alpha\epsilon u^{*2}}{(\alpha u^*+v^*)^2}$ and $J_{21} = \frac{\epsilon v^{*2}}{(\alpha u^*+v^*)^2}$.

In space $\mathbf{C} = \mathbf{C}([-1, 0], \mathbf{R}^2)$, the system (7.1a)–(7.1b) is transformed into a functional differential equation as

$$\dot{u}(t) = L_\mu(u_t) + f(\mu, u_t), \tag{7.2}$$

where $u(t) = (u_1(t), v_1(t))^T \in \mathbf{R}^2$ and $L_\mu : \mathbf{C} \to \mathbf{R}$, $f : \mathbf{R} \times \mathbf{C} \to \mathbf{R}$ are respectively represented by

$$L_\mu(\phi) = \left(\tau^* + \mu\right)\begin{pmatrix} J_{11} & J_{12} \\ 0 & -\gamma - 2\delta v^* \end{pmatrix}\begin{pmatrix} \phi_1(0) \\ \phi_2(0) \end{pmatrix} + \left(\tau^* + \mu\right)\begin{pmatrix} 0 & 0 \\ J_{21} & -J_{12} \end{pmatrix}\begin{pmatrix} \phi_1(-1) \\ \phi_2(-1) \end{pmatrix}, \tag{7.3}$$

and

$$f(\mu, \phi) = \left(\tau^* + \mu\right)\times \begin{pmatrix} a_{11}\phi_1^2(0) + a_{12}\phi_1(0)\phi_2(0) + a_{22}\phi_2^2(0) \\ b_{11}\phi_1^2(-1) + b_{12}\phi_1(-1)\phi_2(-1) + b_{22}\phi_2^2(-1) - \delta\phi_2^2(0) \end{pmatrix}. \tag{7.4}$$

Here, $\phi(\theta) = (\phi_1(\theta), \phi_2(\theta))^T \in \mathbf{C}$; the entries a_{ij} and b_{ij} are given by

$$a_{11} = -1 + \frac{\alpha\epsilon v^{*2}}{(\alpha u^* + v^*)^3}; \qquad a_{12} = -\frac{2\alpha\epsilon u^* v^*}{(\alpha u^* + v^*)^3};$$

$$a_{22} = \frac{\alpha\epsilon u^{*2}}{(\alpha u^* + v^*)^3}; \qquad b_{11} = -\frac{\alpha\epsilon v^{*2}}{(\alpha u^* + v^*)^3};$$

$$b_{12} = \frac{2\alpha\epsilon u^* v^*}{(\alpha u^* + v^*)^3}; \qquad b_{22} = -\frac{\alpha\epsilon u^{*2}}{(\alpha u^* + v^*)^3}.$$

By the Riesz representation theorem, there exist a function $\eta(\theta, \mu)$ of bounded variation for $\theta \in [-1, 0]$ such that

$$L_\mu\phi = \int_{-1}^{0} d\eta(\theta, 0)\phi(\theta), \quad \text{for } \phi \in \mathbf{C}. \tag{7.5}$$

In fact, we can choose

$$\eta(\theta, \mu) = \left(\tau^* + \mu\right)\begin{pmatrix} J_{11} & J_{12} \\ 0 & -\gamma - 2\delta v^* \end{pmatrix}\delta(\theta) - \left(\tau^* + \mu\right)\begin{pmatrix} 0 & 0 \\ J_{21} & -J_{12} \end{pmatrix}\delta(\theta + 1), \tag{7.6}$$

where δ is a Dirac delta function. For $\phi \in \mathbf{C}^1([-1, 0], \mathbf{R}^2)$, define

$$A(\mu)\phi = \begin{cases} \frac{d\phi(\theta)}{d\theta} & \text{for } \theta \in [-1, 0), \\ \int_{-1}^{0} d\eta(\mu, s)\phi(s) & \text{for } \theta = 0, \end{cases} \tag{7.7}$$

and

$$R(\mu)\phi = \begin{cases} 0 & \text{for } \theta \in [-1, 0), \\ f(\mu, \phi) & \text{for } \theta = 0. \end{cases} \tag{7.8}$$

Then system (7.2) is equivalent to

$$\dot{u}_t = A(\mu)u_t + R(\mu)u_t, \tag{7.9}$$

where $u_t(\theta) = u(t + \theta)$ for $\theta \in [-1, 0]$.

For $\psi \in \mathbf{C}^1([0, 1], (\mathbf{R}^2)^*)$, define

$$A^*\psi(s) = \begin{cases} -\frac{d\psi(s)}{ds} & \text{for } s \in (0, 1], \\ \int_{-1}^{0} d\eta^T(t, 0)\psi(-t) & \text{for } s = 0, \end{cases} \tag{7.10}$$

and a bilinear inner product

$$\langle\psi(s),\phi(\theta)\rangle=\bar{\psi}(0)\phi(0)-\int_{-1}^{0}\int_{\xi=0}^{\theta}\bar{\psi}(\xi-\theta)\,d\eta(\theta)\phi(\xi)\,d\xi, \tag{7.11}$$

where $\eta(\theta)=\eta(\theta,0)$. Then $A(0)$ and A^* are adjoint operators. Suppose that $q(\theta)$ and $q^*(\theta)$ are eigenvectors of A and A^* corresponding to $+i\eta^*\tau^*$ and $-i\eta^*\tau^*$, respectively. By direct computation, we have

$$q(\theta)=\left(1,-\frac{J_{11}-i\eta^*}{J_{12}}\right)^T e^{i\eta^*\tau^*\theta},$$

$$q^*(s)=D\left(\frac{\gamma+2\delta v^*+J_{12}e^{i\eta^*\tau^*}-i\eta^*}{J_{21}},1\right)e^{i\eta^*\tau^*s},$$

where

$$\bar{D}=\frac{1}{-\frac{J_{11}-i\eta^*}{J_{12}}+\frac{\gamma+2\delta v^*+i\eta^*+J_{12}e^{-i\eta^*\tau^*}}{J_{21}}-\tau^*(J_{21}+J_{11}-i\eta^*)e^{-i\eta^*\tau^*}}, \tag{7.12}$$

and $\langle q^*(s),q(\theta)\rangle=1$, $\langle q^*(s),\bar{q}(\theta)\rangle=0$. Let u_t be the solution of (7.9) when $\mu=0$. Define

$$z(t)=\langle q^*,u_t\rangle,\qquad W(t,\theta)=u_t(\theta)-2\operatorname{Re}\{z(t)q(\theta)\}. \tag{7.13}$$

On the center manifold $\mathbf{C}_0$, we have $W(t,\theta)=W(z(t),\bar{z}(t),\theta)$ where

$$W(z,\bar{z},\theta)=W_{20}(\theta)\frac{z^2}{2}+W_{11}(\theta)z\bar{z}+W_{02}(\theta)\frac{\bar{z}^2}{2}+W_{30}(\theta)\frac{z^3}{6}+\cdots, \tag{7.14}$$

z and $\bar{z}$ being local coordinates for the center manifold $\mathbf{C}_0$ in the direction of q^* and $\bar{q}^*$. Note that W is real if u_t is real. We consider only real solutions. For solution $u_t\in\mathbf{C}_0$ of (7.9) (since $\mu=0$), we have

$$\dot{z}(t)=i\eta^*\tau^*z+\bar{q}^*(0)f\big(0,W(z,\bar{z},0)+2\operatorname{Re}\{zq(\theta)\}\big)\stackrel{\text{def}}{=}i\eta^*\tau^*z+\bar{q}^*(0)f_0(z,\bar{z}).$$

We rewrite this equation as

$$\dot{z}(t)=i\eta^*\tau^*z(t)+g(z,\bar{z}),$$

where

$$g(z,\bar{z})=g_{20}\frac{z^2}{2}+g_{11}z\bar{z}+g_{02}\frac{\bar{z}^2}{2}+g_{21}\frac{z^2\bar{z}}{2}+\cdots. \tag{7.15}$$

It follows from (7.13) and (7.14) that

$$\begin{aligned}u_t(\theta)&=W(t,\theta)+2\operatorname{Re}\{z(t)q(\theta)\}\\&=W_{20}(\theta)\frac{z^2}{2}+W_{11}(\theta)z\bar{z}+W_{02}(\theta)\frac{\bar{z}^2}{2}\\&\quad+(1,q_1)^T e^{i\eta^*\tau^*\theta}z\\&\quad+(1,\bar{q}_1)^T e^{-i\eta^*\tau^*\theta}\bar{z}+\cdots,\end{aligned} \tag{7.16}$$

where $q_1=-\frac{J_{11}-i\eta^*}{J_{12}}$.

It follows together with (7.4) that

$$\begin{aligned}g(z,\bar{z})&=\bar{q}^*f_0(z,\bar{z})=\bar{q}^*f(0,u_t)\\&=\tau^*\bar{D}\Big[\big\{\bar{q}_2\big(a_{11}+a_{12}q_1+a_{22}q_1^2\big)\\&\quad+\big(b_{11}e^{-i2\eta^*\tau^*}+b_{12}q_1e^{-i2\eta^*\tau^*}\\&\quad+b_{22}q_1^2e^{-i2\eta^*\tau^*}-\delta q_1^2\big)\big\}z^2\\&\quad+\big\{\bar{q}_2\big(2a_{11}+2a_{12}\operatorname{Re}(q_1)+2a_{22}|q_1|^2\big)\\&\quad+\big(2b_{11}+2b_{12}\operatorname{Re}(q_1)\\&\quad+2b_{22}|q_1|^2-2\delta|q_1|^2\big)\big\}z\bar{z}\\&\quad+\big\{\bar{q}_2\big(a_{11}+a_{12}\bar{q}_1+a_{22}\bar{q}_1^2\big)\\&\quad+\big(b_{11}e^{i2\eta^*\tau^*}+b_{12}\bar{q}_1e^{i2\eta^*\tau^*}\\&\quad+b_{22}\bar{q}_1^2e^{i2\eta^*\tau^*}-\delta\bar{q}_1^2\big)\big\}\bar{z}^2\\&\quad+\Big\{\bar{q}_2\Big(a_{11}\big(2W_{11}^{(1)}(0)+W_{20}^{(1)}(0)\big)\end{aligned}$$

$$+ a_{12}\bigg(\frac{1}{2}\big(\bar{q}_1 W_{20}^{(1)}(0) + W_{20}^{(2)}(0)\big) + \big(q_1 W_{11}^{(1)}(0) + W_{11}^{(2)}(0)\big)\bigg) + (\bar{q}_2 a_{22} - \delta)\big(2W_{11}^{(2)}(0)q_1 + W_{20}^{(2)}(0)\bar{q}_1\big)\bigg) + b_{11}\big(2W_{11}^{(1)}(-1)e^{-i\eta^*\tau^*} + W_{20}^{(1)}(-1)e^{i\eta^*\tau^*}\big) + b_{12}\bigg(\frac{1}{2}\big(\bar{q}_1 W_{20}^{(1)}(-1)e^{i\eta^*\tau^*} + W_{20}^{(2)}(-1)e^{i\eta^*\tau^*}\big) + \big(q_1 e^{-i\eta^*\tau^*} W_{11}^{(1)}(-1) + W_{11}^{(2)}(-1)e^{-i\eta^*\tau^*}\big)\bigg) + b_{22}\big(2W_{11}^{(2)}(-1)q_1 e^{-i\eta^*\tau^*} + W_{20}^{(2)}(-1)\bar{q}_1 e^{i\eta^*\tau^*}\big)\bigg\} z^2\bar{z}\bigg], \tag{7.17}$$

where $q_2 = \frac{\gamma + 2\delta v^* + J_{12}e^{i\eta^*\tau^*} - i\eta^*}{J_{21}}$.

Comparing the coefficients of z^2, $\bar{z}^2$, $z\bar{z}$, and $z^2\bar{z}$ with (7.15), we have

$$\begin{aligned}
g_{20} &= 2\tau^*\bar{D}\big(\bar{q}_2\big(a_{11} + a_{12}q_1 + a_{22}q_1^2\big) + \big(b_{11}e^{-i2\eta^*\tau^*} + b_{12}q_1 e^{-i2\eta^*\tau^*} + b_{22}q_1^2 e^{-i2\eta^*\tau^*} - \delta q_1^2\big)\big);\\
g_{11} &= 2\tau^*\bar{D}\big(\bar{q}_2\big(a_{11} + a_{12}\operatorname{Re}(q_1) + a_{22}|q_1|^2\big) + \big(b_{11} + b_{12}\operatorname{Re}(q_1) + b_{22}|q_1|^2 - \delta|q_1|^2\big)\big);\\
g_{02} &= 2\tau^*\bar{D}\big(\bar{q}_2\big(a_{11} + a_{12}\bar{q}_1 + a_{22}\bar{q}_1^2\big) + \big(b_{11}e^{i2\eta^*\tau^*} + b_{12}\bar{q}_1 e^{i2\eta^*\tau^*} + b_{22}\bar{q}_1^2 e^{i2\eta^*\tau^*} - \delta\bar{q}_1^2\big)\big);\\
g_{21} &= \tau^*\bar{D}\big(\bar{q}_2\big(2a_{11}\big(2W_{11}^{(1)}(0) + W_{20}^{(1)}(0)\big) + a_{12}\big(\big(\bar{q}_1 W_{20}^{(1)}(0) + W_{20}^{(2)}(0)\big) + 2\big(q_1 W_{11}^{(1)}(0) + W_{11}^{(2)}(0)\big)\big) + 2(\bar{q}_2 a_{22} - \delta)\big(2W_{11}^{(2)}(0)q_1 + W_{20}^{(2)}(0)\bar{q}_1\big)\big)\\
&\quad + 2b_{11}\big(2W_{11}^{(1)}(-1)e^{-i\eta^*\tau^*} + W_{20}^{(1)}(-1)e^{i\eta^*\tau^*}\big) + b_{12}\big(\big(\bar{q}_1 W_{20}^{(1)}(-1)e^{i\eta^*\tau^*} + W_{20}^{(2)}(-1)e^{i\eta^*\tau^*}\big) + 2\big(q_1 W_{11}^{(1)}(-1)e^{-i\eta^*\tau^*} + W_{11}^{(2)}(-1)e^{-i\eta^*\tau^*}\big)\big)\\
&\quad + 2b_{22}\big(2W_{11}^{(2)}(-1)q_1 e^{-i\eta^*\tau^*} + W_{20}^{(2)}(-1)\bar{q}_1 e^{i\eta^*\tau^*}\big)\big).
\end{aligned} \tag{7.18}$$

Since there are $W_{20}(\theta)$ and $W_{11}(\theta)$ in g_{21}, we need to find out their values at $\theta = 0$ and $\theta = -1$.

From the definition given by (7.9) and (7.13), we have

$$\begin{aligned}
\dot{W} &= \dot{u}_t - \dot{z}q - \dot{\bar{z}}\bar{q}\\
&= \begin{cases} AW - 2\operatorname{Re}\{\bar{q}^*(0) f_0 q(\theta)\} \\ \quad \text{for } \theta \in [-1, 0), \\ AW - 2\operatorname{Re}\{\bar{q}^*(0) f_0 q(0)\} + f_0 \quad \text{for } \theta = 0 \end{cases}\\
&= AW + H(z, \bar{z}, \theta),
\end{aligned} \tag{7.19}$$

where

$$H(z, \bar{z}, \theta) = H_{20}(\theta)\frac{z^2}{2} + H_{11}(\theta)z\bar{z} + H_{02}(\theta)\frac{\bar{z}^2}{2} + \cdots. \tag{7.20}$$

Substituting the above series and computing the corresponding coefficients, we have

$$\big(A - 2i\eta^*\tau^*\big)W_{20} = -H_{20}(\theta), \quad AW_{11}(\theta) = -H_{11}(\theta), \ldots. \tag{7.21}$$

For $\theta \in [-1, 0)$, we know that

$$H(z, \bar{z}, \theta) = \bar{q}^*(0) f_0 q(\theta) - q^*(0)\bar{f_0}\bar{q}(\theta) = -g(z, \bar{z}, \theta)q(\theta) - \bar{g}(z, \bar{z}, \theta)\bar{q}(\theta). \tag{7.22}$$

Comparing the coefficients, we have

$$H_{20}(\theta) = -g_{20}(\theta)q(\theta) - \bar{g}_{02}(\theta)\bar{q}(\theta) \quad \text{and} \quad H_{11}(\theta) = -g_{11}(\theta)q(\theta) - \bar{g}_{11}(\theta)\bar{q}(\theta). \tag{7.23}$$

From (7.21), (7.23) and the definition of A, it follows that

$$\dot{W}_{20}(\theta) = 2i\eta^*\tau^* W_{20}(\theta) + g_{20}(\theta)q(\theta) + \bar{g}_{02}(\theta)\bar{q}(\theta).$$

We know that $q(\theta) = (1, q_1)^T e^{i\eta^*\tau^*\theta}$. Hence,

$$W_{20}(\theta) = \frac{ig_{20}}{\eta^*\tau^*}q(0)e^{i\eta^*\tau^*\theta} + \frac{i\bar{g}_{02}}{3\eta^*\tau^*}\bar{q}(0)e^{-i\eta^*\tau^*\theta} + E_1 e^{2i\eta^*\tau^*\theta}, \tag{7.24}$$

where $E_1 = (E_1^1, E_1^2) \in \mathbf{R}^2$ is a constant vector.

Similarly, we can obtain

$$W_{11}(\theta) = -\frac{ig_{11}}{\eta^*\tau^*}q(0)e^{i\eta^*\tau^*\theta} + \frac{i\bar{g}_{11}}{\eta^*\tau^*}\bar{q}(0)e^{-i\eta^*\tau^*\theta} + E_2, \qquad (7.25)$$

where $E_2 = (E_2^1, E_2^2) \in \mathbf{R}^2$ is also a constant vector.

Now we seek the appropriate values of E_1 and E_2. From the definition of A and (7.21), we obtain

$$\int_{-1}^{0} d\eta(\theta)W_{20}(\theta) = 2i\eta^*\tau^*W_{20}(0) - H_{20}(0), \quad (7.26)$$

$$\int_{-1}^{0} d\eta(\theta)W_{11}(\theta) = -H_{11}(0), \qquad (7.27)$$

where $\eta(\theta) = \eta(0, \theta)$. From (7.19), we have

$$H_{20}(0) = -g_{20}q(0) - \bar{g}_{02}\bar{q}(0) + 2\tau^* \times \begin{pmatrix} a_{11} + a_{12}q_1 + a_{22}{q_1}^2 \\ b_{11}e^{-2i\eta^*\tau^*} + b_{12}q_1e^{-2i\eta^*\tau^*} + b_{22}q_1^2e^{-2i\eta^*\tau^*} - \delta q_1^2 \end{pmatrix}, \qquad (7.28)$$

$$H_{11}(0) = -g_{11}q(0) - \bar{g}_{11}\bar{q}(0) + 2\tau^* \begin{pmatrix} a_{11} + a_{12}\operatorname{Re}(q_1) + a_{22}|q_1|^2 \\ b_{11} + b_{12}\operatorname{Re}(q_1) + b_{22}|q_1|^2 - \delta|q_1|^2 \end{pmatrix}. \qquad (7.29)$$

Substituting (7.24) and (7.28) into (7.26) and using the relations

$$\left(i\eta^*\tau^*I - \int_{-1}^{0} e^{i\eta^*\tau^*\theta}\, d\eta(\theta)\right)q(0) = 0 \quad \text{and}$$

$$\left(-i\eta^*\tau^*I - \int_{-1}^{0} e^{-i\eta^*\tau^*\theta}\, d\eta(\theta)\right)\bar{q}(0) = 0,$$

we obtain

$$\left(i2\eta^*\tau^*I - \int_{-1}^{0} e^{2i\eta^*\tau^*\theta}\, d\eta(\theta)\right)E_1 = 2\tau^*\begin{pmatrix} B_1 \\ B_2 \end{pmatrix}, \qquad (7.30)$$

where $B_1 = a_{11} + a_{12}q_1 + a_{22}{q_1}^2$, $B_2 = b_{11}e^{-2i\eta^*\tau^*} + b_{12}q_1e^{-2i\eta^*\tau^*} + b_{22}q_1^2e^{-2i\eta^*\tau^*} - \delta q_1^2$.

Hence,

$$\begin{pmatrix} i2\eta^* - J_{11} & -J_{12} \\ -J_{21}e^{-2i\eta^*\tau^*} & 2i\eta^* + \gamma + 2\delta v^* + J_{12}e^{-2i\eta^*\tau^*} \end{pmatrix} E_1 = 2\begin{pmatrix} B_1 \\ B_2 \end{pmatrix}.$$

By using Crammer's rule, we have

$$E_1^{(1)} = \frac{2}{A}\begin{vmatrix} B_1 & -J_{12} \\ B_2 & \gamma + 2\delta v^* + J_{12}e^{-2i\eta^*\tau^*} + 2i\eta^* \end{vmatrix},$$

$$E_1^{(2)} = \frac{2}{A}\begin{vmatrix} 2i\eta^* - J_{11} & B_1 \\ -J_{21}e^{-2i\eta^*\tau^*} & B_2 \end{vmatrix},$$

where

$$A = \begin{vmatrix} 2i\eta^* - J_{11} & -J_{12} \\ -J_{21}e^{-2i\eta^*\tau^*} & \gamma + 2\delta v^* + J_{12}e^{-2i\eta^*\tau^*} + 2i\eta^* \end{vmatrix}.$$

Similarly, substituting (7.25) and (7.29) into (7.27), we have

$$\begin{pmatrix} J_{11} & J_{12} \\ J_{21} & -\gamma - 2\delta v^* - J_{12} \end{pmatrix} E_2 = -2\begin{pmatrix} a_{11} + a_{12}\operatorname{Re}(q_1) + a_{22}|q_1|^2 \\ b_{11} + b_{12}\operatorname{Re}(q_1) + b_{22}|q_1|^2 - \delta|q_1|^2 \end{pmatrix},$$

and hence, we have

$$E_2^{(1)} = -\frac{2}{A^*} \times \begin{vmatrix} a_{11} + a_{12}\operatorname{Re}(q_1) + a_{22}|q_1|^2 & J_{12} \\ b_{11} + b_{12}\operatorname{Re}(q_1) + b_{22}|q_1|^2 - \delta|q_1|^2 & -\gamma - 2\delta v^* - J_{12} \end{vmatrix},$$

$$E_2^{(2)} = -\frac{2}{A^*} \times \begin{vmatrix} J_{11} & a_{11} + a_{12}\operatorname{Re}(q_1) + a_{22}|q_1|^2 \\ J_{21} & b_{11} + b_{12}\operatorname{Re}(q_1) + b_{22}|q_1|^2 - \delta|q_1|^2 \end{vmatrix},$$

where $A^* = -A|_{\theta=0,\eta^*=0}$.

Thus, we can find out $W_{20}(0)$ and $W_{11}(0)$ from relations (7.24) and (7.25). Furthermore, we can determine g_{21} by the system parameters and delay in (7.18). Thus, we can compute the following results:

$$C_1(0) = \frac{i}{2\tau^*\eta^*}\left(g_{11}g_{20} - 2|g_{11}|^2 - \frac{|g_{02}|^2}{3}\right) + \frac{g_{21}}{2}, \qquad (7.31a)$$

$$\mu_2 = -\frac{\mathrm{Re}\{C_1(0)\}}{\mathrm{Re}\{\lambda'(\tau^*)\}}, \tag{7.31b}$$

$$\beta_2 = 2\,\mathrm{Re}\{C_1(0)\}, \tag{7.31c}$$

$$\tau_2 = -\frac{\mathrm{Im}\{C_1(0)\} + \mu_2\,\mathrm{Im}\{\lambda'(\tau^*)\}}{\tau^*\eta^*}, \tag{7.31d}$$

which determine the nature of the stability and direction of bifurcating periodic solutions in the center manifold at the critical value τ^*, i.e., μ_2 determines the direction of Hopf-bifurcation. If $\mu_2 > 0$ ($\mu_2 < 0$), then the Hopf-bifurcations is supercritical (subcritical) and the bifurcating periodic solutions exist for $\tau > \tau^*$ ($\tau < \tau^*$). Again β_2 determines the stability of the bifurcating periodic solutions. The bifurcating periodic solution are stable (unstable) if $\beta_2 < 0$ ($\beta_2 > 0$). Also, τ_2 determines the period of periodic solutions: the period increases (decreases) if $\tau_2 > 0$ ($\tau_2 < 0$).

8 Global existence of periodic solutions

In this section, we investigate the global existence of the periodic solution of the system of the system (2.5a)–(2.5b) by the global Hopf-bifurcation theorem due to Wu [1]. For notational simplicity, we set $z_t = (u_t, v_t)^T$, and rewrite the system (2.5a)–(2.5b) as the following functional differential equation:

$$\dot{z}(t) = F(z, \tau, p), \tag{8.1}$$

where $z_t(\theta) = z(t+\theta) \in \mathrm{C}([-\tau, 0], \mathrm{R}^2)$. The system (8.1) has only one equilibrium $z^* = E^*(u^*, v^*)$ under the conditions (i) $\gamma\alpha + 2(1-\epsilon) + \delta\alpha^2 > 0$ and (ii) $\gamma\alpha(1-\epsilon) + (1-\epsilon)^2 < 0$. We now define

$$\mathbf{X} = \mathrm{C}\big([-\tau, 0], \mathrm{R}^2\big),$$

$$\boldsymbol{\Sigma} = \mathrm{cl}\big\{(z, \tau, p) \in X \times \mathrm{R} \times \mathrm{R}^+ : z \text{ is a p periodic solution of (8.1)}\big\},$$

$$\mathbf{N} = \big\{(z, \tau, p) : F(z, \tau, p) = 0\big\},$$

and let $\ell(z^*, \tau_n^*, 2\pi/\eta^*)$ is a connected component of $(z^*, \tau_n^*, 2\pi/\eta^*)$ in Σ, where η^* and τ_n^* are defined in (5.8) and (5.11), respectively.

Lemma 2 *If* (i) $\gamma\alpha + 2(1-\epsilon) + \delta\alpha^2 > 0$ *and* (ii) $\gamma\alpha(1-\epsilon) + (1-\epsilon)^2 < 0$ *hold and* τ *is bounded, then all the nontrivial periodic solutions of the system* (2.5a)–(2.5b) *are uniformly bounded.*

Proof Let $(u(t), v(t))$ be any nontrivial periodic solution of (2.5a)–(2.5b). Then we can find them as follows:

$$u(t) = u(0)\exp\left\{\int_0^t \left(1 - u(s) - \frac{\epsilon v(s)}{\alpha u(s) + \beta v(s)}\right) ds\right\},$$

$$v(t) = v(0)\exp\left\{\int_0^t \left(-\gamma - \delta v(s) + \frac{\epsilon u(s-\tau)v(s-\tau)}{v(s)(\alpha u(s-\tau) + \beta v(s-\tau))}\right) ds\right\},$$

which implies that the solution of (2.5a)–(2.5b) cannot cross u axis and v axis. Thus, all nonconstant periodic solutions are confined in the interior of each quadrant.

Suppose that $(u(t), v(t))$ is a non constant periodic solution of (2.5a)–(2.5b). Then we have $u(t)v(t) > 0$, otherwise the second subequation of the system (2.5a)–(2.5b) implies that $v'(t) > 0$ if $v(t) > 0$ or $v'(t) < 0$ if $v(t) < 0$. In addition, if $u(t) < 0$, $v(t) < 0$, then the first subequation of (2.5a)–(2.5b) implies that $u'(t) < 0$, which is a contradiction, since $u(t)$ is a periodic solution. Thus, the periodic solution of (2.5a)–(2.5b) lie only on the first quadrant. If $(u(t), v(t))$ is a solution with $u(t) > 0$, $v(t) > 0$, then it is easy to find that there exist a $T > 0$ such that for any $t > T$, $u(t) < 1$.

Recalling Lemma 1, the second subequation immediately follows that $v(t) \le \frac{(\epsilon-\gamma\alpha)}{\alpha\delta} = M_2$. Thus, all possible positive periodic solutions are uniformly bounded. Hence, the lemma is completed. □

Lemma 3 *If* (i) $\gamma\alpha + 2(1-\epsilon) + \delta\alpha^2 > 0$ *and* (ii) $\gamma\alpha(1-\epsilon) + (1-\epsilon)^2 < 0$ *hold, then system* (2.5a)–(2.5b) *has no nontrivial* τ *periodic solution.*

Proof Suppose that the system (2.5a)–(2.5b) has τ periodic solution. Then the following system has periodic solution:

$$\frac{du(t)}{dt} = u(t) - \frac{\epsilon u(t)v(t)}{\alpha u(t) + v(t)} - u^2(t), \tag{8.2}$$

$$\frac{dv(t)}{dt} = -\gamma v(t) + \frac{\epsilon u(t)v(t)}{\alpha u(t) + v(t)} - \delta v^2(t), \tag{8.3}$$

which has the same equilibria as the system (2.5a)–(2.5b), i.e., $\bar{z}^1 = (0,0)$, $\bar{z}^2 = (0, -\gamma/\delta)$, $\bar{z}^3 = (1,0)$, and $\bar{z}^* = (u^*, v^*)$. Note that u axis, i.e., $v = 0$ and v axis, i.e., $u = 0$ are the solution of the system (8.2)–

(8.3) and their solution curve never intersect each other. Hence, there are no solutions crossing the coordinate axes. On the other hand, if the system (8.2)–(8.3) has periodic solution, then the interior equilibrium $\bar{z}^*$ is in its interior and other equilibria $\bar{z}^1$, $\bar{z}^2$, $\bar{z}^3$ are located on the coordinate axis. Then we can conclude that the periodic orbit of the system (8.2)–(8.3) must lie on the first quadrant. It is well known that interior equilibrium $\bar{z}^*$ is globally stable in the first quadrant (cf. Wang and Ma [38]). Thus, there is no periodic orbit in the first quadrant. This discussion ensures that the system (8.2)–(8.3) has no periodic solutions. Hence, the proof. □

Theorem 8.1 *Suppose the conditions* (i) $\gamma\alpha + 2(1-\epsilon) + \delta\alpha^2 > 0$ *and* (ii) $\gamma\alpha(1-\epsilon) + (1-\epsilon)^2 < 0$ *hold. Then for each* $\tau > \tau_n^*$ $(n = 1, 2, 3, \ldots)$, *system* (2.5a)–(2.5b) *has at least* $(n-1)$ *periodic solutions.*

Proof It is sufficient to prove that the projection $\ell(z_*, \tau_n^*, 2\pi/\eta^*)$ onto τ space is $[\tau^*, \infty)$ for $n \geq 1$ where $\tau^* \leq \tau_n^*$. Note that

$$F(z, \tau, p) = \begin{cases} u(t) - \frac{\epsilon u(t)v(t)}{\alpha u(t)+v(t)} - u^2(t), \\ -\gamma v(t) + \frac{\epsilon u(t-\tau)v(t-\tau)}{\alpha u(t-\tau)+v(t-\tau)} - \delta v^2(t), \end{cases} \tag{8.4}$$

satisfying the hypothesis (A_1)–(A_3) in Wu [1], with

$$(z_0, \alpha_0, p_0) = (z_*, \tau_n^*, 2\pi/\eta^*) \quad \text{and}$$

$$\det(\Delta_{(z_*, \tau_n^*, 2\pi/\eta^*)}(\lambda)) = 0,$$

i.e., $\lambda^2 + S_1\lambda + S_2 = (S_3 + S_4\lambda)e^{-\lambda\tau}$ (the expressions of S_i, $i = 1, 2, 3, 4$, are given in the Appendix). $(z_*, \tau_n^*, 2\pi/\eta^*)$ are isolated centers as verified in Wu [1]. Hence, by Theorem 5.1, there exist $\epsilon > 0$, $\delta_* > 0$, and a smooth curve $\lambda : (\tau_n^* - \delta_*, \tau_n^* + \delta_*) \longrightarrow \mathbf{C}$ such that $\det(\Delta(\lambda(\tau))) = 0$, $|\lambda(\tau) - \eta^*| < \epsilon$,

$$\lambda(\tau_n^*) = i\eta^*, \qquad \frac{d}{d\tau}\big(\mathrm{Re}(\lambda(\tau))\big)\big|_{\tau=\tau_n^*} > 0 \quad \text{for all}$$
$$\tau \in [\tau_n - \delta, \tau_n + \delta].$$

Let $\Omega_{\epsilon, 2\pi/\eta^*} = \{(\upsilon, p) : 0 < \upsilon < \epsilon, |p - 2\pi/\eta^*| < \epsilon\}$.

It is easy to verify that on $[\tau_n^* - \delta_*, \tau_n^* + \delta_*] \times \partial\Omega_{\epsilon, 2\pi/\eta^*}$, $\det(\Delta_{(z_*, \tau_n^*, 2\pi/\eta^*)}(\upsilon + 2\pi i/p)) = 0$ if and only if $\upsilon = 0$, $\tau = \tau_n^*$ and $p = 2\pi/\eta^*$. Therefore, the hypothesis (A_1)–(A_4) in Wu [1] are satisfied. Moreover, if we define

$$\begin{aligned} &H^{\pm}\big(z^*, \tau_n^*, 2\pi/\eta^*\big)(\upsilon, p) \\ &\quad = \det\big(\Delta\big(z^*, \tau_n^* \pm \delta_*, p\big)(\upsilon + 2\pi i/p\big), \end{aligned}$$

then we have the crossing number of isolated center $(z_*, \tau_n^*, 2\pi/\eta^*)$ as

$$\begin{aligned} &\gamma\big(z^*, \tau_n^*, 2\pi/\eta^*\big) \\ &\quad = \deg_B\big(H^-\big(z^*, \tau_n^*, 2\pi/\eta^*\big), \Omega_{\epsilon, 2\pi/\eta^*}\big) \\ &\qquad - \deg_B\big(H^+\big(z^*, \tau_n^*, 2\pi/\eta^*\big), \Omega_{\epsilon, 2\pi/\eta^*}\big) \\ &\quad = -1. \end{aligned}$$

Thus, we have

$$\sum_{(\bar{z}, \tau^*, \bar{p}) \in \ell(z^*, \tau_n^*, 2\pi/\eta^*)} \gamma\big(\bar{z}, \tau^*, \bar{p}\big) < 0,$$

where $(\bar{z}, \tau^*, \bar{p})$, in fact, takes the form of $(z^*, \tau_n^*, 2\pi/\eta^*)$, $n = 1, 2, \ldots$. It follows from Theorem 3.3 in Wu [1], that the connected component $\ell(z^*, \tau_n^*, 2\pi/\eta^*)$ through $(z^*, \tau_n^*, 2\pi/\eta^*)$ in Σ is unbounded. From (A.2),

$$\tau_n^* = \frac{1}{\eta^*}\arccos\left(\frac{(S_1S_4 - S_3)\eta^{*2} + S_2S_3}{(S_4\eta^*)^2 + (S_3)^2}\right) + \frac{2\pi n}{\eta^*},$$
$$n = 0, 1, 2, \ldots.$$

Thus, when $n > 0$, we have $2\pi/\eta^* < \tau_n^*$. Now we prove the projection of onto τ-space is $[\tau^*, \infty)$ where $\tau^* \leq \tau_n^*$. Clearly, it follows from Lemma 3 that the system (2.5a)–(2.5b) with $\tau = 0$ has no nontrivial periodic solution. Hence, the projection of $\ell(z^*, \tau_n^*, 2\pi/\eta^*)$ onto τ-space is always away from zero.

For a contradiction, we suppose that the projection of τ-space is $[\tau^*, \infty]$ on to τ is bounded. This means that the projection $\ell(z^*, \tau_n^*, 2\pi/\eta^*)$ onto τ space is included in an interval $(0, \tau^*)$. Note that $2\pi/\eta^* < \tau_n^*$. By applying Lemma 3, we have $0 < p < \tau^*$ for (z, τ, p) belonging to $\ell(z^*, \tau_n^*, 2\pi/\eta^*)$. This implies that the projection of $\ell(z^*, \tau_n^*, 2\pi/\eta^*)$ onto p-space is bounded. Then by applying Lemma 2, we have the connected component $\ell(z^*, \tau_n^*, 2\pi/\eta^*)$ is bounded. Hence, the proof. □

8.1 Existence of switching stability

The characteristic equation around the interior equilibrium E^* of the system (2.5a)–(2.5b) with positive delay is

$$\lambda^2 + \big(\gamma + 2\delta v^* - J_{11}\big)\lambda - J_{11}\big(\gamma + 2\delta v^*\big)$$
$$= J_{12}(J_{11} + J_{21} - \lambda)e^{-\lambda\tau}.$$

This equation can be written as

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

where

$$P(\lambda) = \lambda^2 + \big(\gamma + 2\delta v^* - J_{11}\big)\lambda - J_{11}\big(\gamma + 2\delta v^*\big),$$
$$Q(\lambda) = -J_{12}(J_{11} + J_{21} - \lambda).$$

Clearly, $P(\lambda)$ and $Q(\lambda)$ are both analytic function in $\mathrm{Re}(\lambda) > 0$.

Now we have the following results:

(i) $P(0) + Q(0)$

$$= -J_{11}\big(\gamma + 2\delta v^*\big) - J_{12}(J_{11} + J_{21})$$
$$= -J_{11}\big(\gamma + 2\delta v^*\big) + \frac{\epsilon u^*(1+\alpha u^*)(1-2u^*)}{(1+\alpha u^* + \beta v^*)^2}$$
$$\neq 0, \quad \text{if } u^* < 1/2,$$

(ii) $P(-iy) = \bar{P}(iy), \qquad Q(-iy) = \bar{Q}(iy),$ and

(iii) $\limsup_{|\lambda|\to+\infty} \left|\frac{Q(\lambda)}{P(\lambda)}\right| = 0 < 1.$

Therefore,

$$F(y) = \big|P(iy)\big|^2 - \big|Q(iy)\big|^2$$
$$= y^4 + \big(\big(\gamma + 2\delta v^*\big)^2 + J_{11}^2 - J_{12}^2\big)y^2$$
$$+ J_{11}^2\big(\gamma + 2\delta v^*\big)^2 - J_{12}^2(J_{11} + J_{22})^2,$$

which is a quadratic expression in y^2.

Therefore, $F(y) = 0$, has at least one positive root if $|J_{11}(\gamma + 2\delta v^*)| < |J_{12}(J_{11} + J_{22})|$. Hence, by applying Theorem 4.1 in Kuang [8], we see that the system (2.5a)–(2.5b) possesses at most finite number of stability switches.

9 Numerical simulations

In this section, the numerical experiments are performed on the system (2.5a)–(2.5b) to confirm our theoretical findings. We now present some numerical results of the system for different values of τ. From the above discussion, we may determine the direction of Hopf-bifurcation and the direction of bifurcating periodic solution. We now consider the following systems:

$$\begin{cases} \frac{du}{dt} = u - \frac{uv}{7.0u+v} - u^2, \\ \frac{dv}{dt} = -0.01v + \frac{u(t-\tau)v(t-\tau)}{7.0u(t-\tau)+v(t-\tau)} - 0.005v^2, \end{cases} \tag{9.1}$$

which has a positive equilibrium $E^*(0.2530120482, 5.228915660)$. When τ passes through the critical value $\tau = \tau^* = 103.4701397$ and $\frac{d}{d\tau}(\mathrm{Re}(\lambda(\tau)))|_{\tau=\tau^*} = 0.3064100971 \times 10^{-5} > 0$, the equilibrium E^* losses its stability and the system (2.5a)–(2.5b) experiences Hopf-bifurcation. From Sect. 7, we can determine the nature of the stability and direction of the periodic solution bifurcating from the interior equilibrium at the critical point τ^*. Using (7.31), we can compute $C_1(0) = 24.22376196 - 1.4651764i$, $\beta_2 = 48.44752392 > 0$, $\mu_2 = -7.905667009 \times 10^6 < 0$ and $\tau_2 = -72.81028465$. Hence, the bifurcating periodic solution exists and the corresponding periodic solution is supercritical and unstable as evident from Fig. 1(a)–(c). The period of the periodic solution is 72.81028465. The negative sign of τ indicates the decreasing period of the periodic solution of the system. Moreover, this system is globally asymptotically stable around the interior equilibrium E^*, which is clearly depicted from Fig. 2(a)–(b) for $\tau = 92.32767179 < \tau^*$.

10 Conclusion and comment

The delay process is reflected in the survey and experimental studies in ecology. During population density studies of phytoplankton, zooplankton, and fish, many ecologists observed that the month/period where phytoplankton density is encountered maximum, the zooplankton and fish densities are not maximum at the same period, sometimes after this period zooplankton shows the peak and little after the fish peak is noticed (cf. Bhunia [39], Roy et al. [40], Mandal et al. [41]). Phytoplankton-zooplankton-fish is a classical example of food chain; here, zooplankton is predator of phytoplankton and fish is predator of zooplankton. From the above observations, it is obvious that there is delay in the transformation process of energy from prey to predator and this realistic aspect is incorporated in the present model.

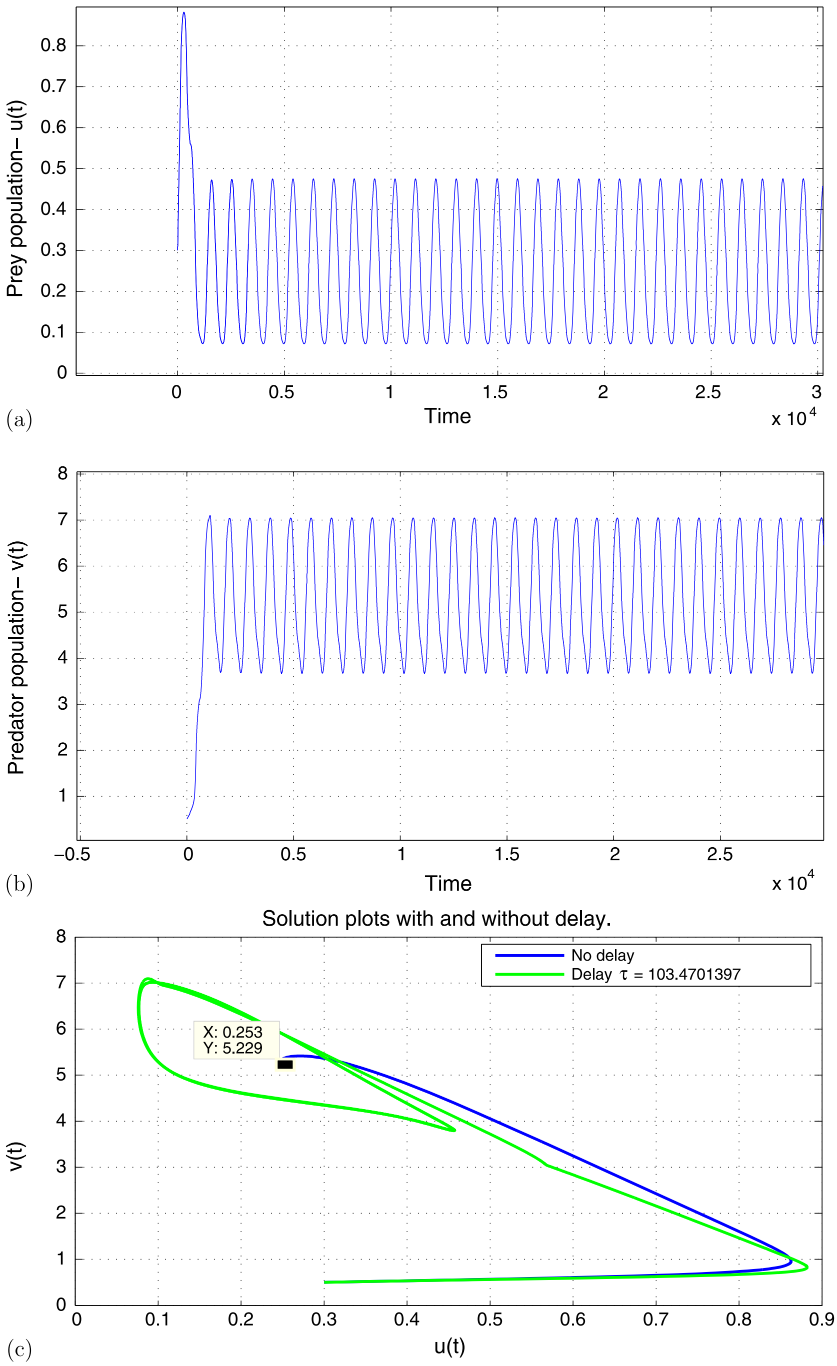

Fig. 1 (**a**)–(**b**) Hopf-bifurcation behavior of the system (2.5a)–(2.5b) around the interior equilibrium E^* at $\tau = \tau^* = 103.4701397$. The other parameter values are given in (9.1). (**c**) Existence of unstable supercritical bifurcating periodic solution around the interior equilibrium E^* with the same parameter values as in (9.1)

In this paper, the properties of Hopf bifurcations in a modified Bazykin's model system [27] with delay in predator's equation have been studied. Although bifurcations in a population dynamics without delay have been investigated by many researchers (cf. Sun et al. [42], Song et al. [43], Song and Yuan [44]), there are few papers on the bifurcations of a population dynamics with delay, which have shown the local, global stability, and direction of global Hopf-bifurcation simultaneously. For this system, we have dealt with all the said dynamics in an orderly manner. In this paper, we discuss all about the existence and stability of Hopf-

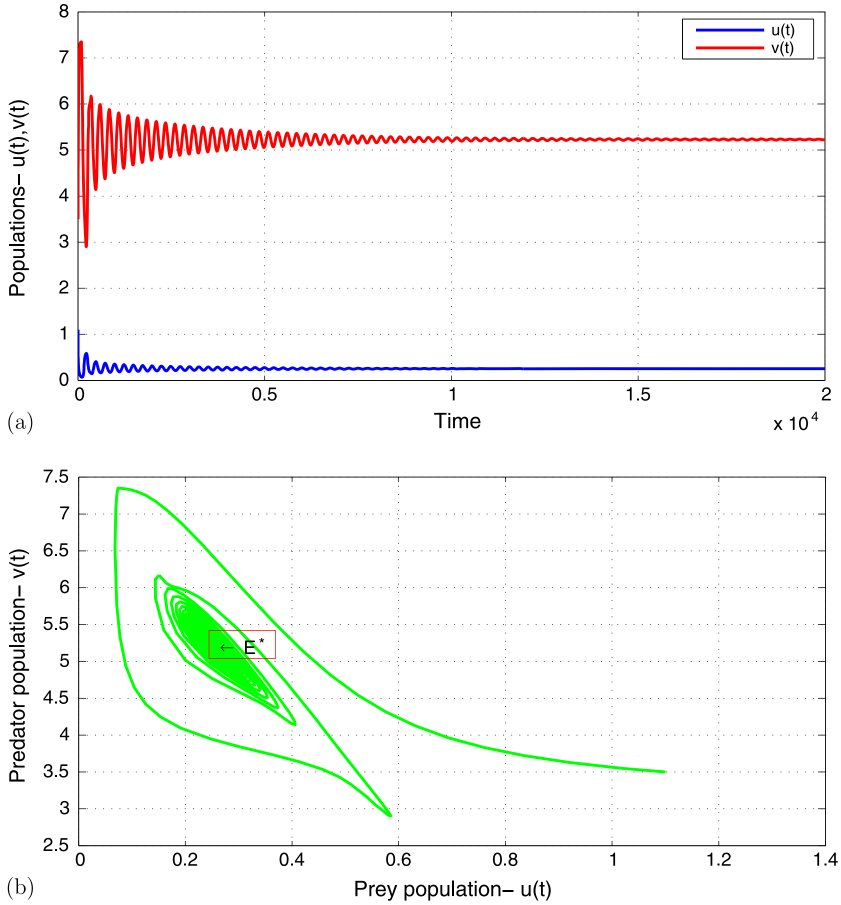

Fig. 2 (**a**)–(**b**) The system (2.5a)–(2.5b) is globally asymptotically stable around the interior equilibrium E^* at $\tau = 92.32767179 < \tau^* = 103.4701397$. The other parameter values are given in (9.1)

bifurcation for a system of modified Bazykin's model with delay. We have shown in Sect. 5 that the system (2.5a)–(2.5b) experiences the Hopf-bifurcation as the delay τ crosses some critical values τ^*. The normal form theory and center manifold reduction have been made use of and we have derived the explicit formulae which determine the stability, direction, and other properties of bifurcating periodic solutions. We hope that the theoretical investigations which have been carried out in this manuscript will certainly help the experimental ecologists to do some experimental studies and as a consequence the theoretical ecology may be developed to some extent.

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Appendix: Alternative method for determining the sign of $\frac{d}{d\tau}(\mathrm{Re}(\lambda(\tau)))$

The characteristic equation (5.3) can be written as

$$\lambda^2 + S_1\lambda + S_2 = (S_3 + S_4\lambda)e^{-\lambda\tau}, \tag{A.1}$$

where $S_1 = \gamma + 2\delta v^* - J_{11}$, $S_2 = -J_{11}(\gamma + 2\delta v^*)$, $S_3 = J_{12}(J_{11} + J_{21})$, and $S_4 = -J_{12}$. By using the previous technique, we can easily obtain the value of τ^* ($\min(\tau_n^*)$) in terms of S_i $(i = 1, \dots, 4)$ as

$$\tau_n^* = \frac{1}{\eta^*}\arccos\left(\frac{(S_1S_4 - S_3)\eta^{*2} + S_2S_3}{(S_4\eta^*)^2 + (S_3)^2}\right) + \frac{2\pi n}{\eta^*}, \tag{A.2}$$

where $n = 0, 1, 2, \dots$.

To determine the sign of $\frac{d}{d\tau}(\mathrm{Re}(\lambda(\tau)))|_{\tau=\tau^*}$, we differentiate (A.1) with respect to τ, which results in the following:

$$(2\lambda + S_1)\frac{d\lambda}{d\tau} = e^{-\lambda\tau}\big(-\tau(S_3 + S_4\lambda) + S_4\big)\frac{d\lambda}{d\tau} - \lambda e^{-\lambda\tau}(S_3 + S_4\lambda), \tag{A.3}$$

which gives

$$\left(\frac{d\lambda}{d\tau}\right)^{-1} = \frac{2\lambda + S_1}{-\lambda(\lambda^2 + S_1\lambda + S_2)} - \frac{\tau}{\lambda} + \frac{S_4}{\lambda(S_3 + S_4\lambda)} = -\frac{\lambda^2 - S_2}{\lambda^2(\lambda^2 + S_1\lambda + S_2)} - \frac{S_3}{\lambda^2(S_3 + S_4\lambda)} - \frac{\tau}{\lambda}.$$

Thus,

$$\begin{aligned}
&\mathrm{sign}\left\{\frac{d(\mathrm{Re}(\lambda(\tau)))}{d\tau}\right\}_{\lambda=i\eta^*} \\
&= \mathrm{sign}\left[\mathrm{Re}\left(\frac{d\lambda}{d\tau}\right)^{-1}\right]_{\lambda=i\eta^*} \\
&= \mathrm{sign}\left\{\mathrm{Re}\left[-\frac{\lambda^2 - S_2}{\lambda^2(\lambda^2 + S_1\lambda + S_2)}\right]_{\lambda=i\eta^*} + \mathrm{Re}\left[-\frac{S_3}{\lambda^2(S_3 + S_4\lambda)}\right]_{\lambda=i\eta^*}\right\} \\
&= \mathrm{sign}\left\{\mathrm{Re}\left[\frac{-\eta^{*2} - S_2}{(-\eta^{*2} + S_1\eta^* i + S_2)}\right] + \mathrm{Re}\left[\frac{S_3}{(S_3 + S_4\eta^* i)}\right]\right\} \\
&= \mathrm{sign}\left\{\frac{\eta^{*4} - (S_2)^2 + (S_3)^2}{(S_3)^2 + (S_4\eta^*)^2}\right\}, \quad \text{since} \\
&(S_3)^2 + \big(S_4\eta^*\big)^2 = \big(S_2 - \eta^{*2}\big)^2 + \big(S_1\eta^*\big)^2.
\end{aligned}$$

Now if $|S_3| > |S_2|$, i.e., $-J_{11}(\gamma + 2\delta v^*) < J_{12}(J_{11} + J_{21})$ holds, what is considered earlier for the positivity of η^*, then we have

$$\frac{d}{d\tau}\big(\mathrm{Re}\big(\lambda(\tau)\big)\big)\big|_{\tau=\tau^*,\eta=\eta^*} > 0.$$

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