Bifurcation dynamics in a modified Leslie type predator-prey model with predator harvesting and delay

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Abstract. In this article, the bifurcation behaviors of a modified Leslie type predator-prey model with harvesting and gestation delay of predator are discussed. The model takes the form of delayed differential-algebra equations. First, the existence of Hopf bifurcations in the model is studied by choosing the delay as a bifurcation parameter. It reveals that a sequence of stability switches and Hopf bifurcations can occur as the delay increases monotonously from zero. Next, the direction of the Hopf bifurcations and the stability of the bifurcating periodic orbits are also investigated. Moreover, we present several numerical simulations to support the theoretical results with the help of Matlab software. Lastly, the significances of our findings are discussed.

Keywords: predator-prey, differential-algebra, delay, bifurcations, periodic orbits.
MSC 2020: 92D25, 34A09, 37G05.

1. Introduction

Recently, there is a wide-range of interest in analysis and modelling of population interactions, since many complex dynamical behaviors have been discovered in this area, such as coexistence, instability, extinction, persistence, periodic oscillations, various bifurcations, chaos, etc. — cf. Refs. [11, 34, 5, 25, 15, 27, 56, 53, 37, 38, 1, 52, 18, 39, 41, 30, 55, 6, 45, 28, 42]. In this paper, we aim to investigate the bifurcation dynamics of a delayed predator-prey model with predator harvesting, which will be modelled by a differential-algebra system with delay in the following. The basic model that we consider is the famous Leslie's population model [34, 5, 27], which is given by

$$
\begin{cases} \dot{x}(t) = x(t)\left(r_1 - ay(t)\right), \\ \dot{y}(t) = y(t)\left(r_2 - \dfrac{b\,y(t)}{x(t)}\right), \end{cases} \tag{1.1}
$$

where $x(t)$ and $y(t)$ represent the respective population densities of prey and predator at time t; the parameters r_1, a, r_2, and b are all positive constants, where $r_1 > 0$ is the intrinsic growth rate of prey, a is the catch rate of predator, r_2 is the intrinsic growth rate of predator, and b is the conversion rate of consumed preys into the newborns of predator.

It is well known that the dynamical behaviors of population models depend on the current conditions, as well as the past information. In order to reflect the population dynamics depending on the past history, time delay of one type or another is often incorporated into population models due to gestation period, maturation time, or other reasons [25, 15]. Just as Kuang [25] pointed out: any model of species dynamics and interactions without delay is an approximation at best. Therefore, the introduction of time delay into population models would be more realistic to model population interactions. Moreover, it is notable that time delay has complicated impacts on the dynamics of a system, which can induce various interesting dynamical behaviors, for instances, stability switch, limit cycle, oscillations, Neimark-Sacker bifurcation, Takens-Bogdanov bifurcation, chaotic behavior and so on [25, 15, 1, 52, 51, 54, 50, 49, 46, 29, 42, 17]. Time delay due to gestation is a common situation, since normally the consumption of preys by the predator species throughout its past history governs the present birth rate of predator. Therefore, we introduce the gestation delay τ of predator population to model (1.1) — viz.

$$\begin{cases} \dot{x}(t) = x(t)\left(r_1 - ay(t)\right), \\ \dot{y}(t) = y(t)\left(r_2 - \dfrac{b\,y(t-\tau)}{x(t)}\right). \end{cases} \tag{1.2}$$

Furthermore, we consider human harvesting effort $E(t)$ on predator population for model (1.2), since people usually harvest predators to avoid the extinction of prey species. In fact, biological resources are often harvested to satisfy the material life of humans [9, 8]. Consequently, we have

$$\begin{cases} \dot{x}(t) = x(t)\left(r_1 - ay(t)\right), \\ \dot{y}(t) = y(t)\left(r_2 - \dfrac{b\,y(t-\tau)}{x(t)} - E(t)\right). \end{cases} \tag{1.3}$$

In the light of Refs[9, 8, 31, 12], we can study the harvesting effort $E(t)$ from an economic viewpoint. Let $P(t)$ and $C(t)$ denote the unit selling price of harvested predators, and the unit harvesting cost at time t, respectively. The number of harvested predators can be expressed as $E(t)y(t)$. And we assume that the market has a constant demand for the harvested predators, which means that the catches can always be sold out in the market. Note that the unit selling price $P(t)$ is inversely associated with the market supply $E(t)y(t)$, and the unit harvesting cost $C(t)$ is reversely relative to the population density of predator species $y(t)$. Hence, we take $P(t)$ and $C(t)$ as $p/(l + E(t)y(t))$ and $c/y(t)$ respectively, where p, l and c are positive parameters, p/l can be regarded as the maximum unit selling price. Subsequently,

$$\text{Total Revenue} = P(t)E(t)y(t) = \frac{pE(t)y(t)}{l+E(t)y(t)}, \text{Total Cost} = C(t)E(t)y(t) = cE(t).$$

Thus, the net economic revenue v produced by harvesting can be written as

$$E(t)y(t)\left(\frac{p}{l + E(t)y(t)} - \frac{c}{y(t)}\right) = v. \tag{1.4}$$

Combining (1.3) and (1.4), we can establish the following delayed differential-algebra predator-prey model with predator harvesting:

$$
\begin{cases}
\dot{x}(t) = x(t)\left(r_1 - ay(t)\right), \\
\dot{y}(t) = y(t)\left(r_2 - \dfrac{b\,y(t-\tau)}{x(t)} - E(t)\right), \\
\quad 0 = E(t)y(t)\left(\dfrac{p}{l+E(t)y(t)} - \dfrac{c}{y(t)}\right) - v.
\end{cases}
\tag{1.5}
$$

The initial values of system (1.5) are given by

$$
x(0) > 0, \;\; y(\theta) > 0, \;\; \theta \in [\,-\tau,\, 0\,], \;\; E(0) > 0,
\tag{1.6}
$$

where $y(\theta) \in C([\,-\tau,\, 0\,], \mathrm{R})$ is a continuous bounded function.

In existing literature, most of the predator-prey models with harvesting are modelled by systems of differential equations [37, 38, 1, 52, 18, 39, 41, 30, 43, 33], which have not considered human harvesting from economic perspective. In contrast to such models, our modified Leslie's predator-prey model (1.5) is described by a system of delayed differential-algebra equations due to the economic revenue from predator harvesting is introduced. It should be noted that the analysis of differential-algebra system is more difficult than the corresponding system of differential equations, and normally differential-algebra systems possess more complicated dynamical behaviours compared with the systems of differential equations [40, 22, 23, 24, 3]. In the research of the dynamic behaviors of related models, Refs[53, 55, 6, 45, 28, 36] have studied the issues of the classification of fixed points, Neimark-Sacker bifurcation, invariant closed curve, Flip bifurcation, period windows, maximum Lyapunov exponents, phase portraits, saddle-node bifurcation, etc. However, the formulae for determining the properties of possible Hopf bifurcations in the delayed differential-algebra predator-prey models have not yet appeared. By applying differential-algebra system theory and center manifold argument, we investigate the properties such as stability, direction, and period of Hopf bifurcations in the delayed differential-algebra predator-prey model (1.5) where the delay is chosen as a bifurcation parameter. In some senses, our study supplements and extends the research work of the articles [53, 37, 38, 1, 52, 18, 39, 41, 30, 55, 6, 45, 28, 36, 43, 33].

We organize the rest of this paper as follows. Section 2 is devoted to analyze the stability of equilibrium point and existence of Hopf bifurcations in model (1.5) with gestation delay. Continue with Section 2, Section 3 deals with the stability and direction of the Hopf bifurcations by applying center manifold argument. Some numerical simulations are presented in Section 4 to make the derived findings more complete. Finally, in Section 5 we explain the significances of our results.

2. Stability analysis

In this section, we analyze the asymptotic stability of the delayed predator-prey model (1.5), as well as the occurrence conditions of Hopf bifurcations in the model. At first, we prove the positiveness of the solutions of model (1.5).

Lemma 2.1. *The trajectories of model* (1.5) *with initial values* (1.6) *and* $v > 0$ *stay in* $\mathrm{R}_+^3 = \{(x(t), y(t), E(t)) \mid x(t) > 0,\, y(t) > 0,\, E(t) > 0\}$, *for* $\forall\, t > 0$.

Proof. In view of model (1.5), we have

$$\frac{\mathrm{d}x(t)}{x(t)} = (r_1 - ay(t))\ \mathrm{d}t.$$

Due to the initial value $x(0) > 0$, by integrating above equation in the interval $[0, t]$, we obtain

$$x(t) = x(0)\ \exp\left\{\int_0^t (r_1 - ay(s))\ \mathrm{d}s\right\} > 0, \ \text{ for } \forall\, t > 0.$$

Similarly, we can get

$$y(t) = y(0)\ \exp\left\{\int_0^t \left(r_2 - \frac{b\,y(s-\tau)}{x(s)} - E(s)\right)\ \mathrm{d}s\right\} > 0, \ \text{ for } \forall\, t > 0.$$

Clearly, harvesting effort $E(t)$ is also positive for $\forall\, t > 0$, since the harvesting profit $v > 0$ here. $\square$

Lemma 2.1 suggests that only the positive equilibrium point of model (1.5) is required to be considered. If $X_0 := (x_0, y_0, E_0)^T$ is an equilibrium point of model (1.5), then we have

$$\begin{cases} r_1 - ay_0 = 0, \\ r_2 - b\dfrac{y_0}{x_0} - E_0 = 0, \\ \dfrac{pE_0y_0}{l + E_0y_0} - cE_0 - v = 0. \end{cases}$$

By solving the set of linear equations, model (1.5) has an equilibrium point $X_0 = (x_0, y_0, E_0)^T = (by_0/(r_2 - E_0), r_1/a, E_0)^T$, where $E_0 = \big\{(py_0 - vy_0 - cl) \pm \sqrt{\Delta}\,\big\}/2cy_0$, and $\Delta = (cl + vy_0 - py_0)^2 - 4clvy_0$.

To make such an equilibrium point X_0 is positive, we suppose that

$$r_2 > E_0,\ py_0 > cl + vy_0,\ (cl + vy_0 - py_0)^2 \geq 4clvy_0. \tag{2.1}$$

According to the theory of differential-algebra system [22, 23, 24], model (1.5) can be locally equivalent to the following constrained system near the point X_0:

$$
\begin{cases}
\dot{x}(t) = x(t)\left(r_1 - ay(t)\right), \\
\dot{y}(t) = y(t)\left(r_2 - \dfrac{b\,y(t-\tau)}{x(t)} - E(t)\right), \\
\dot{E}(t) = f_3(x(t), y(t), E(t)), \\
\quad 0 = E(t)y(t)\left(\dfrac{p}{l+E(t)y(t)} - \dfrac{c}{y(t)}\right) - v,
\end{cases}
\tag{2.2}
$$

where f_3 is a continuously differentiable function and satisfies $f_3(X_0) = 0$. The explicit expression of f_3 is no need to be defined, which can be seen from Eq. (2.11) below.

For the convenience of discussion, we denote

$$
\begin{aligned}
f(X) &= \begin{pmatrix} f_1(X) \\ f_2(X) \\ f_3(X) \end{pmatrix} = \begin{pmatrix} x(t)\left(r_1 - ay(t)\right) \\ y(t)\left(r_2 - \dfrac{b\,y(t-\tau)}{x(t)} - E(t)\right) \\ f_3(x(t), y(t), E(t)) \end{pmatrix}, \\
g(X) &= E(t)y(t)\left(\dfrac{p}{l+E(t)y(t)} - \dfrac{c}{y(t)}\right) - v, \quad X = (x(t), y(t), E(t))^T.
\end{aligned}
\tag{2.3}
$$

Thus, system (2.2) can be written as

$$
\begin{cases}
\dot{X} = f(X), \\
0 = g(X).
\end{cases}
\tag{2.4}
$$

In the light of Refs. [2, 7], we can consider the following parameterisation ψ for system (2.4):

$$
X = \psi(Y) = X_0 + U_0 Y + V_0 h(Y),
\tag{2.5}
$$

$$
g(\psi(Y)) = 0,
\tag{2.6}
$$

where $Y = (y_1, y_2)^T \in \mathrm{R}^2$, $U_0 = \begin{pmatrix} I_2 \\ 0 \end{pmatrix}$, I_2 denotes an identity matrix of dimension 2×2, $V_0 = \begin{pmatrix} 0 \\ 0 \\ 1 \end{pmatrix}$, $h : \mathrm{R}^2 \to \mathrm{R}$ is a smooth mapping. Then substituting $X = \psi(Y)$ into system (2.4) yields

$$
D_Y \psi(Y) \dot{Y} = f(\psi(Y)),
\tag{2.7}
$$

Differentiating Eq. (2.5) regarding Y, and then left multiplying U_0^T to the differentiated equation, which lead to

$$
U_0^T D_Y \psi(Y) = I_2.
\tag{2.8}
$$

Differentiating Eq. (2.6) regarding Y, we derive

$$D_X g(X) D_Y \psi(Y) = 0. \tag{2.9}$$

By Eqs. (2.7)-(2.9), we get

$$\begin{pmatrix} D_X g(X) \\ U_0^T \end{pmatrix}^{-1} \begin{pmatrix} 0 \\ I_2 \end{pmatrix} \dot{Y}(t) = f(\psi(Y)). \tag{2.10}$$

Eqs. (2.7), (2.9) and (2.10) suggest that (2.4) can be locally equivalent to

$$\dot{Y} = U_0^T f(\psi(Y)). \tag{2.11}$$

From the parameterised system (2.11), we can obtain that the Taylor expansions of the parameterised system of system (2.2) at X_0 takes the form

$$\dot{Y} = U_0^T D_X f(X_0) D_Y \psi(0) Y + o(|Y|), \tag{2.12}$$

where D denotes the differential operator, and $D_X f(X)$ represents the Jacobian matrix of function $f(X)$ regarding X. It is notable that the equilibrium point X_0 of model (1.5) corresponds to the equilibrium point $Y = 0$ of parameterised system (2.12).

Next, we calculate the Jacobian matrix $\bar{\mathrm{P}}$ of model (1.5) with $\tau > 0$ at its positive equilibrium point X_0. From the formula (2.12), we can obtain the Jacobian matrix $\bar{\mathrm{P}}$, which takes the form

$$\bar{\mathrm{P}} = \begin{pmatrix} 0 & -ax_0 \\ \dfrac{by_0^2}{x_0^2} & -\dfrac{by_0}{x_0} e^{-\lambda\tau} + \dfrac{plE_0 y_0}{ply_0 - c(l + E_0 y_0)^2} \end{pmatrix}.$$

Hence, the characteristic equation of Jacobi matrix $\bar{\mathrm{P}}$ is

$$\lambda^2 + \left(\frac{by_0}{x_0} e^{-\lambda\tau} - \frac{plE_0 y_0}{ply_0 - c(l + E_0 y_0)^2} \right) \lambda + \frac{aby_0^2}{x_0} = 0. \tag{2.13}$$

To investigate the local asymptotic stability of equilibrium point X_0, in what follows, we shall analyze the roots of characteristic equation (2.13).

For $\tau > 0$, we assume that $\pm i\omega$ (ω is a positive real number) are a pair of purely imaginary roots of Eq. (2.13), then we have the following equation:

$$-\omega^2 + \left[\frac{by_0}{x_0} (\cos\omega\tau - i \sin\omega\tau) - \frac{plE_0 y_0}{ply_0 - c(l + E_0 y_0)^2} \right] i\omega + \frac{aby_0^2}{x_0} = 0.$$

Separating the real and imaginary parts of the above equation, we get

$$-\omega^2 + \frac{by_0}{x_0} \omega \sin\omega\tau + \frac{aby_0^2}{x_0} + i \left[\frac{by_0}{x_0} \omega \cos\omega\tau - \frac{plE_0 y_0 \omega}{ply_0 - c(l + E_0 y_0)^2} \right] = 0,$$

which gives

$$\sin\omega\tau = \frac{x_0\omega}{by_0} - \frac{ay_0}{\omega}, \tag{2.14}$$

$$\cos\omega\tau = \frac{plx_0E_0}{b(ply_0 - c(l+E_0y_0)^2)}. \tag{2.15}$$

Squaring and adding Eqs. (2.14) and (2.15), we have

$$\omega^4 + \left[\frac{p^2l^2E_0^2y_0^2}{(ply_0 - c(l+E_0y_0)^2)^2} - \frac{b^2y_0^2}{x_0^2} - \frac{2aby_0^2}{x_0}\right]\omega^2 + \frac{a^2b^2y_0^4}{x_0^2} = 0. \tag{2.16}$$

Lemma 2.2. *For model* (1.5) *with* $\tau > 0$,

(*i*) *if*

$$\frac{by_0}{x_0} > \frac{plE_0y_0}{ply_0 - c(l+E_0y_0)^2}$$

and

$$\frac{p^2l^2E_0^2y_0^2}{(ply_0 - c(l+E_0y_0)^2)^2} > \frac{b^2y_0^2}{x_0^2} + \frac{2aby_0^2}{x_0},$$

then all the roots of Eq. (2.13) *have negative real parts;*

(*ii*) *if*

$$\left[\frac{p^2l^2E_0^2y_0^2}{(ply_0 - c(l+E_0y_0)^2)^2} - \frac{b^2y_0^2}{x_0^2} - \frac{2aby_0^2}{x_0}\right]^2 > \frac{4a^2b^2y_0^4}{x_0^2}$$

and

$$\frac{p^2l^2E_0^2y_0^2}{(ply_0 - c(l+E_0y_0)^2)^2} < \frac{b^2y_0^2}{x_0^2} + \frac{2aby_0^2}{x_0},$$

then Eq. (2.16) *has two positive roots* ω^+ *and* ω^-. *Substituting* $\omega^\pm$ *into* Eq. (2.15), *we obtain the values of time delay* τ *corresponding to the pair of purely imaginary roots* $\pm i\omega$:

$$\tau_m^\pm = \frac{1}{\omega^\pm}\arccos\left(\frac{plx_0E_0}{b(ply_0 - c(l+E_0y_0)^2)}\right) + \frac{2n\pi}{\omega^\pm}, \quad m = 0, 1, 2, \cdots.$$

Proof. From Eq. (2.16), we know that if

$$\frac{p^2l^2E_0^2y_0^2}{(ply_0 - c(l+E_0y_0)^2)^2} > \frac{b^2y_0^2}{x_0^2} + \frac{2aby_0^2}{x_0},$$

then Eq. (2.16) doesn't have positive roots. Thus, Eq. (2.13) with $\tau > 0$ doesn't have purely imaginary roots. Further, if we suppose that

$$\frac{by_0}{x_0} > \frac{plE_0y_0}{ply_0 - c(l+E_0y_0)^2},$$

then we can derive from Routh-Hurwitz stability criteria [34, 5, 16] that all the roots of the characteristic equation (2.13) with $\tau = 0$ have negative real parts. Consequently, Eq. (2.13) with $\tau > 0$ also have negative real parts according to Rouche's theorem [32, 47, 48, 19].

For the second case (ii), we have

$$\left[\frac{p^2l^2E_0^2y_0^2}{(ply_0 - c(l + E_0y_0)^2)^2} - \frac{b^2y_0^2}{x_0^2} - \frac{2aby_0^2}{x_0}\right]^2 - \frac{4a^2b^2y_0^4}{x_0^2} > 0.$$

Add that to

$$\frac{p^2l^2E_0^2y_0^2}{(ply_0 - c(l + E_0y_0)^2)^2} < \frac{b^2y_0^2}{x_0^2} + \frac{2aby_0^2}{x_0},$$

then it is easy to show that Eq. (2.16) has two positive roots:

$$\begin{aligned}\omega^{\pm} = \Bigg\{ \frac{1}{2}\Bigg[& \frac{b^2y_0^2}{x_0^2} + \frac{2aby_0^2}{x_0} - \frac{p^2l^2E_0^2y_0^2}{(ply_0 - c(l + E_0y_0)^2)^2} \\ & \pm \sqrt{\left[\frac{p^2l^2E_0^2y_0^2}{(ply_0 - c(l + E_0y_0)^2)^2} - \frac{b^2y_0^2}{x_0^2} - \frac{2aby_0^2}{x_0}\right]^2 - \frac{4a^2b^2y_0^4}{x_0^2}}\Bigg]\Bigg\}^{\frac{1}{2}}.\end{aligned}$$

Substituting $\omega^{\pm}$ into (2.15) and solving for τ, then the proof is completed. □

Further, we differentiate Eq. (2.13) with respect to τ, it follows that

$$2\lambda\frac{\mathrm{d}\lambda}{\mathrm{d}\tau} - \frac{plE_0y_0}{ply_0 - c(l + E_0y_0)^2}\frac{\mathrm{d}\lambda}{\mathrm{d}\tau} + \frac{by_0}{x_0}e^{-\lambda\tau}\frac{\mathrm{d}\lambda}{\mathrm{d}\tau} + \frac{by_0}{x_0}\lambda e^{-\lambda\tau}\left(-\lambda - \tau\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right) = 0.$$

As a consequence, we get

$$\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)^{-1} = \frac{2\lambda e^{\lambda\tau}x_0 - \dfrac{plx_0y_0E_0}{ply_0 - c(l + E_0y_0)^2}e^{\lambda\tau} + by_0(1 - \lambda\tau)}{by_0\lambda^2}.$$

Consequently, $\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)^{-1}|_{\lambda = i\omega}$ equals

$$\begin{aligned}&\frac{2i\omega(\cos\omega\tau + i\sin\omega\tau)x_0 - \dfrac{plx_0y_0E_0}{ply_0 - c(l + E_0y_0)^2}(\cos\omega\tau + i\sin\omega\tau) + by_0(1 - \tau\omega i)}{-by_0\omega^2} \\ &= \frac{2x_0}{by_0\omega}\sin\omega\tau + \frac{plx_0E_0}{b\omega^2(ply_0 - c(l + E_0y_0)^2)}\cos\omega\tau - \frac{1}{\omega^2} \\ &\quad + i\left[\frac{plx_0E_0}{b\omega^2(ply_0 - c(l + E_0y_0)^2)}\sin\omega\tau - \frac{2x_0}{b\omega y_0}\cos\omega\tau + \frac{\tau}{\omega}\right].\end{aligned}$$

Associated with Eqs. (2.14) and (2.15), we have

$$\begin{aligned}\mathrm{Re}\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)^{-1}\Bigg|_{\lambda=i\omega} &= \frac{2x_0}{by_0\omega}\left(\frac{x_0\omega}{by_0}-\frac{ay_0}{\omega}\right)\\ &\quad+\frac{plx_0E_0}{b\omega^2(ply_0-c(l+E_0y_0)^2)}\left(\frac{plx_0E_0}{b(ply_0-c(l+E_0y_0)^2)}\right)-\frac{1}{\omega^2}\\ &=\frac{x_0^2}{b^2\omega^2y_0^2}\left[2\omega^2-\frac{2aby_0^2}{x_0}-\frac{b^2y_0^2}{x_0^2}+\frac{p^2l^2E_0^2y_0^2}{(ply_0-c(l+E_0y_0)^2)^2}\right].\end{aligned}$$

Accordingly,

$$\begin{aligned}\mathrm{sign}\left\{\mathrm{Re}\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)\right\}_{\lambda=i\omega} &= \mathrm{sign}\left\{\mathrm{Re}\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)^{-1}\right\}_{\lambda=i\omega}\\ =\mathrm{sign}\left\{2\omega^2-\frac{2aby_0^2}{x_0}-\frac{b^2y_0^2}{x_0^2}+\frac{p^2l^2E_0^2y_0^2}{(ply_0-c(l+E_0y_0)^2)^2}\right\}.\end{aligned}$$

Hence, the following transversality conditions hold:

$$\mathrm{sign}\left\{\mathrm{Re}\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)\right\}_{\tau=\tau_m^+,\ \omega=\omega^+}>0,\quad \mathrm{sign}\left\{\mathrm{Re}\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)\right\}_{\tau=\tau_m^-,\ \omega=\omega^-}<0. \tag{2.17}$$

Combining (2.17) with Lemma 2.2, we can derive the following results:

Theorem 2.1. *For model* (1.5) *with* $\tau>0$, *suppose that*

$$\frac{by_0}{x_0}>\frac{plE_0y_0}{ply_0-c(l+E_0y_0)^2},$$

(*i*) *if*

$$\frac{p^2l^2E_0^2y_0^2}{(ply_0-c(l+E_0y_0)^2)^2}>\frac{b^2y_0^2}{x_0^2}+\frac{2aby_0^2}{x_0},$$

then the equilibrium point X_0 *is locally asymptotically stable due to all the roots of* Eq. (2.13) *have negative real parts*;

(*ii*) *if*

$$\left[\frac{p^2l^2E_0^2y_0^2}{(ply_0-c(l+E_0y_0)^2)^2}-\frac{b^2y_0^2}{x_0^2}-\frac{2aby_0^2}{x_0}\right]^2>\frac{4a^2b^2y_0^4}{x_0^2}$$

and

$$\frac{p^2l^2E_0^2y_0^2}{(ply_0-c(l+E_0y_0)^2)^2}<\frac{b^2y_0^2}{x_0^2}+\frac{2aby_0^2}{x_0},$$

then there exists a positive integer N, *such that the equilibrium point* X_0 *is locally asymptotically stable when the delay* $\tau\in[0,\tau_0^+)\cup(\tau_0^-,\tau_1^+)\cup(\tau_1^-,\tau_2^+)\cup\cdots\cup(\tau_{N-1}^-,\tau_N^+)$, *and it is unstable when the delay* $\tau\in(\tau_0^+,\tau_0^-)\cup(\tau_1^+,\tau_1^-)\cup(\tau_2^+,\tau_2^-)\cup\cdots\cup(\tau_{N-1}^+,\tau_{N-1}^-)\cup(\tau_N^+,+\infty)$.

Proof. Since the proof of Theorem 2.1 is similar to the Hopf bifurcation theorems for functional differential equations in [19, 10], so it is omitted here. □

Remark 2.1. Theorem 2.1 shows that stability switches would occur at the equilibrium point X_0 when the delay τ takes the critical values τ_0^+, τ_0^-, τ_1^+, $\cdots$, τ_{N-1}^-, τ_N^+. This means that, around these critical values, Hopf bifurcations can take place in model (1.5) with $\tau > 0$.

3. Stability and direction of Hopf bifurcations

In this section, we further study the properties of the Hopf bifurcations appearing in the previous section, such as the direction, stability and period of the bifurcations. For these issues, the research tool that we will use is the center manifold theorem due to Hassard, Kazarinoff and Wan [21].

Without loss of generality, we use τ_n to represent any one of the critical values in Theorem 2.1, and in the following discussion we always suppose that a Hopf bifurcation can occur in model (1.5) when $\tau = \tau_n$. Besides, $i\omega$ is assumed to be the purely imaginary root of Eq. (2.13) corresponding to τ_n.

If we let $\mu = \tau - \tau_n$, $y_1(t) = x(\tau t) - x_0$, $y_2(t) = y(\tau t) - y_0$, then the second order Taylor expansions of parameterised system (2.12) with $\tau > 0$ can be rewritten as the following functional differential equation in the phase space $C([-1, 0], \mathrm{R}^2)$:

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

where $Y(t) = (y_1(t), y_2(t))^T$, $Y_t = Y(t + \theta) = (y_1(t + \theta), y_2(t + \theta))$, $\theta \in [-1, 0]$.

For $\Phi(\theta) = (\Phi_1(\theta), \Phi_2(\theta)) \in C([-1, 0], \mathrm{R}^2)$, we define

$$L_\mu\Phi = (\tau_n + \mu)\begin{pmatrix} 0 & -ax_0 \\ \dfrac{by_0^2}{x_0^2} & \dfrac{plE_0y_0}{ply_0 - c(l + E_0y_0)^2} \end{pmatrix}\Phi^T(0) + (\tau_n + \mu)\begin{pmatrix} 0 & 0 \\ 0 & -\dfrac{by_0}{x_0} \end{pmatrix}$$
$$\times\, \Phi^T(-1), \text{ and } F(\mu, \Phi(\theta)) = (\tau_n + \mu)\begin{pmatrix} F_{11} \\ F_{22} \end{pmatrix},$$

where $F_{11} = -a\Phi_1(0)\Phi_2(0)$,

$$\begin{aligned} F_{22} = &-\frac{by_0^2}{x_0^3}\Phi_1^2(0) + \frac{by_0}{x_0^2}\Phi_1(0)\Phi_2(0) + \frac{by_0}{x_0^2}\Phi_1(0) \times \Phi_2(-1) - \frac{b}{x_0}\Phi_2(0)\Phi_2(-1) \\ &+ \left(\frac{plE_0}{ply_0 - c(l + E_0y_0)^2} + \frac{plE_0y_0[cE_0(l + E_0y_0) - pl]}{[ply_0 - c(l + E_0y_0)^2]^2}\right. \\ &\left.- \frac{p^2cl^2E_0^2y_0^2(l + E_0y_0)}{[ply_0 - c(l + E_0y_0)^2]^3}\right)\Phi_2^2(0) + \cdots . \end{aligned}$$

It is easy to verify that L_μ: $C([-1, 0], \mathrm{R}^2) \to \mathrm{R}^2$ is a continuous linear operator mapping. In the light of Riesz representation theorem in Ref[35], there exists a

2×2 matrix function $\eta(\theta,\mu)$ with elements of bounded variation for $\theta\in[-1,0]$, such that

$$L_\mu\Phi=\int_{-1}^{0}[\mathrm{d}\eta(\theta,\mu)]\,\Phi(\theta),\ \text{for }\Phi(\theta)\in C([-1,0],\mathrm{R}^2). \tag{3.2}$$

As a matter of fact, if we choose $\eta(\theta,\mu)$ as

$$(\tau_n+\mu)\begin{pmatrix}0 & -ax_0\\ \dfrac{by_0^2}{x_0^2} & \dfrac{plE_0y_0}{ply_0-c(l+E_0y_0)^2}\end{pmatrix}\delta(\theta)+(\tau_n+\mu)\begin{pmatrix}0 & 0\\ 0 & -\dfrac{by_0}{x_0}\end{pmatrix}\delta(\theta+1),$$

where $\delta(\theta)$ denotes delta function, i.e., $\delta(\theta)=\begin{cases}0, & \theta\in[-1,0),\\ 1, & \theta=0\end{cases}$, then the equation (3.2) is satisfied.

For $\Phi(\theta)\in C^1([-1,0],\mathrm{R}^2)$, we define the operator $A(\mu)$:

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

and the operator $R(\mu)$:

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

then system (3.1) can be expressed as

$$\dot{Y}(t)=A(\mu)Y_t+R(\mu)Y_t. \tag{3.3}$$

From the theoretical analysis in the previous section, we can find that the operator $A(0)$ has a pair of simple purely imaginary eigenvalues $\pm i\omega\tau_n$.

For $\Psi(s)\in(C^1([-1,0],\mathrm{R}^2))^*=C^1([0,1],(\mathrm{R}^2)^*)$, the formal adjoint of operator A is defined as

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

under the bilinear pairing

$$<\Psi(s),\Phi(\theta)>=\bar{\Psi}(0)\Phi(0)-\int_{\theta=-1}^{0}\int_{\xi=0}^{\theta}\bar{\Psi}(\xi-\theta)\mathrm{d}\eta(\theta)\Phi(\xi)\mathrm{d}\xi, \tag{3.4}$$

where $\Psi(s)\in C^1([0,1],(\mathrm{R}^2)^*)$, $\Phi(\theta)\in C^1([-1,0],\mathrm{R}^2)$, $\eta(\theta)=\eta(\theta,0)$. Consequently, the operators $A(0)$ and A^* are a pair of adjoint operators [21], which means that the purely imaginary roots $\pm i\omega\tau_n$ of operator $A(0)$ are also the eigenvalues of operator A^*.

Next, we should calculate the eigenvectors of operators $A(0)$ and A^* associated with the eigenvalues $i\omega\tau_n$ and $-i\omega\tau_n$, respectively. We assume that the vectors $q(\theta) = (1, q_2)^T e^{i\omega\tau_n\theta}$ ($\theta \in [-1, 0]$) and $q^*(s) = \frac{1}{D}(q_2^*, 1)e^{i\omega\tau_n s}$ ($s \in [0, 1]$) respectively denote the eigenvectors of operators $A(0)$ and A^* corresponding to the eigenvalues $i\omega\tau_n$ and $-i\omega\tau_n$. And combining with the definitions of operators $A(0)$ and A^*, we can derive the expressions for q_2 and q_2^* through some simple calculations: $q_2 = -\frac{i\omega}{ax_0}$ and $q_2^* = \frac{i\omega}{ax_0} + \dfrac{plE_0y_0}{ax_0[ply_0 - c(l + E_0y_0)^2]} - \frac{by_0}{ax_0^2}e^{-i\omega}$.

Moreover, it follows from the bilinear form (3.4) that $< q^*(s), q(\theta) >$ equals

$$\frac{1}{\bar{D}}(\bar{q_2^*}, 1)(1, q_2)^T - \int_{\theta=-1}^{0}\int_{\xi=0}^{\theta}\frac{1}{\bar{D}}(\bar{q_2^*}, 1)e^{-i\omega\tau_n(\xi-\theta)}\mathrm{d}\eta(\theta)(1, q_2)^T e^{i\omega\tau_n\xi}\mathrm{d}\xi$$
$$=\frac{1}{\bar{D}}\left\{q_2+\bar{q_2^*}-\int_{\theta=-1}^{0}(\bar{q_2^*}, 1)\, e^{i\omega\tau_n\theta}\theta\mathrm{d}\eta(\theta)(1, q_2)^T\right\}=\frac{1}{\bar{D}}\left(q_2+\bar{q_2^*}-\frac{bq_2y_0\tau_n e^{-i\omega\tau_n}}{x_0}\right).$$

Hence, in order to guarantee $< q^*(s), q(\theta) >= 1$, we should choose $\bar{D} = q_2 + \bar{q_2^*} - (bq_2y_0\tau_n e^{-i\omega\tau_n}/x_0)$. And we can verify that $< q^*(s), \bar{q}(\theta) >= 0$.

In the remainder of this section, we employ the ideas and notations of Hassard et al.[21] to construct the coordinates describing the center manifold C_0 at the Hopf bifurcation value $\mu = 0$ — viz. $\tau = \tau_n$. Define

$$z(t) = < q^*, Y_t > \quad \text{and} \quad W(t, \theta) = Y_t - 2\mathrm{Re}\{z(t)q(\theta)\}, \tag{3.5}$$

then, on the center manifold C_0, one has

$$W(t, \theta) = W(z(t), \bar{z}(t), \theta) = W_{20}(\theta)\frac{z^2}{2} + W_{11}(\theta)z\bar{z} + W_{02}(\theta)\frac{\bar{z}^2}{2} + \cdots , \tag{3.6}$$

where z and $\bar{z}$ are the local coordinates for manifold C_0 in the directions of q and $\bar{q}^*$.

In view of Eqs. (3.5) and (3.6), we can see that $W(z(t), \bar{z}(t), \theta)$ is real if Y_t is real. For the real solution $Y_t \in C_0$, due to $\mu = 0$, then from Eqs. (3.3)-(3.6), we get

$$\dot{z}(t) = i\omega\tau_n z(t) + \bar{q}^*(0)F_0(z, \bar{z}) := i\omega\tau_n z(t) + g(z, \bar{z}), \tag{3.7}$$

where

$$g(z, \bar{z}) = g_{20}(\theta)\frac{z^2}{2} + g_{11}(\theta)z\bar{z} + g_{02}(\theta)\frac{\bar{z}^2}{2} + g_{21}(\theta)\frac{z^2\bar{z}}{2} + \cdots . \tag{3.8}$$

Furthermore, we can obtain from Eq. (3.7) that

$$g(z, \bar{z}) = \bar{q}^*(0)F_0(z, \bar{z}) = \frac{\tau_n}{\bar{D}}(1, \bar{q_2^*})\begin{pmatrix} F_{11}^0 \\ F_{22}^0 \end{pmatrix} = \frac{\tau_n}{\bar{D}}(F_{11}^0 + \bar{q_2^*}F_{22}^0), \tag{3.9}$$

where $F_{11}=-ay_{1t}(0)y_{2t}(0)$,

$$
\begin{aligned}
F_{22} = & -\frac{by_0^2}{x_0^3}y_{1t}^2(0)+\frac{by_0}{x_0^2}y_{1t}(0)y_{2t}(0)+\frac{by_0}{x_0^2}y_{1t}(0)\times y_{2t}(-1)-\frac{b}{x_0}y_{2t}(0)y_{2t}(-1)\\
& +\bigg(\frac{plE_0}{ply_0-c(l+E_0y_0)^2}+\frac{plE_0y_0[cE_0(l+E_0y_0)-pl]}{[ply_0-c(l+E_0y_0)^2]^2}\\
& -\frac{p^2cl^2E_0^2y_0^2(l+E_0y_0)}{[ply_0-c(l+E_0y_0)^2]^3}\bigg)y_{2t}^2(0)+\cdots .
\end{aligned}
$$

According to the literature [21], we have

$$
\begin{aligned}
y_{1t}(0) &= z+\bar{z}+W_{20}^{(1)}(0)\frac{z^2}{2}+W_{11}^{(1)}(0)z\bar{z}+W_{02}^{(1)}(0)\frac{\bar{z}^2}{2}+\cdots ,\\
y_{2t}(0) &= q_2z+\bar{q}_2\bar{z}+W_{20}^{(2)}(0)\frac{z^2}{2}+W_{11}^{(2)}(0)z\bar{z}+W_{02}^{(2)}(0)\frac{\bar{z}^2}{2}+\cdots ,\\
y_{1t}(-1) &= ze^{-i\omega\tau_n\theta}+\bar{z}e^{i\omega\tau_n\theta}+W_{20}^{(1)}(-1)\frac{z^2}{2}+W_{11}^{(1)}(-1)z\bar{z}\\
&\quad +W_{02}^{(1)}(-1)\frac{\bar{z}^2}{2}+\cdots ,\\
y_{2t}(-1) &= q_2ze^{-i\omega\tau_n\theta}+\bar{q}_2\bar{z}e^{i\omega\tau_n\theta}+W_{20}^{(2)}(-1)\frac{z^2}{2}+W_{11}^{(2)}(-1)z\bar{z}\\
&\quad +W_{02}^{(2)}(-1)\frac{\bar{z}^2}{2}+\cdots .
\end{aligned}
\tag{3.10}
$$

Substituting Eq. (3.10) into Eq. (3.9), we gain

$$
\begin{aligned}
& g(z,\bar{z})\\
& =\frac{\tau_n}{\bar{D}}\bigg\{\left(-a\bar{q}_2^*+\frac{by_0}{x_0^2}\right)\left[z+\bar{z}+W_{20}^{(1)}(0)\frac{z^2}{2}+W_{11}^{(1)}(0)z\bar{z}+W_{02}^{(1)}(0)\frac{\bar{z}^2}{2}\right]\\
& \times\left[q_2z+\bar{q}_2\bar{z}+W_{20}^{(2)}(0)\frac{z^2}{2}+W_{11}^{(2)}(0)z\bar{z}+W_{02}^{(2)}(0)\frac{\bar{z}^2}{2}\right]\\
& -\frac{by_0^2}{x_0^3}\left[z+\bar{z}+W_{20}^{(1)}(0)\frac{z^2}{2}+W_{11}^{(1)}(0)z\bar{z}+W_{02}^{(1)}(0)\frac{\bar{z}^2}{2}\right]^2\\
& +\frac{by_0}{x_0^2}\left[z+\bar{z}+W_{20}^{(1)}(0)\frac{z^2}{2}+W_{11}^{(1)}(0)z\bar{z}+W_{02}^{(1)}(0)\frac{\bar{z}^2}{2}\right]\\
& \times\left[q_2ze^{-i\omega\tau_n\theta}+\bar{q}_2\bar{z}e^{i\omega\tau_n\theta}+W_{20}^{(2)}(-1)\frac{z^2}{2}+W_{11}^{(2)}(-1)z\bar{z}+W_{02}^{(2)}(-1)\frac{\bar{z}^2}{2}\right]\\
& -\frac{b}{x_0}\left[q_2z+\bar{q}_2\bar{z}+W_{20}^{(2)}(0)\frac{z^2}{2}+W_{11}^{(2)}(0)z\bar{z}+W_{02}^{(2)}(0)\frac{\bar{z}^2}{2}\right]\\
& \times\left[q_2ze^{-i\omega\tau_n\theta}+\bar{q}_2\bar{z}e^{i\omega\tau_n\theta}+W_{20}^{(2)}(-1)\frac{z^2}{2}+W_{11}^{(2)}(-1)z\bar{z}+W_{02}^{(2)}(-1)\frac{\bar{z}^2}{2}\right]
\end{aligned}
$$

$$+\left[\frac{plE_0}{ply_0-c(l+E_0y_0)^2}+\frac{plE_0y_0[cE_0(l+E_0y_0)-pl]}{[ply_0-c(l+E_0y_0)^2]^2}-\frac{p^2cl^2E_0^2y_0^2(l+E_0y_0)}{[ply_0-c(l+E_0y_0)^2]^3}\right]$$
$$\times\left[q_2z+\bar{q}_2\bar{z}+W_{20}^{(2)}(0)\frac{z^2}{2}+W_{11}^{(2)}(0)z\bar{z}+W_{02}^{(2)}(0)\frac{\bar{z}^2}{2}\right]^2+\cdots\Bigg\},$$

which yields

$$\begin{aligned}
&g(z,\bar{z})\\
&=\frac{\tau_n}{\bar{D}}\Bigg\{z^2\Bigg[-aq_2\bar{q}_2^*+\frac{bq_2y_0}{x_0^2}-\frac{by_0^2}{x_0^3}+\frac{bq_2y_0}{x_0^2}e^{-i\omega\tau_n\theta}-\frac{bq_2^2}{x_0}e^{-i\omega\tau_n\theta}\\
&+\frac{plq_2^2E_0}{ply_0-c(l+E_0y_0)^2}+\frac{plq_2^2E_0y_0[cE_0(l+E_0y_0)-pl]}{[ply_0-c(l+E_0y_0)^2]^2}\\
&-\frac{p^2cl^2q_2^2E_0^2y_0^2(l+E_0y_0)}{[ply_0-c(l+E_0y_0)^2]^3}\Bigg]+z\bar{z}\Bigg[-2a\bar{q}_2^*\mathrm{Re}(q_2)+\frac{2by_0}{x_0^2}\mathrm{Re}(q_2)\\
&-\frac{2by_0^2}{x_0^3}+\frac{2by_0}{x_0^2}\mathrm{Re}(\bar{q}_2e^{i\omega\tau_n\theta})-\frac{2b}{x_0}\mathrm{Re}(q_2\bar{q}_2e^{i\omega\tau_n\theta})\\
&+\frac{2plq_2\bar{q}_2E_0}{ply_0-c(l+E_0y_0)^2}+\frac{2plq_2\bar{q}_2E_0y_0[cE_0(l+E_0y_0)-pl]}{[ply_0-c(l+E_0y_0)^2]^2}\Bigg]\\
&-\frac{2p^2cl^2q_2\bar{q}_2E_0^2y_0^2(l+E_0y_0)}{[ply_0-c(l+E_0y_0)^2]^3}+\bar{z}^2\Bigg[-a\bar{q}_2\bar{q}_2^*+\frac{b\bar{q}_2y_0}{x_0^2}-\frac{by_0^2}{x_0^3}+\frac{b\bar{q}_2y_0}{x_0^2}e^{i\omega\tau_n\theta}\\
&+\frac{pl\bar{q}_2^2E_0}{ply_0-c(l+E_0y_0)^2}-\frac{b\bar{q}_2^2}{x_0}e^{i\omega\tau_n\theta}+\frac{pl\bar{q}_2^2E_0y_0[cE_0(l+E_0y_0)-pl]}{[ply_0-c(l+E_0y_0)^2]^2}\Bigg]\\
&-\frac{p^2cl^2\bar{q}_2^2E_0^2y_0^2(l+E_0y_0)}{[ply_0-c(l+E_0y_0)^2]^3}+z^2\bar{z}\Bigg[\Bigg(-aq_2\bar{q}_2^*+\frac{bq_2y_0}{x_0^2}-\frac{2by_0^2}{x_0^3}\\
&+\frac{bq_2y_0}{x_0^2}e^{-i\omega\tau_n\theta}\Bigg)W_{11}^{(1)}(0)+\Bigg(-a\bar{q}_2^*+\frac{by_0}{x_0^2}-\frac{bq_2}{x_0}e^{-i\omega\tau_n\theta}\\
&+\frac{2plq_2E_0}{ply_0-c(l+E_0y_0)^2}+\frac{2plq_2E_0y_0[cE_0(l+E_0y_0)-pl]}{[ply_0-c(l+E_0y_0)^2]^2}\\
&-\frac{2p^2cl^2q_2E_0^2y_0^2(l+E_0y_0)}{[ply_0-c(l+E_0y_0)^2]^3}\Bigg)W_{11}^{(2)}(0)+\Bigg(-\frac{a\bar{q}_2\bar{q}_2^*}{2}+\frac{b\bar{q}_2y_0}{2x_0^2}-\frac{by_0^2}{x_0^3}\\
&+\frac{b\bar{q}_2y_0}{2x_0^2}e^{i\omega\tau_n\theta}\Bigg)W_{20}^{(1)}(0)+\Bigg(-\frac{a\bar{q}_2^*}{2}+\frac{by_0}{2x_0^2}+\frac{pl\bar{q}_2E_0}{ply_0-c(l+E_0y_0)^2}\\
&-\frac{b\bar{q}_2}{2x_0}e^{i\omega\tau_n\theta}+\frac{pl\bar{q}_2E_0y_0[cE_0(l+E_0y_0)-pl]}{[ply_0-c(l+E_0y_0)^2]^2}-\frac{p^2cl^2\bar{q}_2E_0^2y_0^2(l+E_0y_0)}{[ply_0-c(l+E_0y_0)^2]^3}\Bigg)\\
&\times W_{20}^{(2)}(0)+\left(\frac{by_0}{x_0^2}-\frac{bq_2}{x_0}\right)W_{11}^{(2)}(-1)+\left(\frac{by_0}{2x_0^2}-\frac{b\bar{q}_2}{2x_0}\right)W_{20}^{(2)}(-1)\Bigg]+\cdots\Bigg\}.
\end{aligned}\tag{3.11}$$

Comparing the coefficients of Eqs. (3.8) and (3.11) gives

$$
\begin{aligned}
g_{20} =& \frac{2\tau_n}{\bar{D}}\bigg[-aq_2\bar{q}_2^* + \frac{bq_2y_0}{x_0^2} - \frac{by_0^2}{x_0^3} + \frac{bq_2y_0}{x_0^2}e^{-i\omega\tau_n\theta} \\
& - \frac{bq_2^2}{x_0}e^{-i\omega\tau_n\theta} + \frac{plq_2^2E_0}{ply_0 - c(l+E_0y_0)^2} + \frac{plq_2^2E_0y_0[cE_0(l+E_0y_0) - pl]}{[ply_0 - c(l+E_0y_0)^2]^2} \\
& - \frac{p^2cl^2q_2^2E_0^2y_0^2(l+E_0y_0)}{[ply_0 - c(l+E_0y_0)^2]^3}\bigg], \\
g_{11} =& \frac{\tau_n}{\bar{D}}\bigg[-2a\bar{q}_2^*\mathrm{Re}(q_2) + \frac{2by_0}{x_0^2}\mathrm{Re}(q_2) - \frac{2by_0^2}{x_0^3} + \frac{2by_0}{x_0^2}\mathrm{Re}(\bar{q}_2e^{i\omega\tau_n\theta}) \\
& - \frac{2b}{x_0}\mathrm{Re}(q_2\bar{q}_2e^{i\omega\tau_n\theta}) + \frac{2plq_2\bar{q}_2E_0}{ply_0 - c(l+E_0y_0)^2} \\
& + \frac{2plq_2\bar{q}_2E_0y_0[cE_0(l+E_0y_0) - pl]}{[ply_0 - c(l+E_0y_0)^2]^2} - \frac{2p^2cl^2q_2\bar{q}_2E_0^2y_0^2(l+E_0y_0)}{[ply_0 - c(l+E_0y_0)^2]^3}\bigg], \\
g_{02} =& \frac{2\tau_n}{\bar{D}}\bigg[-a\bar{q}_2\bar{q}_2^* + \frac{b\bar{q}_2y_0}{x_0^2} - \frac{by_0^2}{x_0^3} + \frac{b\bar{q}_2y_0}{x_0^2}e^{i\omega\tau_n\theta} - \frac{b\bar{q}_2^2}{x_0}e^{i\omega\tau_n\theta} \\
& + \frac{pl\bar{q}_2^2E_0}{ply_0 - c(l+E_0y_0)^2} + \frac{pl\bar{q}_2^2E_0y_0[cE_0(l+E_0y_0) - pl]}{[ply_0 - c(l+E_0y_0)^2]^2} \\
& - \frac{p^2cl^2\bar{q}_2^2E_0^2y_0^2(l+E_0y_0)}{[ply_0 - c(l+E_0y_0)^2]^3}\bigg], \\
g_{21} =& \frac{2\tau_n}{\bar{D}}\bigg[\bigg(-aq_2\bar{q}_2^* + \frac{bq_2y_0}{x_0^2} - \frac{2by_0^2}{x_0^3} + \frac{bq_2y_0}{x_0^2}e^{-i\omega\tau_n\theta}\bigg)W_{11}^{(1)}(0) \\
& + \bigg(-a\bar{q}_2^* + \frac{by_0}{x_0^2} - \frac{bq_2}{x_0}e^{-i\omega\tau_n\theta} + \frac{2plq_2E_0}{ply_0 - c(l+E_0y_0)^2} \\
& + \frac{2plq_2E_0y_0[cE_0(l+E_0y_0) - pl]}{[ply_0 - c(l+E_0y_0)^2]^2} - \frac{2p^2cl^2q_2E_0^2y_0^2(l+E_0y_0)}{[ply_0 - c(l+E_0y_0)^2]^3}\bigg)W_{11}^{(2)}(0) \\
& + \bigg(-\frac{a\bar{q}_2\bar{q}_2^*}{2} + \frac{b\bar{q}_2y_0}{2x_0^2} - \frac{by_0^2}{x_0^3} + \frac{b\bar{q}_2y_0}{2x_0^2}e^{i\omega\tau_n\theta}\bigg)W_{20}^{(1)}(0) \\
& + \bigg(-\frac{a\bar{q}_2^*}{2} + \frac{by_0}{2x_0^2} - \frac{b\bar{q}_2}{2x_0}e^{i\omega\tau_n\theta} + \frac{pl\bar{q}_2E_0}{ply_0 - c(l+E_0y_0)^2} \\
& + \frac{pl\bar{q}_2E_0y_0[cE_0(l+E_0y_0) - pl]}{[ply_0 - c(l+E_0y_0)^2]^2} - \frac{p^2cl^2\bar{q}_2E_0^2y_0^2(l+E_0y_0)}{[ply_0 - c(l+E_0y_0)^2]^3}\bigg)W_{20}^{(2)}(0) \\
& + \bigg(\frac{by_0}{x_0^2} - \frac{bq_2}{x_0}\bigg)W_{11}^{(2)}(-1) + \bigg(\frac{by_0}{2x_0^2} - \frac{b\bar{q}_2}{2x_0}\bigg)W_{20}^{(2)}(-1)\bigg].
\end{aligned}
\tag{3.12}
$$

At present, the expressions of g_{20}, g_{11} and g_{02} have already been obtained. However, it is notable that $W_{20}(\theta)$ and $W_{11}(\theta)$ are unknown in g_{21}, therefore we still need to determine them. By using a computational procedure similar to the algorithms presented in Ref[21], we can obtain

$$W_{20}(\theta) = \frac{ig_{20}}{\omega\tau_n}q(0)e^{i\omega\tau_n\theta} + \frac{i\bar{g}_{02}}{3\omega\tau_n}\bar{q}(0)e^{-i\omega\tau_n\theta} + \mathcal{E}_1e^{2i\omega\tau_n\theta},$$

$$W_{11}(\theta) = -\frac{ig_{11}}{\omega\tau_n}q(0)e^{i\omega\tau_n\theta} + \frac{i\bar{g}_{11}}{\omega\tau_n}\bar{q}(0)e^{-i\omega\tau_n\theta} + \mathcal{E}_2, \tag{3.13}$$

where

$$\mathcal{E}_1 = 2\begin{pmatrix} 2i\omega & ax_0 \\ -\dfrac{by_0^2}{x_0^2} & 2i\omega + \dfrac{by_0}{x_0}e^{-2i\omega\tau_n} - \dfrac{plE_0y_0}{ply_0 - c(l+E_0y_0)^2} \end{pmatrix}^{-1}\begin{pmatrix}\mathcal{P}_{11}\\ \mathcal{P}_{21}\end{pmatrix},$$

$$\mathcal{E}_2 = 2\begin{pmatrix} 0 & ax_0 \\ -\dfrac{by_0^2}{x_0^2} & \dfrac{by_0}{x_0} - \dfrac{plE_0y_0}{ply_0 - c(l+E_0y_0)^2} \end{pmatrix}^{-1}\begin{pmatrix}\mathcal{Q}_{11}\\ \mathcal{Q}_{21}\end{pmatrix},$$

with

$$\begin{aligned}
\mathcal{P}_{11} =& -aq_2, \quad \mathcal{Q}_{11} = -\mathrm{Re}(aq_2),\\
\mathcal{P}_{21} =& -\frac{by_0^2}{x_0^3} + \frac{bq_2y_0}{x_0^2} + \left(\frac{bq_2y_0}{x_0^2} - \frac{bq_2^2}{x_0}\right)e^{-i\omega\tau_n\theta} + \frac{plq_2^2E_0}{ply_0 - c(l+E_0y_0)^2}\\
&+ \frac{plq_2^2E_0y_0[cE_0(l+E_0y_0) - pl]}{[ply_0 - c(l+E_0y_0)^2]^2} - \frac{p^2cl^2q_2^2E_0^2y_0^2(l+E_0y_0)}{[ply_0 - c(l+E_0y_0)^2]^3},\\
\mathcal{Q}_{21} =& -\frac{by_0^2}{x_0^3} + \frac{by_0}{x_0^2}\mathrm{Re}(\bar{q}_2e^{i\omega\tau_n\theta}) + \frac{by_0}{x_0^2}\mathrm{Re}(q_2) - \frac{b}{x_0}\mathrm{Re}(q_2\bar{q}_2e^{i\omega\tau_n\theta})\\
&+ \frac{plq_2\bar{q}_2E_0}{ply_0 - c(l+E_0y_0)^2} + \frac{plq_2\bar{q}_2E_0y_0[cE_0(l+E_0y_0) - pl]}{[ply_0 - c(l+E_0y_0)^2]^2}\\
&- \frac{p^2cl^2q_2\bar{q}_2E_0^2y_0^2(l+E_0y_0)}{[ply_0 - c(l+E_0y_0)^2]^3}.
\end{aligned}$$

Further, we can calculate

$$\mathcal{E}_1 = \begin{pmatrix} \dfrac{2\left(2i\omega + \dfrac{by_0}{x_0}e^{-2i\omega\tau_n} - \dfrac{plE_0y_0}{ply_0 - c(l+E_0y_0)^2}\right)\mathcal{P}_{11} - 2ax_0\mathcal{P}_{21}}{2i\omega\left(\dfrac{by_0}{x_0}e^{-2i\omega\tau_n} - \dfrac{plE_0y_0}{ply_0 - c(l+E_0y_0)^2}\right) + \dfrac{aby_0^2}{x_0} - 4\omega^2} \\ \dfrac{\dfrac{2by_0^2}{x_0^2}\mathcal{P}_{11} + 4i\omega\mathcal{P}_{21}}{2i\omega\left(\dfrac{by_0}{x_0}e^{-2i\omega\tau_n} - \dfrac{plE_0y_0}{ply_0 - c(l+E_0y_0)^2}\right) + \dfrac{aby_0^2}{x_0} - 4\omega^2} \end{pmatrix}_{2\times 1},$$

$$\mathcal{E}_2 = \begin{pmatrix} \dfrac{2x_0}{aby_0^2}\left(\dfrac{by_0}{x_0} - \dfrac{plE_0y_0}{ply_0 - c(l+E_0y_0)^2}\right)\mathcal{Q}_{11} - \dfrac{2x_0^2}{by_0^2}\mathcal{Q}_{21} \\ -\dfrac{2\mathrm{Re}(q_2)}{x_0} \end{pmatrix}_{2\times 1}.$$

Then, $W_{20}(\theta)$ and $W_{11}(\theta)$ can be directly worked out by substituting $\mathcal{E}_1$ and $\mathcal{E}_2$ into Eq. (3.13). Subsequently, g_{21} can be determined from Eq. (3.12). So far, the mathematical quantities g_{20}, g_{11}, g_{02} and g_{21} all have been expressed in terms of known parameters. Hence, we are now able to calculate the following crucial values [21] which determine the properties of the Hopf bifurcation when $\tau = \tau_n$:

$$
\begin{cases}
c_1(0) = \dfrac{i}{2\omega\tau_n}\left(g_{11}g_{20} - 2\left|g_{11}\right|^2 - \dfrac{\left|g_{02}\right|^2}{3}\right) + \dfrac{g_{21}}{2}, \\
\mu_2 = -\dfrac{\mathrm{Re}\{c_1(0)\}}{\mathrm{Re}\{\lambda'(\tau_n)\}}, \\
\beta_2 = 2\mathrm{Re}\{c_1(0)\}, \\
T_2 = -\dfrac{\mathrm{Im}\{c_1(0)\} + \mu_2 \mathrm{Im}\{\lambda'(\tau_n)\}}{\omega\tau_n}.
\end{cases}
\tag{3.14}
$$

Associated with the necessary conditions on the emergence of Hopf bifurcations in model (1.5), we can obtain the following results according to the classical Hopf bifurcation theorem in Ref[21]:

Theorem 3.1. *For the model* (1.5) *with* $\tau > 0$, *if* $\frac{by_0}{x_0} > \frac{plE_0y_0}{ply_0 - c(l+E_0y_0)^2}$,

$$
\left[\frac{p^2l^2E_0^2y_0^2}{(ply_0 - c(l+E_0y_0)^2)^2} - \frac{b^2y_0^2}{x_0^2} - \frac{2aby_0^2}{x_0}\right]^2 > \frac{4a^2b^2y_0^4}{x_0^2},
$$

and $\frac{p^2l^2E_0^2y_0^2}{(ply_0 - c(l+E_0y_0)^2)^2} < \frac{b^2y_0^2}{x_0^2} + \dfrac{2aby_0^2}{x_0}$, *then a Hopf bifurcation can occur at the equilibrium point* X_0 *when time delay* τ *takes the critical value* τ_n. *Furthermore,*

(i) *the direction of the Hopf bifurcation is supercritical* (*subcritical*) *if* $\mu_2 > 0$ ($\mu_2 < 0$);

(ii) *the bifurcating periodic orbits are stable* (*unstable*) *if* $\beta_2 < 0$ ($\beta_2 > 0$);

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

4. Numerical simulations

In this section, we perform several Matlab simulations to complement the analytical results above. In view of the assumptions in (2.1), we choose the coefficients of model (1.5) as follows: $r_1 = 2$, $a = 1$, $r_2 = 7/4$, $b = 3$, $p = 1$, $l = 1$, $c = 4/9$, $v = 2/9$. That is,

$$
\begin{cases}
\dot{x}(t) = x(t)\left(2 - y(t)\right), \\
\dot{y}(t) = y(t)\left(\dfrac{7}{4} - \dfrac{3y(t-\tau)}{x(t)} - E(t)\right), \\
0 = E(t)y(t)\left(\dfrac{1}{1+E(t)y(t)} - \dfrac{4}{9y(t)}\right) - \dfrac{2}{9},
\end{cases}
\tag{4.1}
$$

which has a positive equilibrium point $X_0 = (4, 2, 0.25)^T$. Besides, we can calculate that, $by_0/x_0 = 3/2 > plE_0y_0/[ply_0 - c(l+E_0y_0)^2] = 1/2$, $\{p^2l^2E_0^2y_0^2/[ply_0 - c(l+E_0y_0)^2]^2 - b^2y_0^2/x_0^2 - 2aby_0^2/x_0\}^2 = 64 > 4a^2b^2y_0^4/x_0^2 = 36$, $p^2l^2E_0^2y_0^2/[ply_0 -$

$c(l+E_0y_0)^2]^2 = 1/4 < b^2y_0^2/x_0^2 + 2aby_0^2/x_0 = 33/4$. Thus, system (4.1) satisfies the conditions of Hopf bifurcation given in Theorems 2.1 and 3.1.

For this example, Eq. (2.16) becomes $\omega^4 - 8\omega^2 + 9 = 0$, which has two positive roots $\omega^+ = 2.5779$ and $\omega^- = 1.1637$. Accordingly, $\tau_0^+ = (1/2.5779)\arccos(7/8) = 0.4775$ and $\tau_0^- = (1/1.1637)\arccos(7/8) = 1.0578$. Moreover, with the aid of Matlab 7.0, we can obtain the values in Eq. (3.14): $c_1(0) = 5.9418 - 21.7397i$, $\lambda'(\tau_0^+) = 2.7466 - 0.4665i$, $\mu_2 = -2.1633 < 0$, $\beta_2 = 11.8836 > 0$, $T_2 = 16.8411 > 0$. From Theorem 2.1, we can conclude that the equilibrium point X_0 is locally asymptotically stable when $\tau \in [0, 0.4775)$ and it is unstable when $\tau \in (0.4775, 1.0578)$. Hence, a Hopf bifurcation takes place at the equilibrium point X_0 when τ takes the critical value $\tau_0^+ = 0.4775$. Furthermore, according to Theorem 3.1, the Hopf bifurcation at τ_0^+ is subcritical, and the corresponding bifurcating periodic orbits are unstable and increase.

In order to verify the theoretical results, we present some numerical simulations of the illustrative example (4.1) at different values of the delay τ. Numerical simulations show that the equilibrium point X_0 is locally asymptotically stable when $\tau = 0.4675 < \tau_0^+$ as illustrated in Fig. 1; periodic orbits bifurcate from the equilibrium point X_0 when τ takes the bifurcation value $\tau_0^+ = 0.4775$ as illustrated in Fig. 2; the bifurcating periodic orbits are unstable and increase when $\tau = 0.4783 > \tau_0^+$ as illustrated in Fig. 3; and the equilibrium point X_0 is unstable when $\tau = 0.4875 > \tau_0^+$ as illustrated in Fig. 4.

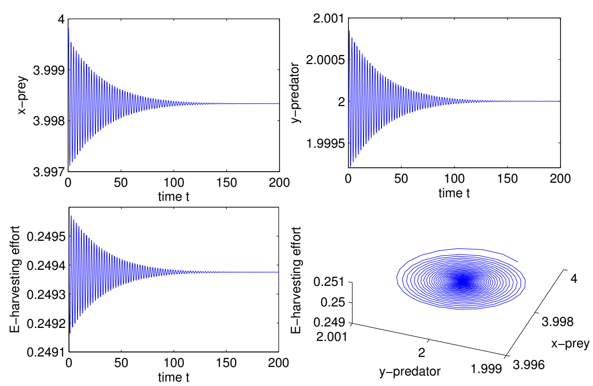

Figure 1: Matlab simulations suggest that the equilibrium point $X_0 = (4, 2, 0.25)^T$ of system (4.1) is locally asymptotically stable when the delay $\tau = 0.4675 < \tau_0^+ = 0.4775$. The initial values $(x(0),\ y(\theta),\ E(0)) = (3.9995,\ 1.9995,\ 0.2495)$ here, where $\theta \in [-\tau, 0]$.

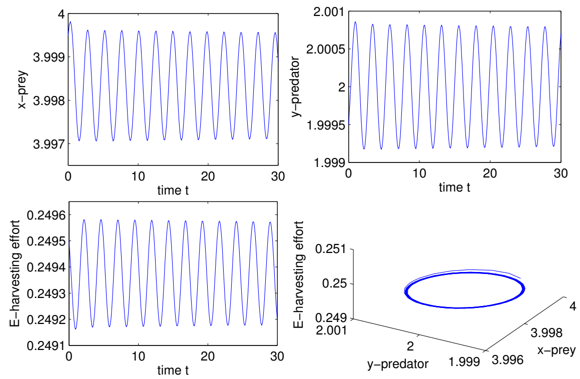

Figure 2: Matlab simulations suggest that periodic orbits bifurcate from the equilibrium point $X_0 = (4, 2, 0.25)^T$ of system (4.1) when the delay $\tau = \tau_0^+ = 0.4775$. The initial values $(x(0),\ y(\theta),\ E(0)) = (3.9995,\ 1.9995,\ 0.2495)$ here, where $\theta \in [-\tau, 0]$.

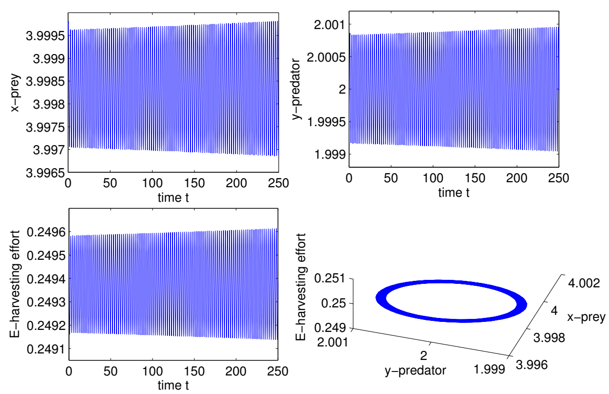

Figure 3: Matlab simulations suggest that the periodic orbits bifurcating from the equilibrium point $X_0 = (4, 2, 0.25)^T$ of system (4.1) are unstable and increase when the delay $\tau = 0.4783 > \tau_0^+ = 0.4775$. The initial values $(x(0),\ y(\theta),\ E(0)) = (3.9995,\ 1.9995,\ 0.2495)$ here, where $\theta \in [-\tau, 0]$.

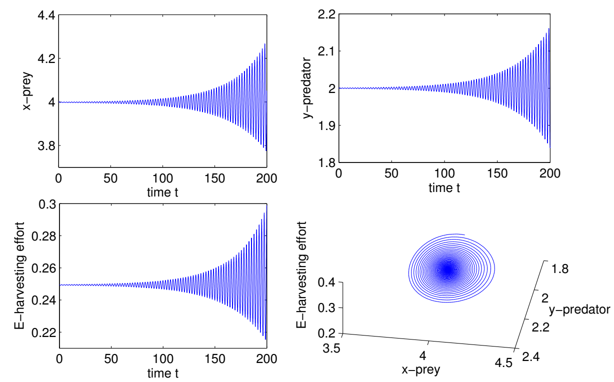

Figure 4: Matlab simulations suggest that the equilibrium point $X_0 = (4, 2, 0.25)^T$ of system (4.1) is unstable when the delay $\tau = 0.4875 > \tau_0^+ = 0.4775$. The initial values $(x(0),\ y(\theta),\ E(0)) = (3.9995,\ 1.9995,\ 0.2495)$ here, where $\theta \in [-\tau, 0]$.

5. Discussion

The present paper has studied the bifurcation dynamics of the delayed differential-algebra predator-prey model (1.5). We can see from Theorem 2.1 that the stability of the equilibrium point X_0 of model (1.5) can switch finite times when the gestation delay τ is treated as a variable bifurcation parameter. The stability would change from stable to unstable to stable, and eventually becomes unstable as the increasing of the delay τ. And large delays have unstabilizing effect on the stability of the equilibrium point X_0.

When the delay τ is small and less than the first critical value τ_0^+, the equilibrium point X_0 is locally asymptotically stable. In this case, the populations of preys and predators, as well as human harvesting are able to coexist in harmony. Hence, the ecological balance can be maintained. However, when the delay τ increases beyond τ_0^+ and within the interval $(\tau_0^+,\ \tau_0^-)$, the equilibrium point becomes unstable. At this moment, the ecological balance would be easily destroyed when it is subject to some external disturbances. Specially, when τ takes the critical value τ_0^+, periodic orbits would arise from the equilibrium point and alter the dynamics of model (1.5) significantly. The appearance of Hopf-bifurcating periodic orbits means that small amplitude oscillations of population densities are currently in progress, which can be understood as the periodic evolution of the populations of preys and predators.

Similar phenomena will also occur around the other critical values τ_0^-, τ_1^+, τ_1^-, $\cdots$, τ_N^+. That is, a finite number of Hopf bifurcations can take place as the delay τ increases from zero. Furthermore, the stability of the periodic orbits is directly related to whether the populations of preys and predators as well as the external harvesting can coexist in an oscillatory mode, so the complex bifurcation behaviors have great significance for the delayed predator-prey model. Hence, stability of the Hopf-bifurcating periodic orbits are further analyzed in Section 3.

6. Concluding remarks

Clearly, our delayed differential-algebra predator-prey model (1.5) can exhibit a sequence of Hopf bifurcations as the increase of the delay τ, which can cause potentially dramatic variations in the dynamical behaviors of the model.

Besides, it is notable that the parameterisation method used in section 2 can reduce the delayed differential-algebra predator-prey model (1.5) to the parameterised system (2.12) near the equilibrium point X_0, which plays an important role in our study. Refs[40, 22, 23, 24, 3] have shown that Differential-Algebraic Equations have widespread applications in constrained dynamical systems, so we expect that the parameterisation method can be employed to investigate the dynamics of more complex constrained systems.

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References

[1] J. F. M. Al-Omari, *The effect of state dependent delay and harvesting on a stage-structured predator-prey model*, Appl. Math. Comput., 271 (2015), 142-153.

[2] W. M. Boothby, *An introduction to differential manifolds and Riemannian geometry*, Academic Press, 1986.

[3] S. Campbell, A. Ilchmann, V. Mehrmann, T. Reis (Eds.), *Applications of differential-algebraic equations: examples and benchmarks*, Springer, 2019.

[4] J. Carr, *Application of center manifold theory*, Springer, 1982.

[5] L. S. Chen, *Mathematical models and methods in ecology*, Science Press, 2017. (in Chinese)

[6] B. S. Chen, J. J. Chen, *Bifurcation and chaotic behavior of a discrete singular biological economic system*, Appl. Math. Comput., 219 (2012), 2371-2386.

[7] B. S. Chen, X. X. Liao, Y. Q. Liu, *Normal forms and bifurcations for the differential-algebraic systems*, Acta Math. Appl. Sin., 23 (2000), 429-443. (in Chinese)

[8] C. W. Clark, *Mathematical models in the economics of renewable resources*, SIAM Rev., 21 (1979), 81-99.

[9] C. W. Clark, *Mathematical bioeconomics: the mathematics of conservation*, Wiley, 2010.

[10] K. L. Cooke, Z. Grossman, *Discrete delay, distributed delay and stability switches*, J. Math. Anal. Appl., 86 (1982), 592-627.

[11] L. Edelstein-Keshet, *Mathematical models in biology*, SIAM, 1988.

[12] M. Fan, K. Wang, *Harvesting problem with price changed with demand and supply*, J. Biomath., 16 (2001), 411-415.

[13] T. Faria, L. T. Maglhalães, *Normal form for retarded functional differential equations with parameters and applications to Hopf bifurcation*, J. Differential Equations, 122 (1995), 181-200.

[14] T. Faria, L. T. Maglhalães, *Normal form for retarded functional differential equations and applications to Bogdanov-Takens singularity*, J. Differential Equations, 122 (1995), 201-224.

[15] K. Gopalswamy, *Stability and oscillations in delay differential equations of population dynamics*, Kluwer Academic Publisher, 1992.

[16] J. Gukenheimer, P. Holmes, *Nonlinear oscillations, dynamical systems, and bifurcations of vector fields*, Springer, 1983.

[17] S. J. Guo, *Bifurcation in a reaction-diffusion model with nonlocal delay effect and nonlinear boundary condition*, J. Differential Equations, 289 (2021), 236-278.

[18] R. P. Gupta, P. Chandra, *Bifurcation analysis of modified Leslie-Gower predator-prey model with Michaelis-Menten type prey harvesting*, J. Math. Anal. Appl., 398 (2013), 278-295.

[19] J. Hale, S. V. Lunel, *Introduction to functional differential equations*, Springer, 1993.

[20] M. Haragus, G. Iooss, *Local bifurcations, center manifolds, and normal forms in infinite-dimensional dynamical systems*, Springer, 2011.

[21] B. D. Hassard, N. D. Kazarinoff, Y. H. Wan, *Theory and applications of Hopf bifurcaton*, Cambridge University Press, Cambridge, 1981.

[22] A. Ilchmann, T. Reis (Eds.), *Surveys in differential-algebraic equations I*, Springer, 2013.

[23] A. Ilchmann, T. Reis (Eds.), *Surveys in differential-algebraic equations II-III*, Springer, 2015.

[24] A. Ilchmann, T. Reis (Eds.), *Surveys in differential-algebraic equations IV*, Springer, 2017.

[25] Y. Kuang, *Delay differential equations with applications in population dynamics*, Academic Press, 1993.

[26] Y. Kuznetsov, *Elements of applied bifurcation theory*, Springer, 2004.

[27] P. H. Leslie, *Some further notes on the use of matrices in population mathematics*, Biometrika, 35 (1948), 213-245.

[28] M. Li, B. S. Chen, H. W. Ye, *A bioeconomic differential algebraic predator-prey model with nonlinear prey harvesting*, Appl. Math. Model., 42 (2017), 17-28.

[29] P. Liu, Z. G. Zeng, J. Wang, *Multistability of recurrent neural networks with nonmonotonic activation functions and unbounded time-varying delays*, IEEE Trans. Neural Netw. Learn. Syst., 29 (2018), 3000-3010.

[30] G. S. Mahapatra, P. Santra, *Prey-predator model for optimal harvesting with functional response incorporating prey refuge*, Int. J. Biomath., 9 (2016), 1650014.

[31] N. G. Mankiw, *Principles of economics*, Peking University Press, 2015.

[32] J. H. Mathews, R. W. Howell, *Complex analysis for mathematics and engineering*, Jones & Bartlett Learning, 2012.

[33] M. G. Mortuja, M. K. Chaube, S. Kumar, *Dynamic analysis of a predator-prey system with nonlinear prey harvesting and square root functional response*, Chaos Solitons Fractals, 148 (2021), 111071.

[34] J. D. Murray, *Mathematical biology: I. an introduction*, Springer, 2002.

[35] J. Muscat, *Functional analysis*, Springer, 2014.

[36] K. Nadjah, A. M. Salah, *Stability and Hopf bifurcation of the coexistence equilibrium for a differential-algebraic biological economic system with predator harvesting*, Electron. Res. Arch., 29 (2021), 1641-1660.

[37] P. Panja, *Dynamics of a predator-prey model with Crowley-Martin functional response, refuge on predator and harvesting of super predator*, J. Biol. Systems, 29 (2021), 631-646.

[38] P. Panja, S. Jana, S. K. Mondal, *Effects of additional food on the dynamics of a three species food chain model incorporating refuge and harvesting*, Int. J. Nonlinear Sci. Numer. Simul., 20 (2019), 787-801.

[39] P. Panja, S. Poria, S. K. Mondal, *Analysis of a harvested tritrophic food chain model in the presence of additional food for top predator*, Int. J. Biomath., 11 (2018), 1850059.

[40] L. Petzold, *Differential/algebraic equations are not ODE's*, SIAM J. Sci. Comput., 3 (1982), 367-384.

[41] S. Sharma, G. P. Samanta, *Optimal harvesting of a two species competition model with imprecise biological parameters*, Nonlinear Dyn., 77 (2014), 1101-1119.

[42] Z. D. Teng, M. Rehim, *Persistence in nonautonomous predator-prey systems with infinite delays*. J. Comput. Appl. Math., 197 (2006), 302-321.

[43] A. A. Thirthar, S. J. Majeed, M. A. Alqudah, P. Panja, T. Abdeljawad, *Fear effect in a predator-prey model with additional food, prey refuge and harvesting on super predator*, Chaos Solitons Fractals, 159 (2022), 112091.

[44] S. Wiggins, *Introduction to applied nonlinear dynamical systems and chaos*, Springer, 2003.

[45] X. Y. Wu, B. S. Chen, *Bifurcations and stability of a discrete singular bioeconomic system*, Nonlinear Dyn., 73 (2013), 1813-1828.

[46] Z. G. Zeng, P. Yu, X. X. Liao, *A new comparison method for stability theory of differential systems with time-varying delays*, Internat. J. Bifur. Chaos Appl. Sci. Engrg., 18 (2008), 169-186.

[47] Z. F. Zhang, T. R. Ding, W. Z. Huang, Z. X. Dong, *Qualitative theory of differential equations*, Science Press, 2018.

[48] J. Y. Zhang, B. Y. Feng, *Geometry theory and bifurcation problems of ordinary differential equations*, Peking University Press, 2000.

[49] G. D. Zhang, J. H. Hu, F. Jiang, *Exponential stability criteria for delayed second-order memristive neural networks*, Neurocomputing, 315 (2018), 439-446.

[50] G. D. Zhang, J. H. Hu, Z. G. Zeng, *New criteria on global stabilization of delayed memristive neural networks with inertial item*, IEEE Trans. Cybern., 50 (2020), 2770-2780.

[51] G. D. Zhang, Y. Shen, *Periodic solutions for a neutral delay Hassell-Varley type predator-prey system*, Appl. Math. Comput., 264 (2015), 443-452.

[52] G. D. Zhang, Y. Shen, B. S. Chen, *Positive periodic solutions in a non-selective harvesting predator-prey model with multiple delays*, J. Math. Anal. Appl., 395 (2012), 298-306.

[53] G. D. Zhang, Y. Shen, B. S. Chen, *Bifurcation analysis in a discrete differential-algebraic predator-prey system*, Appl. Math. Model., 38 (2014), 4835-4848.

[54] G. D. Zhang, Z. G. Zeng, *Stabilization of second-order memristive neural networks with mixed time delays via nonreduced order*, IEEE Trans. Neural Netw. Learn. Syst., 31 (2020), 700-706.

[55] G. D. Zhang, L. L. Zhu, B. S. Chen, *Hopf bifurcation and stability for a differential-algebraic biological economic system*, Appl. Math. Comput., 217 (2010), 330-338.

[56] S. R. Zhou, Y. F. Liu, G. Wang, *The stability of predator-prey systems subject to the Allee effects*, Theor. Popul. Biol., 67 (2005), 23-31.

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