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Dynamics of a Modified Predator-Prey System to allow for a Functional Response and Time Delay

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Abstract. A modified predator-prey system described by two differential equations and an algebraic equation is discussed. Formulae for determining the direction of a Hopf bifurcation and the stability of the bifurcating periodic solutions are derived differential-algebraic system theory, bifurcation theory and centre manifold theory. Numerical simulations illustrate the results, which includes quite complex dynamical behaviour.

AMS subject classifications: 92D25

Key words: Predator-prey system, harvesting, stability, time delay, periodic solutions.

1. Introduction

There has been wide-ranging interest in the modelling of predator-prey systems with harvesting [1, 2, 4, 5, 9–22]. Some type of time delay has often been incorporated into predator-prey systems to account for maturation time, capturing time, or some other factor. Indeed, it is well recognised that time delay can play an important role in many biological dynamical systems. Associated delay differential equations usually exhibit much more complicated dynamics than ordinary differential equations, since a time delay can cause a stable equilibrium to become unstable or cause the population to fluctuate [10, 13, 19]. Refs. [4, 10, 14] proposed the following predator-prey system with time delay:

$$\begin{cases} \dot{x}(t) = x(t)G(x(t-\tau)) - P(x(t))y(t)\,, \\ \dot{y}(t) = y(t)\big[-a + dP(x(t))\big], \end{cases}$$

where $x(t)$ and $y(t)$ denote the respective population densities of the prey and predator at time t, $a > 0$ is the death rate of predator, $d > 0$ is the conversion factor, the delay $\tau \geq 0$

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can be regarded as a gestation period or reaction time of the prey, $G(x(t))$ is the intrinsic growth rate, and $P(x(t))$ is the functional response. Here we choose a traditional logistic form $G(x(t)) = r - kx(t)$, where $r > 0$ is the growth rate of the prey in the absence of the predator and $k > 0$ represents the self-regulation constant of the prey, and $P(x(t)) = \sqrt{x(t)}$ corresponding to the prey interacting with the predator along the outer margin of the herd [5, 9, 15, 16]. Thus we consider the following predator-prey system with time delay:

$$\begin{cases} \dot{x}(t) = x(t)\left(r - kx(t-\tau) - \dfrac{y(t)}{\sqrt{x(t)}} - E(t)\right), \\ \dot{y}(t) = y(t)\left(-a + d\sqrt{x(t)}\right). \end{cases} \tag{1.1}$$

Gordon [6] studied the effect of harvesting on an ecosystem from an economic perspective, and proposed the economic principle

$$\text{Net Economic Revenue (NER)} = \text{Total Revenue (TR)} - \text{Total Cost (TC)}.$$

For the system (1.1), an algebraic equation that represents the economic profit v of the harvesting effort on the prey is

$$E(t)(px(t) - c) = v, \tag{1.2}$$

where $E(t)$ denotes the harvesting effort for the prey, and $p > 0$, $c > 0$ and $v > 0$ are respectively the harvesting reward per unit harvesting effort for a unit weight of prey, the harvesting cost per unit harvesting effort for the prey and the economic profit per unit harvesting effort. Consequently, on combining (1.1) and (1.2) we obtain the following modified predator-prey system with functional response $\sqrt{x}$ and time delay:

$$\begin{cases} \dot{x}(t) = x(t)\left(r - kx(t-\tau) - \dfrac{y(t)}{\sqrt{x(t)}} - E(t)\right), \\ \dot{y}(t) = y(t)\left(-a + d\sqrt{x(t)}\right), \\ 0 = E(t)(px(t) - c) - v. \end{cases} \tag{1.3}$$

The effect of varying the time delay on the dynamics of the system (1.3) in the region $\mathrm{R}^3_+ = \{(x, y, E) |\ x > 0, y > 0, E > 0\}$ is the main focus of this article. In research on the dynamic behaviour of similar predator-prey systems, issues such as saddle-node bifurcation, singularity induced bifurcation, Neimark-Sacker bifurcation and state feedback control have been discussed [12, 20–22]. However, formulae for determining the properties of possible Hopf bifurcation have not yet appeared. By applying a local parameterisation method [3] and centre manifold theory [8], here we investigate the stability and the direction of the Hopf bifurcation of the delayed system (1.3) where τ is a bifurcation parameter, to be defined below. In passing, it is notable that t is occasionally omitted whenever there is no danger of confusion.

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2. Local Stability

The local parameterisation method [3] and the Hopf bifurcation theorem [8] enables an investigation of the local stability of the positive equilibrium point of the system (1.3) and the existence of the Hopf bifurcation at the positive equilibrium point when $\tau > 0$.

The system (1.3) has an equilibrium point

$$X_0 = (x_0, y_0, E_0)^T = \left(\frac{a^2}{d^2}, \frac{a}{d}\left(r - \frac{ka^2}{d^2} - E_0\right), \frac{vd^2}{pa^2 - cd^2}\right)^T,$$

which from the viewpoint of biology should be positive, so that

$$r - \frac{ka^2}{d^2} > E_0, \quad pa^2 - cd^2 > 0 \text{ and } v > 0. \tag{2.1}$$

Under the transformation $X = Q\overline{X}$ where

$$Q = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ -\frac{pE_0}{px_0 - c} & 0 & 1 \end{pmatrix},$$

$X(t) = (x(t), y(t), E(t))^T$ and $\overline{X}(t) = (x(t), y(t), \overline{E}(t))^T$, the system (1.3) becomes

$$\begin{cases} \dot{x}(t) = x(t)\left(r - kx(t-\tau) - \dfrac{y(t)}{\sqrt{x(t)}} + \dfrac{pE_0}{px_0 - c}x(t) - \overline{E}(t)\right), \\ \dot{y}(t) = y(t)\left(-a + d\sqrt{x(t)}\right), \\ 0 = \left(-\dfrac{pE_0}{px_0 - c}x(t) + \overline{E}(t)\right)(px(t) - c) - v. \end{cases} \tag{2.2}$$

For the third equation of system (2.2), we consider the local parameterisation [3]

$$\overline{X}(t) = \psi(Y(t)) = \overline{X}_0 + U_0 Y(t) + V_0 h(Y(t)),$$

with $U_0 = \begin{pmatrix} 1 & 0 \\ 0 & 1 \\ 0 & 0 \end{pmatrix}$, $V_0 = \begin{pmatrix} 0 \\ 0 \\ 1 \end{pmatrix}$, $Y(t) = (y_1(t), y_2(t))^T \in \mathrm{R}^2$, $h(Y(t))$ a smooth mapping from R^2 into R^3, and $h(Y(t)) = (h_1(y_1(t), y_2(t)), h_2(y_1(t), y_2(t)), h_3(y_1(t), y_2(t)))^T$. Thus

$$x(t) = x_0 + y_1(t), \quad y(t) = y_0 + y_2(t) \quad \text{and} \quad \overline{E}(t) = \overline{E}_0 + h_3(y_1(t), y_2(t)))$$

where $\overline{E}_0 = E_0 + (px_0E_0)/(px_0 - c)$, such that the parameterised system obtained from (2.2) is

$$\begin{cases} \dot{y}_1(t) = (x_0 + y_1(t))\Big(r - k(x_0 + y_1(t-\tau)) - \dfrac{(x_0 + y_1(t))}{\sqrt{(x_0 + y_1(t))}} \\ \qquad\qquad + \dfrac{pE_0}{px_0 - c}(x_0 + y_1(t)) - \left(\overline{E}_0 + h_3(y_1(t), y_2(t))\right)\Big), \\ \dot{y}_2(t) = (y_0 + y_2(t))\left(-a + d\sqrt{(x_0 + y_1(t))}\right). \end{cases} \tag{2.3}$$

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The linearised parametric system from (2.3) near the origin $(0,0)$ is therefore

$$\begin{cases} \dot{y}_1(t) = \left(\dfrac{y_0}{2\sqrt{x_0}} + \dfrac{px_0E_0}{px_0 - c}\right) y_1(t) - kx_0 y_1(t-\tau) - \sqrt{x_0}\, y_2(t)\,, \\ \dot{y}_2(t) = \dfrac{dy_0}{2\sqrt{x_0}} y_1(t)\,; \end{cases} \tag{2.4}$$

and the characteristic equation for (2.4) is

$$\lambda^2 + \left(kx_0 e^{-\lambda\tau} - \frac{y_0}{2\sqrt{x_0}} - \frac{px_0E_0}{px_0 - c}\right)\lambda + \frac{dy_0}{2} = 0\,, \tag{2.5}$$

which for $\tau = 0$ reduces to

$$\lambda^2 + \left(kx_0 - \frac{y_0}{2\sqrt{x_0}} - \frac{px_0E_0}{px_0 - c}\right)\lambda + \frac{dy_0}{2} = 0\,. \tag{2.6}$$

From Eq. (2.6) and the Routh-Hurwitz criterion [11] , we readily obtain the following Lemma.

Lemma 2.1. *For the system* (2.2) *with* $\tau = 0$*:*

(i) if $k > \dfrac{pE_0}{px_0 - c} + \dfrac{y_0}{2{x_0}^{3/2}}$*, then the equilibrium point* $\overline{X}_0$ *is locally asymptotically stable — i.e.* X_0 *is locally asymptotically stable;*

(ii) if $k < \dfrac{pE_0}{px_0 - c} + \dfrac{y_0}{2{x_0}^{3/2}}$*, then the equilibrium point* $\overline{X}_0$ *is unstable — i.e.* X_0 *is unstable.*

Let us now consider the local stability of the positive equilibrium point $\overline{X}_0$ when $\tau > 0$. If $\lambda = i\omega$ $(\omega > 0)$ denotes a root of Eq. (2.5), then

$$-\omega^2 + i\omega\left(kx_0(\cos\omega\tau - i\sin\omega\tau) - \frac{y_0}{2\sqrt{x_0}} - \frac{px_0E_0}{px_0 - c}\right) + \frac{dy_0}{2} = 0\,,$$

and separating out the real and imaginary parts gives

$$kx_0\omega\sin\omega\tau = \omega^2 - \frac{dy_0}{2}\,, \tag{2.7}$$

$$kx_0\omega\cos\omega\tau = \frac{y_0\omega}{2\sqrt{x_0}} + \frac{px_0E_0\omega}{px_0 - c}\,. \tag{2.8}$$

From Eqs. (2.7) and (2.8), one has

$$\omega^4 + \left[\left(\frac{y_0}{2\sqrt{x_0}} + \frac{px_0E_0}{px_0 - c}\right)^2 - dy_0 - k^2x_0^2\right]\omega^2 + \frac{d^2y_0^2}{4} = 0\,, \tag{2.9}$$

with two cases to consider as follows.

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Case I. If

$$\left(\frac{y_0}{2\sqrt{x_0}}+\frac{px_0E_0}{px_0-c}\right)^2 > dy_0+k^2x_0^2\,,$$

then Eq. (2.9) has no positive roots such that Eq. (2.5) does not have any purely imaginary root. Furthermore, all roots of the Eq. (2.6) have negative real parts if $k > \frac{pE_0}{px_0-c}+\frac{y_0}{2{x_0}^{3/2}}$, such that from Rouche's theorem [17] the roots of Eq. (2.5) also have negative real parts.

Case II. If

$$\left[\left(\frac{y_0}{2\sqrt{x_0}}+\frac{px_0E_0}{px_0-c}\right)^2-dy_0-k^2x_0^2\right]^2 > d^2y_0^2 \text{ and } \left(\frac{y_0}{2\sqrt{x_0}}+\frac{px_0E_0}{px_0-c}\right)^2 < dy_0+k^2x_0^2\,,$$

it is easy to see that Eq. (2.9) has two positive roots ω^+ and ω^- given by

$$\omega^{\pm}=\left\{\frac{1}{2}\left[dy_0+k^2x_0^2-\left(\frac{y_0}{2\sqrt{x_0}}+\frac{px_0E_0}{px_0-c}\right)^2 \pm\sqrt{\left[\left(\frac{y_0}{2\sqrt{x_0}}+\frac{px_0E_0}{px_0-c}\right)^2-dy_0-k^2x_0^2\right]^2-d^2y_0^2}\ \right]\right\}^{1/2}. \tag{2.10}$$

These results may be summarised in the following Lemma.

Lemma 2.2. *For the system* (2.2)*:*

(i) if $k > \frac{pE_0}{px_0-c}+\frac{y_0}{2{x_0}^{3/2}}$ *and* $\left(\frac{y_0}{2\sqrt{x_0}}+\frac{px_0E_0}{px_0-c}\right)^2 > dy_0+k^2x_0^2$*, then all the roots of Eq.* (2.5) *have negative real parts for all* $\tau > 0$*;*

(ii) if $\left[\left(\frac{y_0}{2\sqrt{x_0}}+\frac{px_0E_0}{px_0-c}\right)^2-dy_0-k^2x_0^2\right]^2 > d^2y_0^2$, $\left(\frac{y_0}{2\sqrt{x_0}}+\frac{px_0E_0}{px_0-c}\right)^2 < dy_0+k^2x_0^2$*, then Eq.* (2.5) *has two positive roots* ω^+ *and* ω^-*. Substituting* $\omega^{\pm}$ *into Eq.* (2.8) *yields*

$$\tau_k^{\pm}=\frac{1}{\omega^{\pm}}\arccos\left(\frac{y_0}{2k{x_0}^{3/2}}+\frac{pE_0}{k(px_0-c)}\right)+\frac{2k\pi}{\omega^{\pm}},\quad k=0,1,2,\cdots. \tag{2.11}$$

Let us now verify the transversality conditions. Differentiating both sides of Eq. (2.5) with respect to τ gives

$$2\lambda\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}+\left(kx_0e^{-\lambda\tau}-\frac{y_0}{2\sqrt{x_0}}-\frac{px_0E_0}{px_0-c}\right)\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}+kx_0\lambda e^{-\lambda\tau}\left(-\lambda-\tau\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)=0\,,$$

which yields

$$\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)^{-1}=\frac{2\lambda+kx_0e^{-\lambda\tau}-\frac{y_0}{2\sqrt{x_0}}-\frac{px_0E_0}{px_0-c}-kx_0\lambda\tau e^{-\lambda\tau}}{kx_0\lambda^2e^{-\lambda\tau}}$$

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such that

$$\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)^{-1}\Big|_{\lambda=i\omega} = \left(-\frac{1}{\omega^2}+\frac{2}{kx_0\omega}\sin\lambda\tau+\left(\frac{pE_0}{k(px_0-c)\omega^2}+\frac{y_0}{2kx_0{}^{\frac{3}{2}}\omega^2}\right)\cos\lambda\tau\right)$$
$$+i\left(\frac{\tau}{\omega}-\frac{2}{kx_0\omega}\cos\lambda\tau+\left(\frac{pE_0}{k(px_0-c)\omega^2}+\frac{y_0}{2kx_0{}^{\frac{3}{2}}\omega^2}\right)\sin\lambda\tau\right).$$

Then associated with Eqs. (2.7) and (2.8) one has

$$\operatorname{sign}\left\{\operatorname{Re}\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)\right\}\Big|_{\lambda=i\omega} = \operatorname{sign}\left\{\operatorname{Re}\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)^{-1}\right\}\Big|_{\lambda=i\omega}$$
$$=\operatorname{sign}\left\{-\frac{1}{\omega^2}+\frac{2}{kx_0\omega}\left(\frac{\omega}{kx_0}-\frac{dy_0}{2kx_0\omega}\right)+\left(\frac{pE_0}{k(px_0-c)\omega^2}+\frac{y_0}{2kx_0{}^{\frac{3}{2}}\omega^2}\right)\left(\frac{y_0}{2kx_0^{\frac{3}{2}}}+\frac{pE_0}{k(px_0-c)}\right)\right\}$$
$$=\operatorname{sign}\left\{\frac{1}{k^2x_0^2\omega^2}\left[2\omega^2-dy_0-k^2x_0^2+\left(\frac{px_0E_0}{px_0-c}+\frac{y_0}{2\sqrt{x_0}}\right)^2\right]\right\}$$

such that

$$\operatorname{sign}\left\{\operatorname{Re}\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)\right\}\Big|_{\tau=\tau_k^+,\ \omega=\omega^+} > 0\,, \qquad \operatorname{sign}\left\{\operatorname{Re}\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)\right\}\Big|_{\tau=\tau_k^-,\ \omega=\omega^-} < 0\,,$$

so the transversality conditions are satisfied and one has the following Theorem.

Theorem 2.1. *Suppose that the system* (2.2) *satisfies* $k > \dfrac{pE_0}{px_0-c}+\dfrac{y_0}{2x_0{}^{3/2}}$.

(i) If $\left(\dfrac{y_0}{2\sqrt{x_0}}+\dfrac{px_0E_0}{px_0-c}\right)^2 > dy_0+k^2x_0^2$, *then all the roots of Eq.* (2.5) *have negative real parts for all* $\tau > 0$ *and the equilibrium point* X_0 *of the system* (1.3) *is asymptotically stable; and*

(ii) if $\left[\left(\dfrac{y_0}{2\sqrt{x_0}}+\dfrac{px_0E_0}{px_0-c}\right)^2 dy_0-k^2x_0^2\right]^2 > d^2y_0^2\,,\ \left(\dfrac{y_0}{2\sqrt{x_0}}+\dfrac{px_0E_0}{px_0-c}\right)^2 < dy_0+k^2x_0^2$, *then there is a positive integer* N *such that the equilibrium point* X_0 *of the system* (1.3) *switches* N *times from stability to instability and then back to stability — i.e.* X_0 *is asymptotically stable when*

$$\tau\in[0,\tau_0^+)\bigcup\left(\bigcup_{n=0}^{N-1}(\tau_n^-,\tau_{n+1}^+)\right),$$

and X_0 *is unstable when*

$$\tau\in\left(\bigcup_{n=0}^{N-1}(\tau_n^+,\tau_n^-)\right)\bigcup(\tau_N^+,+\infty)\,.$$

Thus there are bifurcations at the equilibrium point X_0 *of the system* (1.3) *whenever* $\tau=\tau_n^{\pm}$, $n=0,1,2,\cdots,N$.

Remark 2.1. When $\tau=0$ and the roots of Eq. (2.5) exist with zero real parts, the system (1.3) also undergoes a Hopf bifurcation.

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3. Direction and Stability of the Hopf Bifurcation

Let us now derive formulae that determine the direction, stability and period of the periodic solutions bifurcating from the positive equilibrium point X_0 of the system (1.3). The basic tools used are the normal form method [3,7] and centre manifold theory [8]. It is assumed that the system (1.3) undergoes Hopf bifurcations at the positive equilibrium point X_0 where $\tau = \tau_n$, and $i\omega$ denotes the corresponding purely imaginary root of the characteristic equation at the positive equilibrium point.

If $y_1 = x - x_0$, $y_2 = y - y_0$, $t = t\tau$ and $\tau = \tau_n + \mu$, then the parametric system (2.3) can be transformed into the functional differential equation system in $C = C([-1,0], \mathrm{R}^2)$:

$$\dot{Y}(t) = L_\mu(Y_t) + F(\mu, Y_t) \tag{3.1}$$

where $Y(t) = (y_1(t), y_2(t))^T \in \mathrm{R}^2$, and $L_\mu : C \to \mathrm{R}^2$ and $F : \mathrm{R} \times C \to \mathrm{R}^2$ are given respectively by

$$L_\mu\Phi = (\tau_n + \mu)\begin{pmatrix} \dfrac{y_0}{2\sqrt{x_0}} + \dfrac{px_0E_0}{px_0 - c} & -\sqrt{x_0} \\ \dfrac{dy_0}{2\sqrt{x_0}} & 0 \end{pmatrix}\Phi^T(0) + (\tau_n + \mu)\begin{pmatrix} -kx_0 & 0 \\ 0 & 0 \end{pmatrix}\Phi^T(-1),$$

$$F(\mu, \Phi) = (\tau_n + \mu)\begin{pmatrix} F_{11} \\ F_{22} \end{pmatrix},$$

where $\Phi = (\Phi_1, \Phi_2)$ and

$$F_{11} = \left(\frac{1}{8}x_0^{-3/2}y_0 - \frac{pcE_0}{(px_0 - c)^2}\right)\Phi_1^2(0) - k\Phi_1^2(-1) - \frac{1}{2\sqrt{x_0}}\Phi_1(0)\Phi_2(0) + \cdots,$$

$$F_{22} = -\frac{1}{8}dx_0^{-\frac{3}{2}}y_0\Phi_1^2(0) + \frac{d}{2\sqrt{x_0}}\Phi_1(0)\Phi_2(0) + \cdots.$$

From the Riesz representation theorem, there exists a matrix function $\eta(\theta, \mu)$, $\theta \in [-1, 0]$ with elements of bounded variation, such that

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

Let us choose

$$\eta(\theta, \mu) = (\tau_n + \mu)\begin{pmatrix} \dfrac{y_0}{2\sqrt{x_0}} + \dfrac{px_0E_0}{px_0 - c} & -\sqrt{x_0} \\ \dfrac{dy_0}{2\sqrt{x_0}} & 0 \end{pmatrix}\delta(\theta) + (\tau_n + \mu)\begin{pmatrix} kx_0 & 0 \\ 0 & 0 \end{pmatrix}\delta(\theta + 1),$$

where $\delta(\theta) = \begin{cases} 0, & \theta \neq 0, \\ 1, & \theta = 0. \end{cases}$, and for $\Phi \in C^1([-1,0], \mathrm{R}^2)$ define

$$A(\mu)\Phi = \begin{cases} \dfrac{\mathrm{d}\Phi(\theta)}{\mathrm{d}\theta}, & -1 \le \theta < 0, \\ \int_{-1}^{0} \mathrm{d}\eta(\theta, \mu)\Phi(\theta), & \theta = 0, \end{cases}$$

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$$R(\mu)\Phi = \begin{cases} 0, & -1 \le \theta < 0, \\ F(\mu, \Phi), & \theta = 0. \end{cases}$$

The system (3.1) can then be transformed into the operator equation

$$\dot{Y}(t) = A(\mu)Y_t + R(\mu)Y_t, \tag{3.2}$$

where $Y_t = Y(t+\theta) = (y_1(t+\theta), y_2(t+\theta))$.

For $\Psi \in C^1([-1,0],(\mathrm{R}^2)^*)$ where $(\mathrm{R}^2)^*$ is the 2-dimensional space of row vectors, let us also define the adjoint operator A^* of $A(0)$ — viz.

$$A^*\Psi(s) = \begin{cases} -\dfrac{\mathrm{d}\Psi(s)}{\mathrm{d}s}, & 0 < s \le 1, \\ \int_{-1}^{0} \mathrm{d}\eta^T(s,0)\Psi(-s), & s = 0, \end{cases}$$

and a bilinear inner product

$$< \Psi(s), \Phi(\theta) >= \bar{\Psi}(0)\Phi(0) - \int_{\theta=-1}^{0}\int_{\xi=0}^{\theta} \bar{\Psi}(\xi-\theta)\mathrm{d}\eta(\theta)\Phi(\xi)\mathrm{d}\xi,$$

where $\eta(\theta) = \eta(\theta, 0)$.

From the discussion in Section 2, $\pm i\omega\tau_n$ are eigenvalues of $A(0)$, so they are also eigenvalues of A^*. Let $q(\theta) = (1, q_2)^T e^{i\omega\tau_n\theta}$ denote the eigenvector of $A(0)$ corresponding to $i\omega\tau_n$, and $q^*(s) = \frac{1}{D}(q_2^*, 1)e^{i\omega\tau_n s}$ the eigenvector of A^* corresponding to $-i\omega\tau_n$. Then

$$q_2 = \frac{\dfrac{y_0}{2\sqrt{x_0}} + \dfrac{px_0E_0}{px_0 - c} - i\omega - kx_0e^{-i\omega\tau_n}}{\sqrt{x_0}}, \qquad q_2^* = \frac{i\omega}{\sqrt{x_0}},$$
$$\bar{D} = q_2 + \bar{q_2^*} + kx_0\bar{q_2^*}\tau_n e^{-i\omega\tau_n},$$

and furthermore $< q^*, q >= 1$ and $< q^*, \bar{q} >= 0$.

The coordinates to describe the centre manifold C_0 at $\mu = 0$ may now be calculated as follows. Defining

$$\dot{z}(t) =< q^*, Y_t >, \; W(t,\theta) = Y_t - 2\mathrm{Re}\{z(t)q(\theta)\},$$

on the centre manifold C_0 one has

$$W(t,\theta) = W(z,\bar{z},\theta) = W_{20}(\theta)\frac{z^2}{2} + W_{11}(\theta)z\bar{z} + W_{02}(\theta)\frac{\bar{z}^2}{2} + \cdots, \tag{3.3}$$

where z and $\bar{z}$ are local coordinates for C_0 in the direction of q and $\bar{q}^*$, respectively. It is notable that W is real if Y_t is real, and only real solutions need to be considered. For the solution $Y_t \in C_0$, since $\mu = 0$ from Eq. (3.2) one has

$$\dot{z} = i\omega\tau_n z + \bar{q}^*(0)F_0(z,\bar{z}) := i\omega\tau_n z + g(z,\bar{z}) \tag{3.4}$$

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where

$$g(z,\bar{z}) = g_{20}(\theta)\frac{z^2}{2} + g_{11}(\theta)z\bar{z} + g_{02}(\theta)\frac{\bar{z}^2}{2} + \cdots, \tag{3.5}$$

and from Eq. (3.4)

$$g(z,\bar{z}) = \bar{q}^*(0)F_0(z,\bar{z}) = \frac{1}{\bar{D}}\tau_n(\bar{q}_2^*, 1)\begin{pmatrix} F_{11}^0 \\ F_{22}^0 \end{pmatrix}$$

where

$$F_{11}^0 = \left(\frac{1}{8}x_0^{-\frac{3}{2}}y_0 - \frac{pcE_0}{(px_0-c)^2}\right)y_{1t}^2(0) - ky_{1t}^2(-1) - \frac{1}{2\sqrt{x_0}}y_{1t}(0)y_{2t}(0) + \cdots,$$
$$F_{22}^0 = -\frac{1}{8}dx_0^{-\frac{3}{2}}y_0y_{1t}^2(0) + \frac{d}{2\sqrt{x_0}}y_{1t}(0)y_{2t}(0) + \cdots.$$

Associated with Eq. (3.3), one has

$$\begin{aligned} g(z,\bar{z}) = \frac{\tau_n}{\bar{D}}\Bigg\{ & \left[\frac{1}{8}x_0^{-\frac{3}{2}}y_0\bar{q}_2^* - \frac{pcE_0\bar{q}_2^*}{(px_0-c)^2}\right]\times\left[z+\bar{z}+W_{20}^{(1)}(0)\frac{z^2}{2}+W_{11}^{(1)}(0)z\bar{z}+W_{02}^{(1)}(0)\frac{\bar{z}^2}{2}\right]^2 \\ & - k\bar{q}_2^*\left[ze^{-i\omega\tau_n\theta}+\bar{z}e^{i\omega\tau_n\theta}+W_{20}^{(1)}(-1)\frac{z^2}{2}+W_{11}^{(1)}(-1)z\bar{z}+W_{02}^{(1)}(-1)\frac{\bar{z}^2}{2}\right]^2 \\ & - \frac{\bar{q}_2^*}{2\sqrt{x_0}}\left[z+\bar{z}+W_{20}^{(1)}(0)\frac{z^2}{2}+W_{11}^{(1)}(0)z\bar{z}+W_{02}^{(1)}(0)\frac{\bar{z}^2}{2}\right] \\ & \times\left[q_2z+\bar{q}_2\bar{z}+W_{20}^{(2)}(0)\frac{z^2}{2}+W_{11}^{(2)}(0)z\bar{z}+W_{02}^{(2)}(0)\frac{\bar{z}^2}{2}\right] \\ & - \frac{1}{8}dx_0^{-\frac{3}{2}}y_0\left[z+\bar{z}+W_{20}^{(1)}(0)\frac{z^2}{2}+W_{11}^{(1)}(0)z\bar{z}+W_{02}^{(1)}(0)\frac{\bar{z}^2}{2}\right]^2 \\ & + \frac{d}{2\sqrt{x_0}}\left[z+\bar{z}+W_{20}^{(1)}(0)\frac{z^2}{2}+W_{11}^{(1)}(0)z\bar{z}+W_{02}^{(1)}(0)\frac{\bar{z}^2}{2}\right] \\ & \times\left[q_2z+\bar{q}_2\bar{z}+W_{20}^{(2)}(0)\frac{z^2}{2}+W_{11}^{(2)}(0)z\bar{z}+W_{02}^{(2)}(0)\frac{\bar{z}^2}{2}\right]+\cdots\Bigg\} \end{aligned}$$

— i.e.

$$\begin{aligned} g(z,\bar{z}) = \frac{\tau_n}{\bar{D}}\Bigg\{ & z^2\left[\frac{1}{8}x_0^{-\frac{3}{2}}y_0\bar{q}_2^* - \frac{pcE_0\bar{q}_2^*}{(px_0-c)^2} - k\bar{q}_2^*e^{-2i\omega\tau_n\theta} - \frac{q_2\bar{q}_2^*}{2\sqrt{x_0}} - \frac{1}{8}dx_0^{-\frac{3}{2}}y_0 + \frac{dq_2}{2\sqrt{x_0}}\right] \\ & + z\bar{z}\left[\frac{1}{4}x_0^{-\frac{3}{2}}y_0\bar{q}_2^* - \frac{2pcE_0\bar{q}_2^*}{(px_0-c)^2} - 2k\bar{q}_2^* - \frac{\mathrm{Re}(q_2)\bar{q}_2^*}{\sqrt{x_0}} - \frac{1}{4}dx_0^{-\frac{3}{2}}y_0 + \frac{d\mathrm{Re}(q_2)}{\sqrt{x_0}}\right] \\ & + \bar{z}^2\left[\frac{1}{8}x_0^{-\frac{3}{2}}y_0\bar{q}_2^* - \frac{pcE_0\bar{q}_2^*}{(px_0-c)^2} - k\bar{q}_2^*e^{2i\omega\tau_n\theta} - \frac{\bar{q}_2\bar{q}_2^*}{2\sqrt{x_0}} - \frac{1}{8}dx_0^{-\frac{3}{2}}y_0 + \frac{d\bar{q}_2}{2\sqrt{x_0}}\right] \\ & + z^2\bar{z}\left[\left(\frac{1}{4}x_0^{-\frac{3}{2}}y_0\bar{q}_2^* - \frac{2pcE_0\bar{q}_2^*}{(px_0-c)^2} - \frac{q_2\bar{q}_2^*}{2\sqrt{x_0}} - \frac{1}{4}dx_0^{-\frac{3}{2}}y_0 + \frac{dq_2}{2\sqrt{x_0}}\right)W_{11}^{(1)}(0)\right. \end{aligned}$$

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$$+\left(\frac{d}{2\sqrt{x_0}}-\frac{\bar{q}_2^*}{2\sqrt{x_0}}\right)W_{11}^{(2)}(0)$$
$$+\left(\frac{1}{8}x_0^{-\frac{3}{2}}y_0\bar{q}_2^*-\frac{pcE_0\bar{q}_2^*}{(px_0-c)^2}-\frac{\bar{q}_2\bar{q}_2^*}{4\sqrt{x_0}}-\frac{1}{8}dx_0^{-\frac{3}{2}}y_0+\frac{d\bar{q}_2}{4\sqrt{x_0}}\right)W_{20}^{(1)}(0)$$
$$+\left(\frac{d}{4\sqrt{x_0}}-\frac{\bar{q}_2^*}{4\sqrt{x_0}}\right)W_{20}^{(2)}(0)-2k\bar{q}_2^*e^{-i\omega\tau_n\theta}W_{11}^{(1)}(-1)$$
$$-k\bar{q}_2^*e^{i\omega\tau_n\theta}W_{20}^{(1)}(-1)\Big]+\cdots\Big\}.$$

Comparing the coefficients with (3.5) produces the following coefficients:

$$g_{20}=\frac{2\tau_n}{\bar{D}}\left[\frac{1}{8}x_0^{-\frac{3}{2}}y_0\bar{q}_2^*-\frac{pcE_0\bar{q}_2^*}{(px_0-c)^2}-k\bar{q}_2^*e^{-2i\omega\tau_n\theta}-\frac{q_2\bar{q}_2^*}{2\sqrt{x_0}}-\frac{1}{8}dx_0^{-\frac{3}{2}}y_0+\frac{dq_2}{2\sqrt{x_0}}\right],$$
$$g_{11}=\frac{\tau_n}{\bar{D}}\left[\frac{1}{4}x_0^{-\frac{3}{2}}y_0\bar{q}_2^*-\frac{2pcE_0\bar{q}_2^*}{(px_0-c)^2}-2k\bar{q}_2^*-\frac{\mathrm{Re}(q_2)\bar{q}_2^*}{\sqrt{x_0}}-\frac{1}{4}dx_0^{-\frac{3}{2}}y_0+\frac{d\mathrm{Re}(q_2)}{\sqrt{x_0}}\right],$$
$$g_{02}=\frac{2\tau_n}{\bar{D}}\left[\frac{1}{8}x_0^{-\frac{3}{2}}y_0\bar{q}_2^*-\frac{pcE_0\bar{q}_2^*}{(px_0-c)^2}-k\bar{q}_2^*e^{2i\omega\tau_n\theta}-\frac{\bar{q}_2\bar{q}_2^*}{2\sqrt{x_0}}-\frac{1}{8}dx_0^{-\frac{3}{2}}y_0+\frac{d\bar{q}_2}{2\sqrt{x_0}}\right],$$
$$g_{21}=\frac{2\tau_n}{\bar{D}}\left[\left(\frac{1}{4}x_0^{-\frac{3}{2}}y_0\bar{q}_2^*-\frac{2pcE_0\bar{q}_2^*}{(px_0-c)^2}-\frac{q_2\bar{q}_2^*}{2\sqrt{x_0}}-\frac{1}{4}dx_0^{-\frac{3}{2}}y_0+\frac{dq_2}{2\sqrt{x_0}}\right)W_{11}^{(1)}(0)\right.$$
$$+\left(\frac{d}{2\sqrt{x_0}}-\frac{\bar{q}_2^*}{2\sqrt{x_0}}\right)W_{11}^{(2)}(0)$$
$$+\left(\frac{1}{8}x_0^{-\frac{3}{2}}y_0\bar{q}_2^*-\frac{pcE_0\bar{q}_2^*}{(px_0-c)^2}-\frac{\bar{q}_2\bar{q}_2^*}{4\sqrt{x_0}}-\frac{1}{8}dx_0^{-\frac{3}{2}}y_0+\frac{d\bar{q}_2}{4\sqrt{x_0}}\right)W_{20}^{(1)}(0)$$
$$\left.+\left(\frac{d}{4\sqrt{x_0}}-\frac{\bar{q}_2^*}{4\sqrt{x_0}}\right)W_{20}^{(2)}(0)-2k\bar{q}_2^*e^{-i\omega\tau_n\theta}W_{11}^{(1)}(-1)-k\bar{q}_2^*e^{i\omega\tau_n\theta}W_{20}^{(1)}(-1)\right].$$

The $W_{20}(\theta)$ and $W_{11}(\theta)$ may be calculated using a computation process similar to Ref. [8], to get

$$W_{20}(\theta)=\frac{ig_{20}}{\omega\tau_n}q(0)e^{i\omega\tau_n\theta}+\frac{i\bar{g}_{02}}{3\omega\tau_n}\bar{q}(0)e^{-i\omega\tau_n\theta}+M_1e^{2i\omega\tau_n\theta},$$
$$W_{11}(\theta)=-\frac{ig_{11}}{\omega\tau_n}q(0)e^{i\omega\tau_n\theta}+\frac{i\bar{g}_{11}}{\omega\tau_n}\bar{q}(0)e^{-i\omega\tau_n\theta}+M_2\,,$$

where M_1 and M_2 can be determined from

$$M_1=\begin{pmatrix}2i\omega-\dfrac{y_0}{2\sqrt{x_0}}-\dfrac{px_0E_0}{px_0-c}+kx_0e^{-2i\omega\tau_n} & \sqrt{x_0}\\ -\dfrac{dy_0}{2\sqrt{x_0}} & 2i\omega\end{pmatrix}^{-1}\times 2\begin{pmatrix}G_{11}\\ G_{21}\end{pmatrix},$$

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$$M_2 = \begin{pmatrix} -\dfrac{y_0}{2\sqrt{x_0}} - \dfrac{px_0E_0}{px_0-c} + kx_0 & \sqrt{x_0} \\ -\dfrac{dy_0}{2\sqrt{x_0}} & 0 \end{pmatrix}^{-1} \times 2 \begin{pmatrix} H_{11} \\ H_{21} \end{pmatrix},$$

with

$$\begin{aligned} G_{11} &= \frac{1}{8}x_0^{-\frac{3}{2}}y_0 - \frac{pcE_0}{(px_0-c)^2} - ke^{-2i\omega\tau_n\theta} - \frac{q_2}{2\sqrt{x_0}}, \\ G_{21} &= -\frac{1}{8}dx_0^{-\frac{3}{2}}y_0 + \frac{dq_2}{2\sqrt{x_0}}, \\ H_{11} &= \frac{1}{8}x_0^{-\frac{3}{2}}y_0 - \frac{pcE_0}{(px_0-c)^2} - k - \frac{\mathrm{Re}(q_2)}{2\sqrt{x_0}}, \\ H_{21} &= -\frac{1}{8}dx_0^{-\frac{3}{2}}y_0 + \frac{d\mathrm{Re}(q_2)}{2\sqrt{x_0}}. \end{aligned}$$

Consequently,

$$M_1 = \begin{pmatrix} \dfrac{4G_{11}i\omega - 2\sqrt{x_0}G_{21}}{\dfrac{dy_0}{2} + 2kx_0i\omega e^{-2i\omega\tau_n} - 4\omega^2 - \left(\dfrac{y_0}{\sqrt{x_0}} + \dfrac{2px_0E_0}{px_0-c}\right)i\omega} \\ \dfrac{\dfrac{dy_0}{\sqrt{x_0}}G_{11} + \left(4i\omega - \dfrac{y_0}{\sqrt{x_0}} - \dfrac{2px_0E_0}{px_0-c} + 2kx_0e^{-2i\omega\tau_n}\right)G_{21}}{\dfrac{dy_0}{2} + 2kx_0i\omega e^{-2i\omega\tau_n} - 4\omega^2 - \left(\dfrac{y_0}{\sqrt{x_0}} + \dfrac{2px_0E_0}{px_0-c}\right)i\omega} \end{pmatrix},$$

$$M_2 = \begin{pmatrix} -\dfrac{4\sqrt{x_0}H_{21}}{dy_0} \\ \dfrac{2}{\sqrt{x_0}}H_{11} - \left(\dfrac{2}{d\sqrt{x_0}} + \dfrac{4px_0E_0}{dy_0(px_0-c)} - \dfrac{4kx_0}{dy_0}\right)H_{21} \end{pmatrix}.$$

leading to the following values:

$$\begin{aligned} c_1(0) &= \frac{i}{2\omega\tau_n}\left(g_{11}g_{20} - 2|g_{11}|^2 - \frac{|g_{02}|^2}{3}\right) + \frac{g_{21}}{2}, \qquad \mu_2 = -\frac{\mathrm{Re}\{c_1(0)\}}{\mathrm{Re}\{\lambda'(\tau_n)\}}, \\ \beta_2 &= 2\mathrm{Re}\{c_1(0)\}, \qquad T_2 = -\frac{\mathrm{Im}\{c_1(0)\} + \mu_2\mathrm{Im}\{\lambda'(\tau_n)\}}{\omega\tau_n}. \end{aligned}$$

The above discussion is summarised in the following Theorem.

Theorem 3.1. *(i) The direction of the Hopf bifurcation is determined by the sign of μ_2: if $\mu_2 > 0$ ($\mu_2 < 0$), then the Hopf bifurcation is supercritical (subcritical);*

(ii) the stability of the bifurcating periodic solutions is determined by the sign of β_2: if $\beta_2 < 0$ ($\beta_2 > 0$), then the bifurcating periodic solutions are stable (unstable);

(iii) the period of the bifurcating periodic solutions is determined by the sign of T_2: if $T_2 > 0$ ($T_2 < 0$), then the bifurcating periodic solutions increase (decrease).

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4. Numerical Simulations

Some numerical simulations were undertaken to support the theoretical analysis in Sections 2 and 3. In view of the assumption (2.1) and the conditions in Theorem 2.1, the coefficients of the system (1.3) chosen were

$$r = 5.5\,, \quad k = 1\,, \quad a = 2\,, \quad d = 1\,, \quad p = 1\,, \quad c = 1\,, \quad v = 3\,,$$

when the system (1.3) becomes

$$\begin{cases} \dot{x}(t) = x(t)\left(5.5 - x(t-\tau) - \dfrac{y(t)}{\sqrt{x(t)}} - E(t)\right), \\ \dot{y}(t) = y(t)\left(-2 + \sqrt{x(t)}\right), \\ 0 = E(t)(x(t)-1) - 3\,. \end{cases} \tag{4.1}$$

The system (4.1) has a positive equilibrium point $X_0 = (x_0, y_0, E_0) = (4, 1, 1)$, and from Eq. (2.10) the values $\omega^+ = 3.8047$ and $\omega^- = 0.1314$ were obtained using Matlab 7.0. Substituting $\omega^\pm$ into Eq. (2.11) produces $\tau_0^+ = 0.3059$ and $\tau_0^- = 8.8571$, and according to Theorem 2.1 the positive equilibrium point X_0 of the system (4.1) is asymptotically stable when $\tau \in [0, \tau_0^+) = [0, 0.3059)$ and unstable when $\tau \in (\tau_0^+, \tau_0^-) = (0.3059, 8.8571)$, and Hopf bifurcation occurs at the critical value $\tau = \tau_0^+$.

Matlab 7.0 also produces the values $c_1(0) = 0.1537 - 2.6838i$, $\lambda'(\tau_0^+) = 9.2360 - 7.9150i$ such that $\mu_2 = -0.0166 < 0$, $\beta_2 = 0.3074 > 0$ and $T_2 = 2.1931 > 0$. From Theorem 3.1, the Hopf bifurcation of system (4.1) occurring at the critical value $\tau = \tau_0^+$ is subcritical, and the bifurcating periodic solutions that exist when τ crosses τ_0^+ to the left are unstable and increase.

As Theorems 2.1 and 3.1 state, the positive equilibrium point X_0 of system (4.1) is asymptotically stable when $\tau = 0.305 < \tau_0^+$, as illustrated by the computer simulations in Fig. 1. Thus periodic solutions occur from the positive equilibrium point X_0 when $\tau = 0.3058 < \tau_0^+$, as shown in Fig. 2, but bifurcating periodic solutions are unstable and increase when $\tau = 0.306 > \tau_0^+$ as shown in Fig. 3 and the positive equilibrium point X_0 is unstable when $\tau = 0.31 > \tau_0^+$ as shown in Fig. 4.

5. Discussion

A modified predator-prey system with a time delay acting as a bifurcation parameter has been considered, showing the effect of a gestation delay of the prey on the stability of the model system. It is well known that a time delay affects the dynamical behaviour — and the local stability analysis discussed in this article reveals that the time delay is responsible for a stability switch of the model system, and that a Hopf bifurcation occurs as the time delay increases beyond a certain threshold. Furthermore, formulae that determine the direction of the bifurcation and the stability of the bifurcating periodic solutions when $\tau > 0$ are established. From the viewpoint of biology, both species may coexist in an oscillatory mode when the bifurcating periodic solutions are stable.

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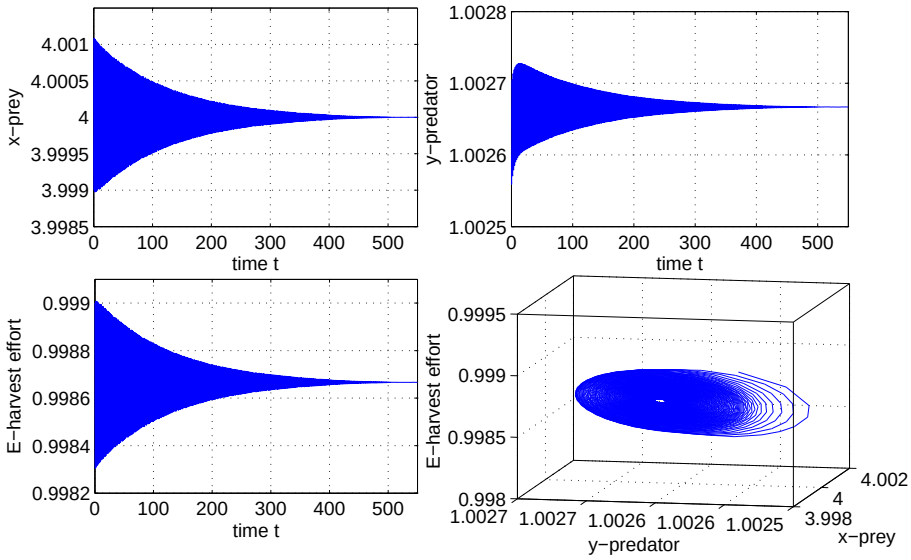


Figure 1: The positive equilibrium point X_0 of the system (4.1) is locally asymptotically stable when $\tau = 0.305 < \tau_0^+$ and the initial conditions are $x_0 = 3.999$, $y_0 = 1.0026$ and $E_0 = 0.999$.

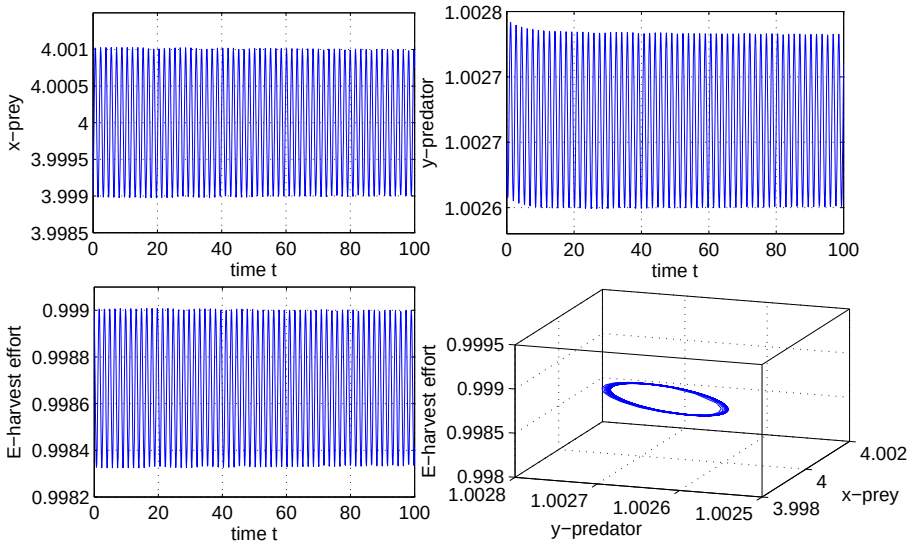


Figure 2: The periodic solutions bifurcating from the positive equilibrium point X_0 of the system (4.1) when $\tau = 0.3058 < \tau_0^+$ and the initial conditions are $x_0 = 3.999$, $y_0 = 1.00265$ and $E_0 = 0.999$.

The main focus is on the study of local Hopf bifurcations in this article. In Ref. [19], not only local Hopf bifurcations but also the global continuation of local Hopf bifurcations for the delayed predator-prey system were investigated, and here the direction and stability of the global Hopf bifurcation for the system (1.3) has been explored. Whether pr not the

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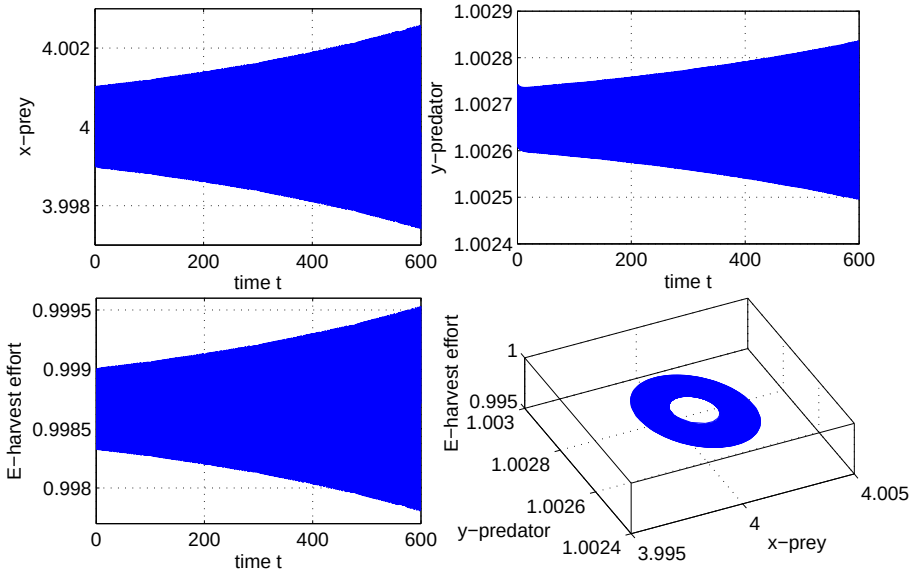


Figure 3: The bifurcating periodic solutions are unstable and increase when $\tau = 0.306 > \tau_0^+$ and the initial conditions are $x_0 = 3.999$, $y_0 = 1.00265$ and $E_0 = 0.999$.

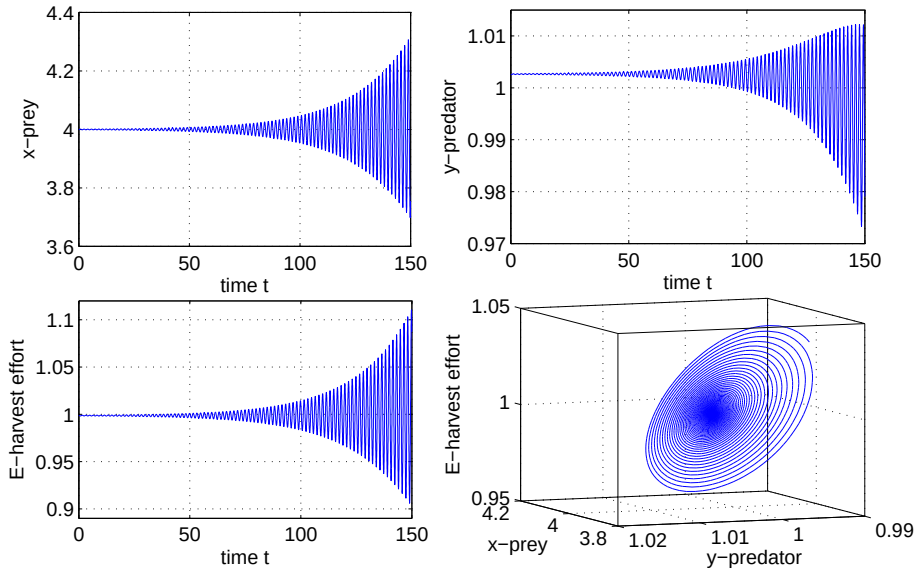


Figure 4: The positive equilibrium point X_0 of the system (4.1) is unstable when $\tau = 0.31 > \tau_0^+$ and the initial conditions are $x_0 = 3.999$, $y_0 = 1.0026$ and $E_0 = 0.999$.

predator and prey species can still coexist in an oscillatory mode for large values of the time delay is of interest.

Wang [18] has suggested that the introduction of stage structure into the predator-

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prey system may cause periodic oscillations of the populations, and Liu *et al.* [13] have also pointed out that stage structure is an important factor affecting the permanence or extinction of population. Thus including stage structure in our predator-prey system with time delay is an issue for future consideration.

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