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Research article

Delayed predator-prey dynamics with Holling type IV functional response and rational nonlinear harvesting

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Abstract: A Holling type IV predator-prey system with a rational nonlinear harvesting rate and gestation delay of prey species is studied, which is formulated by delayed differential-algebra equations. Its dynamical behaviors are investigated in terms of differential-algebra system theory, bifurcation theory, and center manifold theorem. By choosing the gestation delay as a bifurcation parameter, we first show that Hopf bifurcations can occur as the delay increases through a sequence of threshold values. Second, we derive an explicit algorithm for determining the stability and direction of the Hopf bifurcations. Last, some numerical simulations are performed to illustrate the analytical results, and their biological significances are explained.

Keywords: Holling type IV; nonlinear harvesting; stability switches; Hopf bifurcation; periodic orbits

1. Introduction

Predator-prey systems are arguably the most fundamental building blocks of any complex bio- and ecosystems due to their universal existence and importance [1, 2]. Understanding the population dynamics of predator-prey systems will be helpful for studying the multiple-species interactions in biological systems. The dynamical relationships in predator-prey systems have been widely investigated mathematically since the publication of the pioneering work: Lotka-Volterra equations, refer to the literature [1, 2]. In the research of the biological interactions between predators and their preys, it is crucial to determine what specific form of the functional response (describes the average number of preys killed per individual predator per unit of time) is biologically plausible, which provides a sound basis for theoretical development. The classical predator-prey system with functional response [1–5] takes the following form:

$$\begin{cases} \dot{x}(t) = x(t)\left(r - \dfrac{x(t)}{K}\right) - p(x(t))y(t), \\ \dot{y}(t) = \mu p(x(t))y(t) - Dy(t), \end{cases} \tag{1.1}$$

where the variables $x(t)$ and $y(t)$ stand for the prey and predator density at any instant of time t, respectively. The functional response $p(x(t))$ is also called "the trophic function", which satisfies the usual requirements such as nonnegativity, boundedness, monotonic increasing, and $p(0) = 0$. The positive constants r, K, μ, and D represent the intrinsic growth rate of prey species, the environmental carrying capacity, the maximal growth rate, and the death rate of predator species, respectively.

The interaction mechanisms in predator-prey systems indicate that non-monotonic response can often occur since the growth of predator population may be inhibited when the prey density reaches a high level. Under such circumstances, Sokol and Howell [6] proposed the Holling type IV functional response, which incorporates prey interference with predation in that the per capita predation rate increases with the density of prey population to a maximum at a critical prey density beyond which it decreases. In this work, $p(x(t))$ is chosen as the well-known Holling type IV functional response, which has the form $x(t)/(a + x^2(t))$, where $a > 0$ is called the half-saturation constant.

It has been widely known that the past history as well as the current conditions can influence the future dynamical behaviors of systems. In order to reflect that the dynamics of predator-prey systems depending on the past history, various time delays are necessarily incorporated into the biosystems, which would make the biological processes more accurate [7]. On the other hand, time delay may also have complex effects on the dynamical behaviors of a system; for example, it could induce instability, various oscillations, limit cycles, bifurcations (such as saddle-node, Hopf-Andronov, and Bogdanov-Takens, etc.), chaos, multistability, and so on [7–9]. In particular, it has been generally recognized that some kinds of gestation delays are inevitable in predator-prey interactions, which in reality play an important role in mathematical modeling. For instance, the reproduction of predator species after preying is not instantaneous but mediated by some time lag required for gestation. Apparently, the birth rate of the predator population also has great associations with the gestation delay of prey species. It is worth noticing that the class of predator-prey systems with gestation delays appearing in the intra-specific interaction terms of prey equations are viewed as a critical part of delayed predator-prey systems [7]. By referring to the modeling thoughts in [7], we incorporate a time delay τ, denoting the gestation of the prey population into the first differential equation of predator-prey system (1.1). That is,

$$\begin{cases} \dot{x}(t) = x(t)\left(r - \dfrac{x(t-\tau)}{K} - \dfrac{y(t)}{a + x^2(t)}\right), \\ \dot{y}(t) = y(t)\left(\dfrac{\mu x(t)}{a + x^2(t)} - D\right). \end{cases} \tag{1.2}$$

It has been well known that harvesting has a strong impact on the dynamical evolution of biological populations [10–14]. Thus, we consider prey harvesting for delayed predator-prey system (1.2), viz.

$$\begin{cases} \dot{x}(t) = x(t)\left(r - \dfrac{x(t-\tau)}{K} - \dfrac{y(t)}{a + x^2(t)}\right) - H(x(t)), \\ \dot{y}(t) = y(t)\left(\dfrac{\mu x(t)}{a + x^2(t)} - D\right), \end{cases} \tag{1.3}$$

where the harvesting $H(x(t))$ is an increasing function of prey density $x(t)$. The most common harvesting policy is linear harvesting rate, viz. $H(x(t)) = E(t)x(t)$ [1, 2], where $E(t)$ represents the harvesting effort on prey species. The harvesting effort $E(t)$ indicates the human resource cost invested, i.e., the number of workers multiplies their working hours. Thus, when more species become available, harvesting more and more with the linear rate would be unprofitable due to oversupply in the market.

We consider a rational nonlinear harvesting type. Let $\mathbb{t}$ be the total time that one worker requires for harvesting, which contains searching time $\mathbb{t}_s$ and handling time $\mathbb{t}_h$. Suppose that the number of preys caught by a worker is $\mathbb{n}_x = \mathbb{t}_s x(t)$, then $\mathbb{t}_h = m\mathbb{n}_x = m\mathbb{t}_s x(t)$, where m is the average time used for handling one prey. Thus, $\mathbb{t} = \mathbb{t}_s(1 + mx(t))$, and the number of preys caught by per worker per time is $\mathbb{n}_x/\mathbb{t} = x(t)/(1 + mx(t))$. Hence, the catches caught by workers can be expressed as $H(x(t)) = x(t)E(t)/(1 + mx(t))$, which shows that as the population density of prey $x(t)$ increases, the catches also increase but at a decreasing rate.

The harvesting efforts on biological resources are more likely to be commercial behaviors nowadays, so is pretty common that the biological resources in ecological system are harvested and sold in the market to produce economic benefits in our daily life. The bio-economics aspects of renewable resource management have been investigated by Gordon and Clark [15,16], who adopted the following economic equation to study the economic revenue from the harvesting on biological resources:

$$\text{Net Economic Revenue (NER)} = \text{Total Revenue (TR)} - \text{Total Cost (TC)}. \tag{1.4}$$

For the above nonlinear harvesting type, we have $\text{TR} = pH(x(t)) = px(t)E(t)/(1 + mx(t))$ and $\text{TC} = cE(t)$, where the positive parameters p and c represent the unit selling price of the catches and the wage of a worker per unit of time, respectively.

Combining Eqs (1.3) and (1.4) with the nonlinear harvesting, we have the following predator-prey system in which the harvesting term is characterized by an algebraic equation:

$$\begin{cases} \dot{x}(t) = x(t)\left(r - \dfrac{x(t-\tau)}{K} - \dfrac{y(t)}{a + x^2(t)} - \dfrac{E(t)}{1 + mx(t)}\right), \\ \dot{y}(t) = y(t)\left(\dfrac{\mu x(t)}{a + x^2(t)} - D\right), \\ 0 = E(t)\left(\dfrac{px(t)}{1 + mx(t)} - c\right) - v, \end{cases} \tag{1.5}$$

where the positive parameter v denotes the net economic revenue from harvesting.

The initial values for the delayed predator-prey system (1.5) are given as $x(\theta) > 0$ $(\theta \in [-\tau, 0])$, $y(0) > 0$, $E(0) > 0$, where $x(\theta)$ is a continuously bounded function in the interval $[-\tau, 0]$.

In contrast to the familiar predator-prey systems with harvesting [17, 18], which are described by differential equations, the merit of our differential-algebra predator-prey system (1.5) is that it not only includes the predator-prey interactions in the harvested biological system but also considers the harvesting from an economic point of view. Several relevant predator-prey systems have been reported in the literature [19–23], and the references cited therein. In [19, 21, 22], using the forward Euler scheme and Poincaré scheme, the researchers obtained discrete predator-prey systems. Additionally, on the basis of stability and bifurcation theory for discrete dynamical systems [24,25], they investigated the positiveness of solutions, stability of positive fixed points, bifurcation sets, direction and stability of flip bifurcation and Neimark-Sacker bifurcation, period-2 orbits, invariant closed curves, maximum

Lyapunov exponents, bifurcation diagrams, and chaotic sets of the discrete systems. Besides, by applying the normal form theory of Guckenheimer and Holmes [26], as well as the singularity induced bifurcation theorem of Venkatasubramanian et al. [27], the researchers in [20, 23] studied the issues of stability of interior equilibria, the instability mechanism, period solutions, Hopf bifurcations, impulsive phenomena, and singularity induced bifurcations in ordinary predator-prey systems of the types: Ratio-dependent and prey-dependent. Different from [17–23], we plan to investigate the dynamical behaviors of a delayed differential-algebra predator-prey system with Holling type IV functional response and rational nonlinear harvesting, including stability of equilibrium, existence and direction of Hopf bifurcations, stability and period of Hopf-bifurcating periodic orbits. The research tools we use are the functional differential equation theory of Hale and Lunel [28], the center manifold theorem developed by Hassard et al. [29], as well as the parametric procedure due to Chen et al. [30], which also differ from related references [19–23]. The methods enrich the toolbox for analyzing the dynamics of ecological systems. In some sense, the paper complements the relevant research in the literature [17–23].

Before studying the dynamics of predator-prey system (1.5), the following preliminaries are needed: The point $X_0 = (x_0, y_0, E_0)^T$ is an equilibrium of system (1.5) if and only if X_0 satisfies

$$\begin{cases} r - \dfrac{x_0}{K} - \dfrac{y_0}{a + x_0^2} - \dfrac{E_0}{1 + mx_0} = 0, \\ \dfrac{\mu x_0}{a + x_0^2} - D = 0, \\ E_0\left(\dfrac{px_0}{1 + mx_0} - c\right) - v = 0, \end{cases}$$

which shows that (1.5) has an equilibrium $X_0 = \left(x_0, (a+x_0^2)\left(r - \dfrac{x_0}{K} - \dfrac{E_0}{1+mx_0}\right), \dfrac{(1+mx_0)v}{(p-cm)x_0 - c}\right)^T$, where x_0 satisfies the quadratic equation $Dx_0^2 - \mu x_0 + aD = 0$.

In light of the differential-algebra system theory [31–34], system (1.5) can be locally equivalent to the differential-algebra system near its equilibrium X_0:

$$\begin{cases} \dot{x}(t) = x(t)\left(r - \dfrac{x(t-\tau)}{K} - \dfrac{y(t)}{a + x^2(t)} - \dfrac{E(t)}{1 + mx(t)}\right), \\ \dot{y}(t) = y(t)\left(\dfrac{\mu x(t)}{a + x^2(t)} - D\right), \\ \dot{E}(t) = f_3(x(t), y(t), E(t)), \\ \quad 0 = E(t)\left(\dfrac{px(t)}{1 + mx(t)} - c\right) - v, \end{cases} \tag{1.6}$$

where $f_3(x(t), y(t), E(t))$ is a continuously differentiable function, which satisfies $f_3(x_0, y_0, E_0) = 0$. The concrete expression of f_3 does not need to be written and the reason for this will be seen in Section 2.

For convenience, we denote

$$f(X) = \begin{pmatrix} f_1(X) \\ f_2(X) \\ f_3(X) \end{pmatrix} = \begin{pmatrix} x(t)\left(r - \dfrac{x(t-\tau)}{K} - \dfrac{y(t)}{a + x^2(t)} - \dfrac{E(t)}{1 + mx(t)}\right) \\ y(t)\left(\dfrac{\mu x(t)}{a + x^2(t)} - D\right) \\ f_3(x(t), y(t), E(t)) \end{pmatrix},$$

$$g(X) = E(t)\left(\frac{px(t)}{1+mx(t)} - c\right) - v,\ X = (x, y, E)^T.$$

In the following discussion, time t is occasionally omitted whenever there is no danger of confusion.

The rest of the article is organized as follows: In the next section, we consider stability of the interior equilibrium and the existence of local Hopf bifurcations occurring at the equilibrium of system (1.6). In Section 3, we employ the normal form theory and center manifold theorem due to Hassard et al. [29] to analyze the direction, stability, and period of the bifurcating periodic orbits at the threshold values of the gestation delay. To verify our analytical results, several numerical simulations are included in Section 4. Finally, biological explanations of the theoretical findings as well as some possible directions for further studies are discussed in Section 5.

2. Stability and Hopf bifurcations induced by delay

The biological significance of the equilibrium in population ecology requires that X_0 should be an interior equilibrium, which implies that the prey species, the predator species, and the harvesting effort all exist [1, 2]. Thus, the components of equilibrium X_0 should be positive. Accordingly, we suppose that the components satisfy the following assumptions throughout this study:

$$\mu^2 \geq 4aD^2,\ \ r > \frac{x_0}{K} + \frac{E_0}{1+mx_0},\ \ (p-cm)x_0 > c. \tag{2.1}$$

In view of the parameterisation method introduced in the Appendix, we consider the nonsingular transformation $X = \mathcal{P}\overline{X}$ for system (1.6), such that $D_X g(X_0)\mathcal{P} = \left(0, 0, \frac{(p-cm)x_0 - c}{1+mx_0}\right)$, where

$$\mathcal{P} = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ -\frac{pE_0}{(1+mx_0)[(p-cm)x_0-c]} & 0 & 1 \end{pmatrix},\ \ \overline{X} = (x, y, \overline{E})^T,$$

and $D_X g$ denotes the Jacobi matrix of g with respect to X.

Thus, system (1.6) is transformed into

$$\begin{cases} \dot{x}(t) = x(t)\left(r - \frac{x(t-\tau)}{K} - \frac{y(t)}{a+x^2(t)} + \frac{pE_0 x(t)}{(1+mx_0)[(p-cm)x_0-c](1+mx(t))} - \frac{\overline{E}(t)}{1+mx(t)}\right), \\ \dot{y}(t) = y(t)\left(\frac{\mu x(t)}{a+x^2(t)} - D\right), \\ \dot{\overline{E}}(t) = f_3(x(t), y(t), \overline{E}(t)), \\ \ \ 0 = \left(-\frac{pE_0 x(t)}{(1+mx_0)[(p-cm)x_0-c]} + \overline{E}(t)\right)\left(\frac{px(t)}{1+mx(t)} - c\right) - v, \end{cases} \tag{2.2}$$

where $f_3(x(t), y(t), \overline{E}(t))$ is a continuously differentiable function that satisfies $f_3(\overline{X}_0) = 0$, $\overline{X}_0 = (x_0, y_0, \overline{E}_0)^T = \left(x_0, y_0, E_0 + \frac{px_0E_0}{(1+mx_0)[(p-cm)x_0-c]}\right)^T$ and is an equilibrium of system (2.2). The concrete expression of $f_3(x(t), y(t), \overline{E}(t))$ does not need to be written, cf. Eq (2.4) below.

To be consistent with the notations included in Section 1, we let

$$
\begin{aligned}
f(\overline{X}) &= (f_1(\overline{X}),\ f_2(\overline{X}),\ f_3(\overline{X}))^T \\
&= \begin{pmatrix} x(t)\left(r - \dfrac{x(t-\tau)}{K} - \dfrac{y(t)}{a+x^2(t)} + \dfrac{pE_0 x(t)}{(1+mx_0)[(p-cm)x_0-c](1+mx(t))} - \dfrac{\overline{E}(t)}{1+mx(t)}\right) \\ y(t)\left(\dfrac{\mu x(t)}{a+x^2(t)} - D\right) \\ f_3(x(t), y(t), \overline{E}(t)) \end{pmatrix}, \\
g(\overline{X}) &= \left(-\frac{pE_0 x(t)}{(1+mx_0)[(p-cm)x_0-c]} + \overline{E}(t)\right)\left(\frac{px(t)}{1+mx(t)} - c\right) - v.
\end{aligned} \tag{2.3}
$$

Owing to $g(\overline{X}(t))$ is a continuously differentiable function from $\mathrm{R}^3 \to \mathrm{R}$, the regular solution set of $g(\overline{X}(t))$ can define a 2-dimensional smooth manifold $\mathcal{M}$ in R^3, where $\mathcal{M} = \{\overline{X}(t) \in \mathrm{R}^3 : g(\overline{X}(t)) = 0 \text{ and rank } D_{\overline{X}} g(\overline{X}(t)) = 1\}$. Hence, a local parameterisation ψ [30, 35] can be defined as follows: For $\forall\, \overline{X}(t) \in B(\overline{X}_0) \subset \mathcal{M}$, $\exists\, Y(t) \in \mathcal{N} \subset \mathrm{R}^2$, such that

$$
\overline{X}(t) = \psi(Y(t)) = \overline{X}_0 + U_0 Y(t) + V_0 h(Y(t)) \ \text{ and } \ g(\psi(Y(t))) = 0,
$$

where $B(\overline{X}_0)$ is an open neighborhood of $\overline{X}_0$, $\mathcal{N} = \psi^{-1}(B(\overline{X}_0))$, $U_0 = \begin{pmatrix} I_2 \\ 0 \end{pmatrix}_{3\times 2}$, $V_0 = \begin{pmatrix} 0 \\ I_1 \end{pmatrix}_{3\times 1}$, I_n denotes an identity matrix of dimension $n \times n$, $Y = (y_1, y_2)^T \in \mathrm{R}^2$, $h(Y)$ is a smooth mapping from $\mathrm{R}^2 \to \mathrm{R}$, and the existence of h can be guaranteed by the implicit function theorem due to $\mathcal{M}$ being a smooth manifold. Then, from Eq (A.9) in the Appendix, the Taylor series developments of the parameterised system of (2.2) at $\overline{X}_0$ can be expressed as

$$
\dot{Y} = U_0^T D_{\overline{X}} f(\overline{X}_0) \begin{pmatrix} D_{\overline{X}} g(\overline{X}_0) \\ U_0^T \end{pmatrix}^{-1} \begin{pmatrix} 0 \\ I_2 \end{pmatrix} Y + o\,(|Y|). \tag{2.4}
$$

Thus, the Jacobi matrix of the linearized system from parameterised system (2.4) evaluated at $\overline{X}_0$ is

$$
U_0^T D_{\overline{X}} f(\overline{X}_0) \begin{pmatrix} D_{\overline{X}} g(\overline{X}_0) \\ U_0^T \end{pmatrix}^{-1} \begin{pmatrix} 0 \\ I_2 \end{pmatrix} = \begin{pmatrix} D_{\overline{X}} f_1(\overline{X}_0) \\ D_{\overline{X}} f_2(\overline{X}_0) \end{pmatrix} \begin{pmatrix} D_{\overline{X}} g(\overline{X}_0) \\ U_0^T \end{pmatrix}^{-1} \begin{pmatrix} 0 \\ I_2 \end{pmatrix}.
$$

The terms $f_3(x(t), y(t), E(t))$ and $f_3(x(t), y(t), \overline{E}(t))$ are absent here, so that their concrete expressions do not need to be explicitly defined. Moreover, the above Jacobi matrix can be calculated as follows:

$$
\begin{aligned}
&\begin{pmatrix} \Lambda & -\dfrac{x_0}{a+x_0^2} & -\dfrac{x_0}{1+mx_0} \\ \dfrac{\mu y_0(a-x_0^2)}{(a+x_0^2)^2} & 0 & 0 \end{pmatrix} \begin{pmatrix} 0 & 0 & \dfrac{(p-cm)x_0-c}{1+mx_0} \\ 1 & 0 & 0 \\ 0 & 1 & 0 \end{pmatrix}^{-1} \begin{pmatrix} 0 & 0 \\ 1 & 0 \\ 0 & 1 \end{pmatrix} \\
= &\begin{pmatrix} \Lambda & -\dfrac{x_0}{a+x_0^2} & -\dfrac{x_0}{1+mx_0} \\ \dfrac{\mu y_0(a-x_0^2)}{(a+x_0^2)^2} & 0 & 0 \end{pmatrix} \begin{pmatrix} 0 & 1 & 0 \\ 0 & 0 & 1 \\ \dfrac{1+mx_0}{(p-cm)x_0-c} & 0 & 0 \end{pmatrix} \begin{pmatrix} 0 & 0 \\ 1 & 0 \\ 0 & 1 \end{pmatrix}
\end{aligned}
$$

$$= \begin{pmatrix} -\dfrac{x_0}{(p-cm)x_0-c} & \Lambda & -\dfrac{x_0}{a+x_0^2} \\ 0 & \dfrac{\mu y_0(a-x_0^2)}{(a+x_0^2)^2} & 0 \end{pmatrix} \begin{pmatrix} 0 & 0 \\ 1 & 0 \\ 0 & 1 \end{pmatrix} = \begin{pmatrix} \Lambda & -\dfrac{x_0}{a+x_0^2} \\ \dfrac{\mu y_0(a-x_0^2)}{(a+x_0^2)^2} & 0 \end{pmatrix}, \tag{2.5}$$

where $\Lambda = -\dfrac{e^{-\lambda\tau}x_0}{K} + \dfrac{2x_0^2y_0}{(a+x_0^2)^2} + \dfrac{px_0E_0}{(1+mx_0)^3[(p-cm)x_0-c]} + \dfrac{mx_0\overline{E}_0}{(1+mx_0)^2}$.

Note that $\overline{E}_0 = E_0 + \dfrac{px_0E_0}{(1+mx_0)[(p-cm)x_0-c]}$, then the characteristic equation of Jacobi matrix (2.5) is

$$\lambda^2 + \left(\frac{x_0}{K}e^{-\lambda\tau} - \frac{2x_0^2y_0}{(a+x_0^2)^2} - \frac{px_0E_0}{(1+mx_0)^2[(p-cm)x_0-c]} - \frac{mx_0E_0}{(1+mx_0)^2}\right)\lambda + \frac{\mu x_0y_0(a-x_0^2)}{(a+x_0^2)^3} = 0. \tag{2.6}$$

When the gestation delay $\tau = 0$, the characteristic equation (2.6) becomes

$$\lambda^2 + \left(\frac{x_0}{K} - \frac{2x_0^2y_0}{(a+x_0^2)^2} - \frac{px_0E_0}{(1+mx_0)^2[(p-cm)x_0-c]} - \frac{mx_0E_0}{(1+mx_0)^2}\right)\lambda + \frac{\mu x_0y_0(a-x_0^2)}{(a+x_0^2)^3} = 0. \tag{2.7}$$

Associated with Routh-Hurwitz criterion in [1,2] and Eq (2.7), we have:

Lemma 2.1. *For the predator-prey system* (1.5) *with* $\tau = 0$,

(i) *if* $\dfrac{x_0}{K} > \dfrac{2x_0^2y_0}{(a+x_0^2)^2} + \dfrac{px_0E_0}{(1+mx_0)^2[(p-cm)x_0-c]} + \dfrac{mx_0E_0}{(1+mx_0)^2}$ *and* $x_0^2 < a$, *then the interior equilibrium* X_0 *of system* (1.5) *is locally asymptotically stable*;

(ii) *if* $\dfrac{x_0}{K} < \dfrac{2x_0^2y_0}{(a+x_0^2)^2} + \dfrac{px_0E_0}{(1+mx_0)^2[(p-cm)x_0-c]} + \dfrac{mx_0E_0}{(1+mx_0)^2}$, *then the interior equilibrium* X_0 *of system* (1.5) *is unstable.*

Next, we investigate the variation of gestation delay τ on the stability of interior equilibrium X_0. Let $\lambda = i\omega$ ($\omega > 0$) be a root of the characteristic equation (2.6), and substituting it into (2.6), the positive constant ω should satisfy

$$\begin{aligned} -\omega^2 + \Bigg(\frac{x_0}{K}\cos\omega\tau - \frac{x_0}{K}i\sin\omega\tau - \frac{2x_0^2y_0}{(a+x_0^2)^2} - \frac{px_0E_0}{(1+mx_0)^2[(p-cm)x_0-c]} \\ - \frac{mx_0E_0}{(1+mx_0)^2}\Bigg)i\omega + \frac{\mu x_0y_0(a-x_0^2)}{(a+x_0^2)^3} = 0. \end{aligned}$$

Separating the real and imaginary parts of the above equation yields

$$\begin{aligned} -\omega^2 + \frac{x_0}{K}\omega\sin\omega\tau + \frac{\mu x_0y_0(a-x_0^2)}{(a+x_0^2)^3} + \Bigg(\frac{x_0}{K}\omega\cos\omega\tau - \frac{2\omega x_0^2y_0}{(a+x_0^2)^2} \\ - \frac{p\omega x_0E_0}{(1+mx_0)^2[(p-cm)x_0-c]} - \frac{m\omega x_0E_0}{(1+mx_0)^2}\Bigg)i = 0, \end{aligned}$$

which leads to

$$\sin\omega\tau = \frac{K\omega}{x_0} - \frac{K\mu y_0(a-x_0^2)}{\omega(a+x_0^2)^3}, \tag{2.8}$$

$$\cos \omega\tau = \frac{2Kx_0y_0}{(a+x_0^2)^2} + \frac{pKE_0}{(1+mx_0)^2[(p-cm)x_0-c]} + \frac{mKE_0}{(1+mx_0)^2}. \tag{2.9}$$

Adding up the squares of the corresponding sides of Eqs (2.8) and (2.9), one has

$$\omega^4 + \Bigg[\bigg(\frac{2x_0^2y_0}{(a+x_0^2)^2} + \frac{px_0E_0}{(1+mx_0)^2[(p-cm)x_0-c]} + \frac{mx_0E_0}{(1+mx_0)^2}\bigg)^2 - \frac{2\mu x_0y_0(a-x_0^2)}{(a+x_0^2)^3} - \frac{x_0^2}{K^2}\Bigg]\omega^2 + \frac{\mu^2x_0^2y_0^2(a-x_0^2)^2}{(a+x_0^2)^6} = 0, \tag{2.10}$$

with two cases to consider:

Case I. If

$$\bigg(\frac{2x_0^2y_0}{(a+x_0^2)^2} + \frac{px_0E_0}{(1+mx_0)^2[(p-cm)x_0-c]} + \frac{mx_0E_0}{(1+mx_0)^2}\bigg)^2 > \frac{2\mu x_0y_0(a-x_0^2)}{(a+x_0^2)^3} + \frac{x_0^2}{K^2},$$

then Eq (2.10) does not have positive roots. Thus, Eq (2.6) does not have purely imaginary roots. Moreover, if $\frac{x_0}{K} > \frac{2x_0^2y_0}{(a+x_0^2)^2} + \frac{px_0E_0}{(1+mx_0)^2[(p-cm)x_0-c]} + \frac{mx_0E_0}{(1+mx_0)^2}$ and $x_0^2 < a$, then all roots of Eq (2.7) have negative real parts. Thus, by Rouche's theorem in [36], the roots of Eq (2.6) also have negative real parts.

Case II. If

$$\Delta > 0 \text{ and } \bigg(\frac{2x_0^2y_0}{(a+x_0^2)^2} + \frac{px_0E_0}{(1+mx_0)^2[(p-cm)x_0-c]} + \frac{mx_0E_0}{(1+mx_0)^2}\bigg)^2 < \frac{2\mu x_0y_0(a-x_0^2)}{(a+x_0^2)^3} + \frac{x_0^2}{K^2},$$

where

$$\Delta = \Bigg[\bigg(\frac{2x_0^2y_0}{(a+x_0^2)^2} + \frac{px_0E_0}{(1+mx_0)^2[(p-cm)x_0-c]} + \frac{mx_0E_0}{(1+mx_0)^2}\bigg)^2 - \frac{2\mu x_0y_0(a-x_0^2)}{(a+x_0^2)^3} - \frac{x_0^2}{K^2}\Bigg]^2 - \frac{4\mu^2x_0^2y_0^2(a-x_0^2)^2}{(a+x_0^2)^6},$$

then Eq (2.10) has two positive roots ω^+ and ω^-:

$$\omega^{\pm} = \Bigg\{\frac{1}{2}\Bigg[\frac{2\mu x_0y_0(a-x_0^2)}{(a+x_0^2)^3} + \frac{x_0^2}{K^2} - \bigg(\frac{2x_0^2y_0}{(a+x_0^2)^2} + \frac{px_0E_0}{(1+mx_0)^2[(p-cm)x_0-c]} + \frac{mx_0E_0}{(1+mx_0)^2}\bigg)^2 \pm \sqrt{\Delta}\Bigg]\Bigg\}^{1/2}. \tag{2.11}$$

The above two cases can be concluded as the following Lemma 2.2:

Lemma 2.2. *For the predator-prey system* (1.5),

(i) *if*

$$\frac{x_0}{K} > \frac{2x_0^2y_0}{(a+x_0^2)^2} + \frac{px_0E_0}{(1+mx_0)^2[(p-cm)x_0-c]} + \frac{mx_0E_0}{(1+mx_0)^2}, \quad x_0^2 < a \quad \textit{and}$$

$$\left(\frac{2x_0^2y_0}{(a+x_0^2)^2}+\frac{px_0E_0}{(1+mx_0)^2[(p-cm)x_0-c]}+\frac{mx_0E_0}{(1+mx_0)^2}\right)^2>\frac{2\mu x_0y_0(a-x_0^2)}{(a+x_0^2)^3}+\frac{x_0^2}{K^2},$$

then all the roots of the characteristic equation (2.6) *have negative real parts for all* $\tau>0$;

(ii) *if*

$$\Delta>0 \ \textit{and} \ \left(\frac{2x_0^2y_0}{(a+x_0^2)^2}+\frac{px_0E_0}{(1+mx_0)^2[(p-cm)x_0-c]}+\frac{mx_0E_0}{(1+mx_0)^2}\right)^2<\frac{2\mu x_0y_0(a-x_0^2)}{(a+x_0^2)^3}+\frac{x_0^2}{K^2},$$

then the characteristic equation (2.6) *has two positive roots* ω^+ *and* ω^-. *Substituting* $\omega^\pm$ *into the* Eq (2.9) *and solving for* τ*, we have*

$$\tau_k^\pm=\frac{1}{\omega^\pm}\arccos\left(\frac{2Kx_0y_0}{(a+x_0^2)^2}+\frac{pKE_0}{(1+mx_0)^2[(p-cm)x_0-c]}+\frac{mKE_0}{(1+mx_0)^2}\right)+\frac{2k\pi}{\omega^\pm},\ \ k=0,1,2,\cdots. \tag{2.12}$$

Taking the derivative of λ with respect to τ in Eq (2.6), we get

$$\begin{aligned}2\lambda\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}-\Big(\frac{x_0}{K}\lambda\tau e^{-\lambda\tau}+\frac{2x_0^2y_0}{(a+x_0^2)^2}+\frac{px_0E_0}{(1+mx_0)^2[(p-cm)x_0-c]}\\+\frac{mx_0E_0}{(1+mx_0)^2}-\frac{x_0}{K}e^{-\lambda\tau}\Big)\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}-\frac{x_0}{K}\lambda^2e^{-\lambda\tau}=0.\end{aligned}$$

It follows that

$$\begin{aligned}\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)^{-1}=\frac{1}{\lambda^2}-\frac{\tau}{\lambda}+\Big(\frac{2K}{\lambda x_0}-\frac{2Kx_0y_0}{\lambda^2(a+x_0^2)^2}-\frac{mKE_0}{\lambda^2(1+mx_0)^2}\\-\frac{pKE_0}{\lambda^2(1+mx_0)^2[(p-cm)x_0-c]}\Big)e^{\lambda\tau}.\end{aligned}$$

Therefore,

$$\begin{aligned}\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)^{-1}\Bigg|_{\lambda=i\omega}&=\frac{2K}{x_0}\left(-\frac{i}{\omega}\right)(\cos\omega\tau+i\sin\omega\tau)-\frac{1}{\omega^2}+\frac{\tau}{\omega}i+\Big\{\frac{2Kx_0y_0}{\omega^2(a+x_0^2)^2}+\frac{mKE_0}{\omega^2(1+mx_0)^2}\\&\quad+\frac{pKE_0}{\omega^2(1+mx_0)^2[(p-cm)x_0-c]}\Big\}(\cos\omega\tau+i\sin\omega\tau)\\&=-\frac{1}{\omega^2}+\frac{2K}{\omega x_0}\sin\omega\tau+\Big\{\frac{2Kx_0y_0}{\omega^2(a+x_0^2)^2}+\frac{mKE_0}{\omega^2(1+mx_0)^2}\\&\quad+\frac{pKE_0}{\omega^2(1+mx_0)^2[(p-cm)x_0-c]}\Big\}\cos\omega\tau\\&\quad+i\Big\{\frac{\tau}{\omega}-\frac{2K}{\omega x_0}\cos\omega\tau+\Big(\frac{2Kx_0y_0}{\omega^2(a+x_0)^2}+\frac{mKE_0}{\omega^2(1+mx_0)^2}\\&\quad+\frac{pKE_0}{\omega^2(1+mx_0)^2[(p-cm)x_0-c]}\Big)\sin\omega\tau\Big\}.\end{aligned}$$

Substituting Eqs (2.8) and (2.9) into the above equation yields,

$$
\begin{aligned}
&\operatorname{sign}\left\{\operatorname{Re}\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)\right\}\bigg|_{\lambda=i\omega} = \operatorname{sign}\left\{\operatorname{Re}\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)^{-1}\right\}\bigg|_{\lambda=i\omega}\\
&=\operatorname{sign}\bigg\{-\frac{1}{\omega^2}+\frac{2K}{\omega x_0}\left(\frac{K\omega}{x_0}-\frac{\mu K y_0(a-x_0^2)}{\omega(a+x_0^2)^3}\right)\\
&\quad+\frac{1}{\omega^2}\left(\frac{2Kx_0y_0}{(a+x_0^2)^2}+\frac{mKE_0}{(1+mx_0)^2}+\frac{pKE_0}{(1+mx_0)^2[(p-cm)x_0-c]}\right)^2\bigg\}\\
&=\operatorname{sign}\bigg\{\frac{K^2}{\omega^2x_0^2}\bigg[2\omega^2-\frac{x_0^2}{K^2}-\frac{2\mu x_0y_0(a-x_0^2)}{(a+x_0^2)^3}\\
&\quad+\left(\frac{2x_0^2y_0}{(a+x_0^2)^2}+\frac{mx_0E_0}{(1+mx_0)^2}+\frac{px_0E_0}{(1+mx_0)^2[(p-cm)x_0-c]}\right)^2\bigg]\bigg\}.
\end{aligned}
$$

Then we can obtain that

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

Hence, the transversality conditions are satisfied.

Summarizing the above discussion and combining this with the theory of functional differential equations in [28] enable us to derive the main result in this section:

Theorem 2.1. *Suppose that predator-prey system* (1.5) *satisfies*

$$
\frac{x_0}{K} > \frac{2x_0^2y_0}{(a+x_0^2)^2}+\frac{px_0E_0}{(1+mx_0)^2[(p-cm)x_0-c]}+\frac{mx_0E_0}{(1+mx_0)^2} \ \textit{and} \ x_0^2 < a,
$$

(i) *if*

$$
\left(\frac{2x_0^2y_0}{(a+x_0^2)^2}+\frac{px_0E_0}{(1+mx_0)^2[(p-cm)x_0-c]}+\frac{mx_0E_0}{(1+mx_0)^2}\right)^2 > \frac{2\mu x_0y_0(a-x_0^2)}{(a+x_0^2)^3}+\frac{x_0^2}{K^2},
$$

then all the roots of the characteristic equation (2.6) *have negative real parts for all* $\tau > 0$, *and consequently the interior equilibrium* X_0 *of system* (1.5) *is locally asymptotically stable*;

(ii) *if*

$$
\Delta > 0 \ \textit{and} \ \left(\frac{2x_0^2y_0}{(a+x_0^2)^2}+\frac{px_0E_0}{(1+mx_0)^2[(p-cm)x_0-c]}+\frac{mx_0E_0}{(1+mx_0)^2}\right)^2 < \frac{2\mu x_0y_0(a-x_0^2)}{(a+x_0^2)^3}+\frac{x_0^2}{K^2},
$$

then there is a positive integer N, *such that the interior equilibrium* X_0 *of system* (1.5) *is locally asymptotically stable when* $\tau \in [0,\tau_0^+)\bigcup\left(\bigcup_{n=0}^{N-1}(\tau_n^-,\tau_{n+1}^+)\right)$, *and the interior equilibrium* X_0 *is unstable when* $\tau \in \left(\bigcup_{n=0}^{N-1}(\tau_n^+,\tau_n^-)\right)\bigcup(\tau_N^+,+\infty)$. *Thus, Hopf bifurcations occur at the interior equilibrium* X_0 *of system* (1.5) *when* $\tau=\tau_n^\pm$, $n=0,1,2,\cdots,N$.

Remark 2.1. *For the predator-prey system* (1.5) *with* $\tau = 0$*, if*

$$\frac{x_0}{K} = \frac{2x_0^2 y_0}{(a+x_0^2)^2} + \frac{p x_0 E_0}{(1+mx_0)^2[(p-cm)x_0 - c]} + \frac{m x_0 E_0}{(1+mx_0)^2},$$

then Eq (2.7) *has a pair of conjugate complex roots. Consequently, Hopf bifurcation may also occur in this circumstance, and the properties of the Hopf bifurcation can be investigated using the normal form method and Hopf bifurcation theorem of Guckenheimer et al.* [26].

3. Direction and stability of the Hopf bifurcations

It is well-known that the center manifold theorem in [29] is a useful tool for determining the direction and stability of the bifurcating periodic orbits arising through Hopf bifurcations. In order to use the center manifold theorem, we need to derive the second order Taylor series developments of parameterised system (2.4) at the point $\overline{X}_0$, which takes the form of

$$\begin{cases} \dot{y}_1 = \Big(\frac{2x_0^2 y_0}{(a+x_0^2)^2} + \frac{m x_0 E_0}{(1+mx_0)^2} + \frac{p x_0 E_0}{(1+mx_0)^2[(p-cm)x_0-c]}\Big) y_1 \\ \quad -\frac{x_0}{K} y_1(t-\tau) - \frac{x_0}{a+x_0^2} y_2 + \Big(\frac{x_0 y_0 (3a - x_0^2)}{(a+x_0^2)^3} + \frac{mE_0}{(1+mx_0)^3} \\ \quad -\frac{p x_0 E_0 (p-cm)}{2(1+mx_0)^2[(p-cm)x_0-c]^2} + \frac{pE_0(2-mx_0)}{2(1+mx_0)^3[(p-cm)x_0-c]} \\ \quad -\frac{p^2 x_0 E_0}{2(1+mx_0)^3[(p-cm)x_0-c]^2}\Big) y_1^2 - \frac{1}{K} y_1^2(t-\tau) + \frac{x_0^2 - a}{(a+x_0^2)^2} y_1 y_2 + o\,(|Y|^3), \\ \dot{y}_2 = \frac{\mu y_0 (a - x_0^2)}{(a+x_0^2)^2} y_1 + \frac{\mu x_0 y_0 (x_0^2 - 3a)}{(a+x_0^2)^3} y_1^2 + \frac{\mu (a - x_0^2)}{(a+x_0^2)^2} y_1 y_2 + o\,(|Y|^3). \end{cases} \tag{3.1}$$

The computation procedure of Eq (3.1) is provided in Appendix B.

We assume that predator-prey system (1.5) undergoes a Hopf bifurcation at the interior equilibrium X_0 when $\tau = \tau_n$, and let $i\omega$ be the corresponding purely imaginary root of the characteristic equation (2.6). Here, we make the following transformation for the Taylor series developments (3.1):

$$y_1 = x - x_0,\ y_2 = y - y_0,\ t = t\tau,\ \tau = \tau_n + \mu,$$

then system (3.1) is transformed into the functional differential equation system in the phase space $C := C([-1, 0], \mathrm{R}^2)$:

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

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

$$L_\mu \Phi = (\tau_n + \mu) \begin{pmatrix} \frac{2x_0^2 y_0}{(a+x_0^2)^2} + \frac{m x_0 E_0}{(1+mx_0)^2} + \frac{p x_0 E_0}{(1+mx_0)^2[(p-cm)x_0-c]} & -\frac{x_0}{a+x_0^2} \\ \frac{\mu y_0 (a - x_0^2)}{(a+x_0^2)^2} & 0 \end{pmatrix} \Phi^T(0)$$

$$+(\tau_n+\mu)\begin{pmatrix} -\frac{x_0}{K} & 0 \\ 0 & 0 \end{pmatrix}\Phi^T(-1),$$

$$F(\mu,\Phi)=(\tau_n+\mu)\,(F_{11},\ F_{22})^T,$$

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

$$\begin{aligned} F_{11}=&\Big(\frac{x_0(3a-x_0^2)y_0}{(a+x_0^2)^3}+\frac{mE_0}{(1+mx_0)^3}-\frac{p(p-cm)x_0E_0}{2(1+mx_0)^2[(p-cm)x_0-c]^2}\\ &+\frac{p(2-mx_0)E_0}{2(1+mx_0)^3[(p-cm)x_0-c]}-\frac{p^2x_0E_0}{2(1+mx_0)^3[(p-cm)x_0-c]^2}\Big)\Phi_1^2(0)\\ &-\frac{1}{K}\Phi_1^2(-1)+\frac{x_0^2-a}{(a+x_0^2)^2}\Phi_1(0)\Phi_2(0)+\cdots,\\ F_{22}=&\frac{\mu x_0y_0(x_0^2-3a)}{(a+x_0^2)^3}\Phi_1^2(0)+\frac{\mu(a-x_0^2)}{(a+x_0^2)^2}\Phi_1(0)\Phi_2(0)+\cdots. \end{aligned}$$

On the grounds of Riesz representation theorem [28], there exists a matrix function $\eta(\theta,\mu)$ whose elements are bounded variations for $\theta\in[-1,0]$, such that

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

where $\Phi\in C$, and

$$\begin{aligned}\eta(\theta,\mu)=&(\tau_n+\mu)\begin{pmatrix} \frac{2x_0^2y_0}{(a+x_0^2)^2}+\frac{mx_0E_0}{(1+mx_0)^2}+\frac{px_0E_0}{(1+mx_0)^2[(p-cm)x_0-c]} & -\frac{x_0}{a+x_0^2} \\ \frac{\mu y_0(a-x_0^2)}{(a+x_0^2)^2} & 0 \end{pmatrix}\delta(\theta)\\ &+(\tau_n+\mu)\begin{pmatrix} \frac{x_0}{K} & 0 \\ 0 & 0 \end{pmatrix}\delta(\theta+1),\ \text{where}\ \delta(\theta)=\begin{cases}0, & \theta\neq 0,\\ 1, & \theta=0.\end{cases}\end{aligned}$$

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

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

and

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

then the functional differential equation system (3.2) is equivalent to

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

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

For $\Psi \in C^1([0,1],(\mathrm{R}^2)^*)$, let us define the adjoint operator A^* of $A(0)$,

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

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

In view of the theoretical analysis in Section 2, we know that $\pm i\omega\tau_n$ are the eigenvalues of operator $A(0)$. Due to $A(0)$ and A^* being adjoint operators, $\pm i\omega\tau_n$ are also the eigenvalues of operator A^*. Let $q(\theta) = (1, q_2)^T e^{i\omega\tau_n\theta}$ be the eigenvector of operator $A(0)$ corresponding to the eigenvalue $i\omega\tau_n$, and $q^*(s) = \frac{1}{Q}(q_2^*, 1)e^{i\omega\tau_n s}$ be the eigenvector of operator A^* corresponding to the eigenvalue $-i\omega\tau_n$. Then, one can calculate

$$\begin{aligned} q_2 &= \frac{2x_0y_0}{a+x_0^2} + \frac{m(a+x_0^2)E_0}{(1+mx_0)^2} + \frac{p(a+x_0^2)E_0}{(1+mx_0)^2[(p-cm)x_0-c]} - \frac{(a+x_0^2)i\omega}{x_0} - \frac{(a+x_0^2)e^{-i\omega\tau_n}}{K}, \\ q_2^* &= \frac{i\omega(a+x_0^2)}{x_0}, \ \ \bar{Q} = q_2 + \bar{q}_2^* + \frac{\bar{q}_2^* x_0\tau_n e^{-i\omega\tau_n}}{K}, \end{aligned}$$

where q_2 and q_2^* satisfy the requirements $< q^*, q > = 1$ and $< q^*, \bar{q} > = 0$.

In the light of the center manifold theory proposed by Hassard et al. in [29], in what follows, we ought to calculate the coordinates to describe the center manifold C_0 at $\mu = 0$. We define

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

Subsequently, on the center manifold C_0, we have

$$W(t,\theta) = W(z,\bar{z},\theta) = W_{20}(\theta)\frac{z^2}{2} + W_{11}(\theta)z\bar{z} + W_{02}(\theta)\frac{\bar{z}^2}{2} + \cdots, \tag{3.4}$$

where z and $\bar{z}$ are the local coordinates for center manifold C_0 in the directions of q and $\bar{q}^*$, respectively. It is notable that W is real if Y_t is real. Consequently, we consider only real solutions. For the real solution $Y_t \in C_0$, since $\mu = 0$, from system (3.3), we can obtain

$$\dot{z} = i\omega\tau_n z + \bar{q}^*(0)F_0(z,\bar{z}) = i\omega\tau_n z + g(z,\bar{z}), \tag{3.5}$$

where

$$g(z,\bar{z}) = g_{20}(\theta)\frac{z^2}{2} + g_{11}(\theta)z\bar{z} + g_{02}(\theta)\frac{\bar{z}^2}{2} + g_{21}(\theta)\frac{z^2\bar{z}}{2} + \cdots. \tag{3.6}$$

By Eqs (3.5) and (3.6), we have

$$g(z,\bar{z}) = \bar{q}^*(0)F_0(z,\bar{z}) = \frac{1}{\bar{Q}}\tau_n(\bar{q}_2^*, 1)\begin{pmatrix} F_{11}^0 \\ F_{22}^0 \end{pmatrix}, \tag{3.7}$$

where

$$F_{11}^{0} = \Big(\frac{x_0y_0(3a - x_0^2)}{(a + x_0^2)^3} + \frac{mE_0}{(1 + mx_0)^3} - \frac{p(p - cm)x_0E_0}{2(1 + mx_0)^2[(p - cm)x_0 - c]^2} + \frac{pE_0(2 - mx_0)}{2(1 + mx_0)^3[(p - cm)x_0 - c]} - \frac{p^2x_0E_0}{2(1 + mx_0)^3[(p - cm)x_0 - c]^2}\Big)y_{1t}^2(0) - \frac{1}{K}y_{1t}^2(-1) + \frac{x_0^2 - a}{(a + x_0^2)^2}y_{1t}(0)y_{2t}(0) + \cdots,$$

$$F_{22}^{0} = \frac{\mu x_0y_0(x_0^2 - 3a)}{(a + x_0^2)^3}y_{1t}^2(0) + \frac{\mu(a - x_0^2)}{(a + x_0^2)^2}y_{1t}(0)y_{2t}(0) + \cdots.$$

It follows from Eqs (3.4) and (3.7) that

$$\begin{aligned} g(z, \bar{z}) = \frac{\tau_n}{\bar{Q}}\Big\{\Big[&\frac{\bar{q}_2^*x_0y_0(3a - x_0^2)}{(a + x_0^2)^3} + \frac{m\bar{q}_2^*E_0}{(1 + mx_0)^3} - \frac{p\bar{q}_2^*x_0E_0(p - cm)}{2(1 + mx_0)^2[(p - cm)x_0 - c]^2} \\ &+ \frac{p\bar{q}_2^*E_0(2 - mx_0)}{2(1 + mx_0)^3[(p - cm)x_0 - c]} - \frac{p^2\bar{q}_2^*x_0E_0}{2(1 + mx_0)^3[(p - cm)x_0 - c]^2}\Big] \\ &\times\Big[z + \bar{z} + W_{20}^{(1)}(0)\frac{z^2}{2} + W_{11}^{(1)}(0)z\bar{z} + W_{02}^{(1)}(0)\frac{\bar{z}^2}{2}\Big]^2 \\ &- \frac{\bar{q}_2^*}{K}\Big[ze^{-i\omega\tau_n\theta} + \bar{z}e^{i\omega\tau_n\theta} + W_{20}^{(1)}(-1)\frac{z^2}{2} + W_{11}^{(1)}(-1)z\bar{z} + W_{02}^{(1)}(-1)\frac{\bar{z}^2}{2}\Big]^2 \\ &+ \frac{\bar{q}_2^*(x_0^2 - a)}{(a + x_0^2)^2}\Big[z + \bar{z} + W_{20}^{(1)}(0)\frac{z^2}{2} + W_{11}^{(1)}(0)z\bar{z} + W_{02}^{(1)}(0)\frac{\bar{z}^2}{2}\Big] \\ &\times\Big[q_2z + \bar{q}_2\bar{z} + W_{20}^{(2)}(0)\frac{z^2}{2} + W_{11}^{(2)}(0)z\bar{z} + W_{02}^{(2)}(0)\frac{\bar{z}^2}{2}\Big] \\ &+ \frac{\mu x_0y_0(x_0^2 - 3a)}{(a + x_0^2)^3}\Big[z + \bar{z} + W_{20}^{(1)}(0)\frac{z^2}{2} + W_{11}^{(1)}(0)z\bar{z} + W_{02}^{(1)}(0)\frac{\bar{z}^2}{2}\Big]^2 \\ &+ \frac{\mu(a - x_0^2)}{(a + x_0^2)^2}\Big[z + \bar{z} + W_{20}^{(1)}(0)\frac{z^2}{2} + W_{11}^{(1)}(0)z\bar{z} + W_{02}^{(1)}(0)\frac{\bar{z}^2}{2}\Big] \\ &\times\Big[q_2z + \bar{q}_2\bar{z} + W_{20}^{(2)}(0)\frac{z^2}{2} + W_{11}^{(2)}(0)z\bar{z} + W_{02}^{(2)}(0)\frac{\bar{z}^2}{2}\Big] + \cdots\Big\}. \end{aligned}$$

That is,

$$\begin{aligned} g(z, \bar{z}) = \frac{\tau_n}{\bar{Q}}\Big\{z^2\Big[&\frac{\bar{q}_2^*x_0y_0(3a - x_0^2)}{(a + x_0^2)^3} + \frac{m\bar{q}_2^*E_0}{(1 + mx_0)^3} - \frac{p(p - cm)\bar{q}_2^*x_0E_0}{2(1 + mx_0)^2[(p - cm)x_0 - c]^2} \\ &+ \frac{p\bar{q}_2^*(2 - mx_0)E_0}{2(1 + mx_0)^3[(p - cm)x_0 - c]} - \frac{p^2\bar{q}_2^*x_0E_0}{2(1 + mx_0)^3[(p - cm)x_0 - c]^2} \\ &- \frac{\bar{q}_2^*}{K}e^{-2i\omega\tau_n\theta} + \frac{q_2\bar{q}_2^*(x_0^2 - a)}{(a + x_0^2)^2} + \frac{\mu q_2(a - x_0^2)}{(a + x_0^2)^2} + \frac{\mu x_0y_0(x_0^2 - 3a)}{(a + x_0^2)^3}\Big] \\ &+ z\bar{z}\Big[\frac{2\bar{q}_2^*x_0y_0(3a - x_0^2)}{(a + x_0^2)^3} + \frac{2m\bar{q}_2^*E_0}{(1 + mx_0)^3} - \frac{p(p - cm)\bar{q}_2^*x_0E_0}{(1 + mx_0)^2[(p - cm)x_0 - c]^2} \end{aligned}$$

$$
\begin{aligned}
&+ \frac{p(2-mx_0)\bar{q}_2^* E_0}{(1+mx_0)^3[(p-cm)x_0-c]} - \frac{p^2\bar{q}_2^* x_0 E_0}{(1+mx_0)^3[(p-cm)x_0-c]^2} - \frac{2\bar{q}_2^*}{K} \\
&+ \frac{2\bar{q}_2^*(x_0^2-a)}{(a+x_0^2)^2}\mathrm{Re}(q_2) + \frac{2\mu(a-x_0^2)}{(a+x_0^2)^2}\mathrm{Re}(q_2) + \frac{2\mu x_0 y_0(x_0^2-3a)}{(a+x_0^2)^3}\Big] \\
&+ \bar{z}^2\Big[\frac{\bar{q}_2^* x_0 y_0(3a-x_0^2)}{(a+x_0^2)^3} + \frac{m\bar{q}_2^* E_0}{(1+mx_0)^3} - \frac{p(p-cm)\bar{q}_2^* x_0 E_0}{2(1+mx_0)^2[(p-cm)x_0-c]^2} \\
&+ \frac{p\bar{q}_2^*(2-mx_0)E_0}{2(1+mx_0)^3[(p-cm)x_0-c]} - \frac{p^2\bar{q}_2^* x_0 E_0}{2(1+mx_0)^3[(p-cm)x_0-c]^2} \\
&- \frac{\bar{q}_2^*}{K}e^{2i\omega\tau_n\theta} + \frac{(x_0^2-a)}{(a+x_0^2)^2}\bar{q}_2\bar{q}_2^* + \frac{\mu\bar{q}_2(a-x_0^2)}{(a+x_0^2)^2} + \frac{\mu x_0 y_0(x_0^2-3a)}{(a+x_0^2)^3}\Big] \\
&+ z^2\bar{z}\Big[\Big(\frac{2\bar{q}_2^* x_0 y_0(3a-x_0^2)}{(a+x_0^2)^3} + \frac{2m\bar{q}_2^* E_0}{(1+mx_0)^3} - \frac{p(p-cm)\bar{q}_2^* x_0 E_0}{(1+mx_0)^2[(p-cm)x_0-c]^2} \\
&+ \frac{p\bar{q}_2^*(2-mx_0)E_0}{(1+mx_0)^3[(p-cm)x_0-c]} - \frac{p^2\bar{q}_2^* x_0 E_0}{(1+mx_0)^3[(p-cm)x_0-c]^2} \\
&+ \frac{q_2\bar{q}_2^*(x_0^2-a)}{(a+x_0^2)^2} + \frac{\mu q_2(a-x_0^2)}{(a+x_0^2)^2} + \frac{2\mu x_0 y_0(x_0^2-3a)}{(a+x_0^2)^3}\Big)W_{11}^{(1)}(0) \\
&+ \Big(\frac{\bar{q}_2^*(x_0^2-a)}{(a+x_0^2)^2} + \frac{\mu(a-x_0^2)}{(a+x_0^2)^2}\Big)W_{11}^{(2)}(0) \\
&+ \Big(\frac{\bar{q}_2^* x_0 y_0(3a-x_0^2)}{(a+x_0^2)^3} + \frac{m\bar{q}_2^* E_0}{(1+mx_0)^3} - \frac{p(p-cm)\bar{q}_2^* x_0 E_0}{2(1+mx_0)^2[(p-cm)x_0-c]^2} \\
&+ \frac{p\bar{q}_2^*(2-mx_0)E_0}{2(1+mx_0)^3[(p-cm)x_0-c]} - \frac{p^2\bar{q}_2^* x_0 E_0}{2(1+mx_0)^3[(p-cm)x_0-c]^2} \\
&+ \frac{\bar{q}_2\bar{q}_2^*(x_0^2-a)}{2(a+x_0^2)^2} + \frac{\mu\bar{q}_2(a-x_0^2)}{2(a+x_0^2)^2} + \frac{\mu x_0 y_0(x_0^2-3a)}{(a+x_0^2)^3}\Big)W_{20}^{(1)}(0) \\
&+ \Big(\frac{\bar{q}_2^*(x_0^2-a)}{2(a+x_0^2)^2} + \frac{\mu(a-x_0^2)}{2(a+x_0^2)^2}\Big)W_{20}^{(2)}(0) - \frac{2\bar{q}_2^*}{K}e^{-i\omega\tau_n\theta}W_{11}^{(1)}(-1) - \frac{\bar{q}_2^*}{K}e^{i\omega\tau_n\theta}W_{20}^{(1)}(-1)\Big] + \cdots\Big\}.
\end{aligned} \tag{3.8}
$$

Comparing the coefficients of Eqs (3.6) and (3.8) produces

$$
\begin{aligned}
g_{20} = \frac{2\tau_n}{\bar{Q}}\Big[&\frac{\bar{q}_2^* x_0 y_0(3a-x_0^2)}{(a+x_0^2)^3} + \frac{m\bar{q}_2^* E_0}{(1+mx_0)^3} - \frac{p(p-cm)\bar{q}_2^* x_0 E_0}{2(1+mx_0)^2[(p-cm)x_0-c]^2} \\
&+ \frac{p\bar{q}_2^*(2-mx_0)E_0}{2(1+mx_0)^3[(p-cm)x_0-c]} - \frac{p^2\bar{q}_2^* x_0 E_0}{2(1+mx_0)^3[(p-cm)x_0-c]^2} \\
&- \frac{\bar{q}_2^*}{K}e^{-2i\omega\tau_n\theta} + \frac{q_2\bar{q}_2^*(x_0^2-a)}{(a+x_0^2)^2} + \frac{\mu q_2(a-x_0^2)}{(a+x_0^2)^2} + \frac{\mu x_0 y_0(x_0^2-3a)}{(a+x_0^2)^3}\Big], \\
g_{11} = \frac{\tau_n}{\bar{Q}}\Big[&\frac{2\bar{q}_2^* x_0 y_0(3a-x_0^2)}{(a+x_0^2)^3} + \frac{2m\bar{q}_2^* E_0}{(1+mx_0)^3} - \frac{p(p-cm)\bar{q}_2^* x_0 E_0}{(1+mx_0)^2[(p-cm)x_0-c]^2}
\end{aligned}
$$

$$+\frac{p\bar{q}_2^*(2-mx_0)E_0}{(1+mx_0)^3[(p-cm)x_0-c]}-\frac{p^2\bar{q}_2^*x_0E_0}{(1+mx_0)^3[(p-cm)x_0-c]^2}$$
$$-\frac{2\bar{q}_2^*}{K}+\frac{2\bar{q}_2^*(x_0^2-a)}{(a+x_0^2)^2}\mathrm{Re}(q_2)+\frac{2\mu(a-x_0^2)}{(a+x_0^2)^2}\mathrm{Re}(q_2)+\frac{2\mu x_0y_0(x_0^2-3a)}{(a+x_0^2)^3}\Big],$$

$$g_{02}=\frac{2\tau_n}{\bar{Q}}\Big[\frac{\bar{q}_2^*x_0y_0(3a-x_0^2)}{(a+x_0^2)^3}+\frac{m\bar{q}_2^*E_0}{(1+mx_0)^3}-\frac{p(p-cm)\bar{q}_2^*x_0E_0}{2(1+mx_0)^2[(p-cm)x_0-c]^2}$$
$$+\frac{p\bar{q}_2^*(2-mx_0)E_0}{2(1+mx_0)^3[(p-cm)x_0-c]}-\frac{p^2\bar{q}_2^*x_0E_0}{2(1+mx_0)^3[(p-cm)x_0-c]^2}$$
$$-\frac{\bar{q}_2^*}{K}e^{2i\omega\tau_n\theta}+\frac{(x_0^2-a)}{(a+x_0^2)^2}\bar{q}_2\bar{q}_2^*+\frac{\mu\bar{q}_2(a-x_0^2)}{(a+x_0^2)^2}+\frac{\mu x_0y_0(x_0^2-3a)}{(a+x_0^2)^3}\Big],$$

$$g_{21}=\frac{2\tau_n}{\bar{Q}}\Big[\Big(\frac{2\bar{q}_2^*x_0y_0(3a-x_0^2)}{(a+x_0^2)^3}+\frac{2m\bar{q}_2^*E_0}{(1+mx_0)^3}-\frac{p(p-cm)\bar{q}_2^*x_0E_0}{(1+mx_0)^2[(p-cm)x_0-c]^2}$$
$$+\frac{p\bar{q}_2^*(2-mx_0)E_0}{(1+mx_0)^3[(p-cm)x_0-c]}-\frac{p^2\bar{q}_2^*x_0E_0}{(1+mx_0)^3[(p-cm)x_0-c]^2}$$
$$+\frac{q_2\bar{q}_2^*(x_0^2-a)}{(a+x_0^2)^2}+\frac{\mu q_2(a-x_0^2)}{(a+x_0^2)^2}+\frac{2\mu x_0y_0(x_0^2-3a)}{(a+x_0^2)^3}\Big)W_{11}^{(1)}(0)$$
$$+\Big(\frac{\bar{q}_2^*(x_0^2-a)}{(a+x_0^2)^2}+\frac{\mu(a-x_0^2)}{(a+x_0^2)^2}\Big)W_{11}^{(2)}(0)$$
$$+\Big(\frac{\bar{q}_2^*x_0y_0(3a-x_0^2)}{(a+x_0^2)^3}+\frac{m\bar{q}_2^*E_0}{(1+mx_0)^3}-\frac{p(p-cm)\bar{q}_2^*x_0E_0}{2(1+mx_0)^2[(p-cm)x_0-c]^2}$$
$$+\frac{p\bar{q}_2^*(2-mx_0)E_0}{2(1+mx_0)^3[(p-cm)x_0-c]}-\frac{p^2\bar{q}_2^*x_0E_0}{2(1+mx_0)^3[(p-cm)x_0-c]^2}$$
$$+\frac{\bar{q}_2\bar{q}_2^*(x_0^2-a)}{2(a+x_0^2)^2}+\frac{\mu\bar{q}_2(a-x_0^2)}{2(a+x_0^2)^2}+\frac{\mu x_0y_0(x_0^2-3a)}{(a+x_0^2)^3}\Big)W_{20}^{(1)}(0)$$
$$+\Big(\frac{\bar{q}_2^*(x_0^2-a)}{2(a+x_0^2)^2}+\frac{\mu(a-x_0^2)}{2(a+x_0^2)^2}\Big)W_{20}^{(2)}(0)-\frac{2\bar{q}_2^*}{K}e^{-i\omega\tau_n\theta}W_{11}^{(1)}(-1)-\frac{\bar{q}_2^*}{K}e^{i\omega\tau_n\theta}W_{20}^{(1)}(-1)\Big]. \quad (3.9)$$

From Eq (3.9), we can see that the unknown variables $W_{20}(\theta)$ and $W_{11}(\theta)$ appear in the expression of g_{21}. Thus, we need to calculate $W_{20}(\theta)$ and $W_{11}(\theta)$ to determine the concrete expression of g_{21}. Similar to the calculation procedure performed in [29], one can derive that

$$W_{20}(\theta)=\frac{ig_{20}}{\omega\tau_n}q(0)e^{i\omega\tau_n\theta}+\frac{i\bar{g}_{02}}{3\omega\tau_n}\bar{q}(0)e^{-i\omega\tau_n\theta}+M_1e^{2i\omega\tau_n\theta},$$
$$W_{11}(\theta)=-\frac{ig_{11}}{\omega\tau_n}q(0)e^{i\omega\tau_n\theta}+\frac{i\bar{g}_{11}}{\omega\tau_n}\bar{q}(0)e^{-i\omega\tau_n\theta}+M_2, \quad (3.10)$$

where M_1 and M_2 take the forms of

$$M_1=2\begin{pmatrix}2i\omega-\frac{2x_0^2y_0}{(a+x_0^2)^2}-\frac{mx_0E_0}{(1+mx_0)^2}-\frac{px_0E_0}{(1+mx_0)^2[(p-cm)x_0-c]}+\frac{x_0}{K}e^{-2i\omega\tau_n} & \frac{x_0}{a+x_0^2}\\ -\frac{\mu y_0(a-x_0^2)}{(a+x_0^2)^2} & 2i\omega\end{pmatrix}^{-1}\begin{pmatrix}G_{11}\\ G_{21}\end{pmatrix},$$

$$M_2 = 2\begin{pmatrix} \frac{x_0}{K} - \frac{2x_0^2 y_0}{(a+x_0^2)^2} - \frac{mx_0E_0}{(1+mx_0)^2} - \frac{px_0E_0}{(1+mx_0)^2[(p-cm)x_0-c]} & \frac{x_0}{a+x_0^2} \\ -\frac{\mu y_0(a-x_0^2)}{(a+x_0^2)^2} & 0 \end{pmatrix}^{-1} \begin{pmatrix} H_{11} \\ H_{21} \end{pmatrix},$$

with

$$\begin{aligned} G_{11} &= \frac{x_0y_0(3a-x_0^2)}{(a+x_0^2)^3} + \frac{mE_0}{(1+mx_0)^3} - \frac{p(p-cm)x_0E_0}{2(1+mx_0)^2[(p-cm)x_0-c]^2} \\ &\quad + \frac{p(2-mx_0)E_0}{2(1+mx_0)^3[(p-cm)x_0-c]} - \frac{p^2x_0E_0}{2(1+mx_0)^3[(p-cm)x_0-c]^2} \\ &\quad - \frac{1}{K}e^{-2i\omega\tau_n} + \frac{q_2(x_0^2-a)}{(a+x_0^2)^2}, \\ G_{21} &= \frac{\mu q_2(a-x_0^2)}{(a+x_0^2)^2} + \frac{\mu x_0y_0(x_0^2-3a)}{(a+x_0^2)^3}, \\ H_{11} &= \frac{x_0y_0(3a-x_0^2)}{(a+x_0^2)^3} + \frac{mE_0}{(1+mx_0)^3} - \frac{p(p-cm)x_0E_0}{2(1+mx_0)^2[(p-cm)x_0-c]^2} \\ &\quad + \frac{p(2-mx_0)E_0}{2(1+mx_0)^3[(p-cm)x_0-c]} - \frac{p^2x_0E_0}{2(1+mx_0)^3[(p-cm)x_0-c]^2} \\ &\quad - \frac{1}{K} + \frac{x_0^2-a}{(a+x_0^2)^2}\mathrm{Re}(q_2), \\ H_{21} &= \frac{\mu(a-x_0^2)}{(a+x_0^2)^2}\mathrm{Re}(q_2) + \frac{\mu x_0y_0(x_0^2-3a)}{(a+x_0^2)^3}. \end{aligned}$$

Some straightforward calculations give

$$M_1 = \begin{pmatrix} \frac{4G_{11}i\omega}{\xi} - \frac{2x_0}{\xi(a+x_0^2)}G_{21} \\ \frac{2\mu y_0(a-x_0^2)}{\xi(a+x_0^2)^2}G_{11} + \frac{\eta}{\xi}G_{21} \end{pmatrix}_{2\times 1} \quad \text{and} \quad M_2 = \begin{pmatrix} \frac{2(a+x_0^2)^2H_{21}}{\mu y_0(x_0^2-a)} \\ \frac{2(a+x_0^2)H_{11}}{x_0} + \frac{\gamma H_{21}}{\mu x_0y_0(a-x_0^2)} \end{pmatrix}_{2\times 1}, \tag{3.11}$$

where

$$\begin{aligned} \xi &= \frac{\mu x_0y_0(a-x_0^2)}{(a+x_0^2)^3} + \frac{2x_0}{K}i\omega e^{-2i\omega\tau_n} - 4\omega^2 \\ &\quad - \left(\frac{4x_0^2y_0}{(a+x_0^2)^2} + \frac{2mx_0E_0}{(1+mx_0)^2} + \frac{2px_0E_0}{(1+mx_0)^2[(p-cm)x_0-c]}\right)i\omega, \\ \eta &= 4i\omega - \frac{4x_0^2y_0}{(a+x_0^2)^2} - \frac{2mx_0E_0}{(1+mx_0)^2} - \frac{2px_0E_0}{(1+mx_0)^2[(p-cm)x_0-c]} + \frac{2x_0}{K}e^{-2i\omega\tau_n}, \\ \gamma &= \frac{2x_0(a+x_0^2)^3}{K} - 4x_0^2(a+x_0^2)y_0 - \frac{2mx_0(a+x_0^2)^3E_0}{(1+mx_0)^2} - \frac{2px_0(a+x_0^2)^3E_0}{(1+mx_0)^2[(p-cm)x_0-c]}. \end{aligned}$$

Thereupon, $W_{20}(\theta)$ and $W_{11}(\theta)$ can be obtained by means of Eqs (3.10) and (3.11). Thereafter, substituting $W_{20}(\theta)$ and $W_{11}(\theta)$ into Eq (3.9), we derive the concrete expressions of g_{20}, g_{11}, g_{02}, and g_{21}. Accordingly, the following values can be calculated:

$$\begin{aligned} &c_1(0) = \frac{i}{2\omega\tau_n}\left(g_{11}g_{20} - 2|g_{11}|^2 - \frac{|g_{02}|^2}{3}\right) + \frac{g_{21}}{2}, \quad \mu_2 = -\frac{\text{Re}\{c_1(0)\}}{\text{Re}\{\lambda'(\tau_n)\}}, \\ &\beta_2 = 2\text{Re}\{c_1(0)\}, \quad T_2 = -\frac{\text{Im}\{c_1(0)\} + \mu_2\text{Im}\{\lambda'(\tau_n)\}}{\omega\tau_n}, \end{aligned} \tag{3.12}$$

which determine the natures of the bifurcating periodic orbits on the center manifold C_0 at the threshold value τ_n. The sign of μ_2 determines the direction of the Hopf bifurcation, the sign of β_2 determines the stability of the bifurcating periodic orbits, and the sign of T_2 determines the period of the bifurcating periodic orbits.

Taking into account the conditions under which Hopf bifurcations take place in the previous section, when the gestation delay τ takes the threshold values $\tau_n^{\pm}$, $n = 0, 1, 2, \cdots, N$, we have the following results on the direction of the Hopf bifurcation as well as the stability of the bifurcating periodic orbits by referring to the center manifold theorem in [29]:

Theorem 3.1. *For predator-prey system* (1.5), *we suppose that*

$$\frac{x_0}{K} > \frac{2x_0^2y_0}{(a+x_0^2)^2} + \frac{px_0E_0}{(1+mx_0)^2[(p-cm)x_0-c]} + \frac{mx_0E_0}{(1+mx_0)^2}, \quad x_0^2 < a,$$

$$\Delta > 0 \ \text{and} \ \left(\frac{2x_0^2y_0}{(a+x_0^2)^2} + \frac{px_0E_0}{(1+mx_0)^2[(p-cm)x_0-c]} + \frac{mx_0E_0}{(1+mx_0)^2}\right)^2 < \frac{2\mu x_0y_0(a-x_0^2)}{(a+x_0^2)^3} + \frac{x_0^2}{K^2},$$

then a Hopf bifurcation can occur in the system when the delay τ takes any one of the threshold values $\tau_n^{\pm}$, $n = 0, 1, 2, \cdots, N$. Furthermore,

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

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

(iii) *if* $T_2 > 0$ ($T_2 < 0$), *then the bifurcating periodic orbits increase* (*decrease*).

4. A numerical example

In this section, we present a numerical example to justify the analytical predictions derived in Sections 2 and 3. Let us consider the following example:

$$\begin{cases} \dot{x}(t) = x(t)\left(\dfrac{11}{6} - x(t-\tau) - \dfrac{y(t)}{2+x^2(t)} - \dfrac{E(t)}{1+x(t)}\right), \\ \dot{y}(t) = y(t)\left(\dfrac{3x(t)}{2+x^2(t)} - 1\right), \\ 0 = E(t)\left(\dfrac{2x(t)}{1+x(t)} - \dfrac{1}{2}\right) - \dfrac{1}{2}, \end{cases} \tag{4.1}$$

which has an interior equilibrium $X_* = (1, 1, 1)$ and satisfies the assumptions in (2.1). The Hopf bifurcation conditions indicated in Theorems 2.1 and 3.1 are verified as follows: $x_0/K = 1 > 2x_0^2y_0/(a+$

$x_0^2)^2+px_0E_0/\{(1+mx_0)^2[(p-cm)x_0-c]\}+mx_0E_0/(1+mx_0)^2 = 0.9722$, $x_0^2 = 1 < a = 2$, $\Delta = \{[2x_0^2y_0/(a+x_0^2)^2 + px_0E_0/\{(1+mx_0)^2[(p-cm)x_0-c]\} + mx_0E_0/(1+mx_0)^2]^2 - 2\mu x_0y_0(a-x_0^2)/(a+x_0^2)^3 - x_0^2/K^2\}^2 - 4\mu^2x_0^2y_0^2(a-x_0^2)^2/(a+x_0^2)^6 = [(35/36)^2 - 11/9]^2 - 4/81 = 0.0273 > 0$, $\{2x_0^2y_0/(a+x_0^2)^2 + px_0E_0/\{(1+mx_0)^2[(p-cm)x_0-c]\}+mx_0E_0/(1+mx_0)^2\}^2 = 0.9452 < 2\mu x_0y_0(a-x_0^2)/(a+x_0^2)^3+x_0^2/K^2 = 1.2222$. Thus the conditions are satisfied. Moreover, Eq (2.10) becomes $\omega^4+[(35/36)^2-(11/9)]\omega^2+(1/81) = 0$ here, which has two positive roots $\omega^+ = 0.4703$ and $\omega^- = 0.2363$. By the theoretical analysis in Section 2, we have $\tau_0^+ = (1/0.4703)\arccos(35/36) = 0.5023$, $\tau_0^- = (1/0.2363)\arccos(35/36) = 0.9998$, and $\lambda'(\tau_0^+) = 0.1539 + 0.4378i$. Furthermore, with the help of Matlab 7.0, we can obtain the values of the quantities in the computational formulas (3.12): $c_1(0) = 0.0602 - 0.0486i$, $\mu_2 = -0.3912 < 0$, $\beta_2 = 0.1204 > 0$, $T_2 = 0.9307 > 0$.

According to Theorems 2.1 and 3.1, the interior equilibrium $X_*(1,1,1)$ loses its stability, and a subcritical Hopf bifurcation occurs as τ passes through the threshold value τ_0^+. The equilibrium $X_*(1,1,1)$ is locally asymptotically stable when $\tau = 0$ and $\tau = 0.47 \in (0,\tau_0^+) = (0, 0.5023)$ (see Figures 1 and 2); periodic orbits bifurcate from the equilibrium $X_*(1,1,1)$ when $\tau = \tau_0^+ = 0.5023$ (see Figure 3); the bifurcating periodic orbits are unstable and increase when $\tau = 0.5025 > \tau_0^+$ (see Figure 4); and the equilibrium $X_*(1,1,1)$ is unstable when $\tau = 0.54 \in (\tau_0^+,\tau_0^-) = (0.5023, 0.9998)$ (see Figure 5).

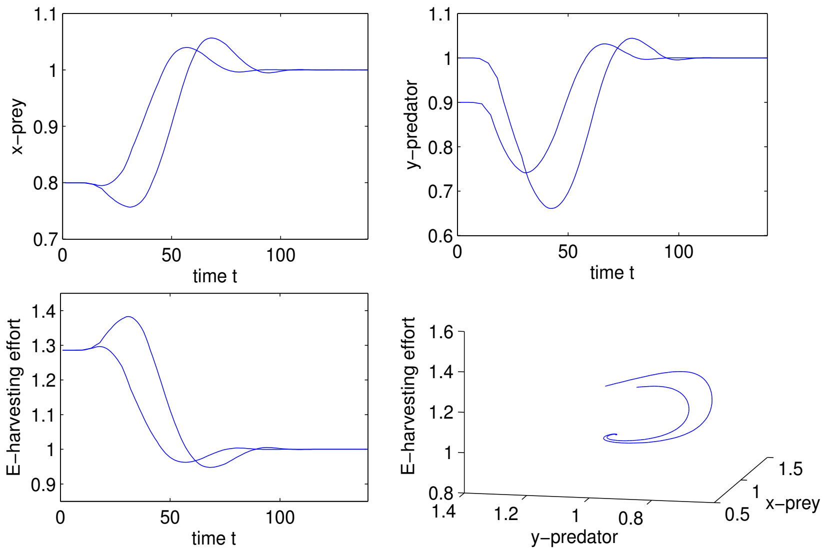

Figure 1. Matlab simulations show that the interior equilibrium $X_*(1,1,1)$ of the numerical example (4.1) is locally asymptotically stable when the gestation delay $\tau = 0$ and the initial values $(x(0), y(0), E(0)) = (0.8, 0.9 + 0.1 * \mathbb{i}, 1.286), \mathbb{i} = 0, 1$.

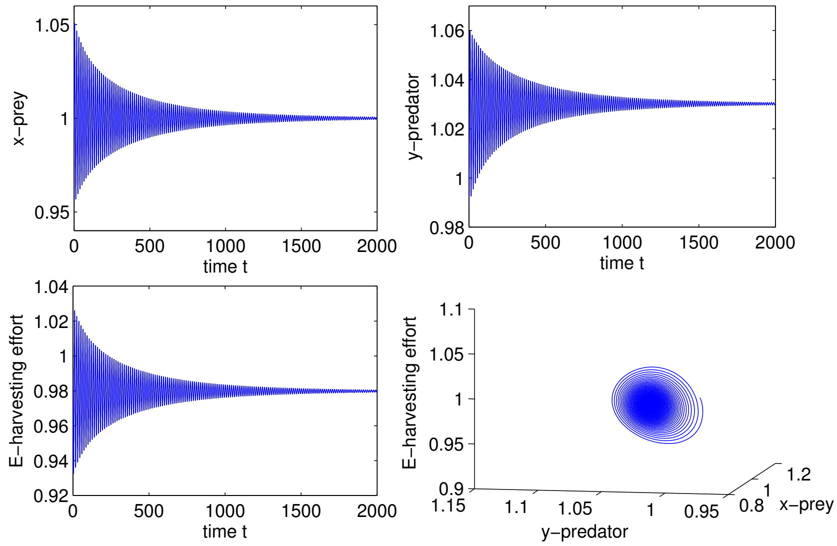

Figure 2. Matlab simulations show that the interior equilibrium $X_*(1, 1, 1)$ of the numerical example (4.1) is locally asymptotically stable when the gestation delay $\tau = 0.47 < \tau_0^+$ and the initial values $(x(\theta), y(0), E(0)) = (0.99, 0.99, 0.99)$, $\theta \in [-\tau, 0]$.

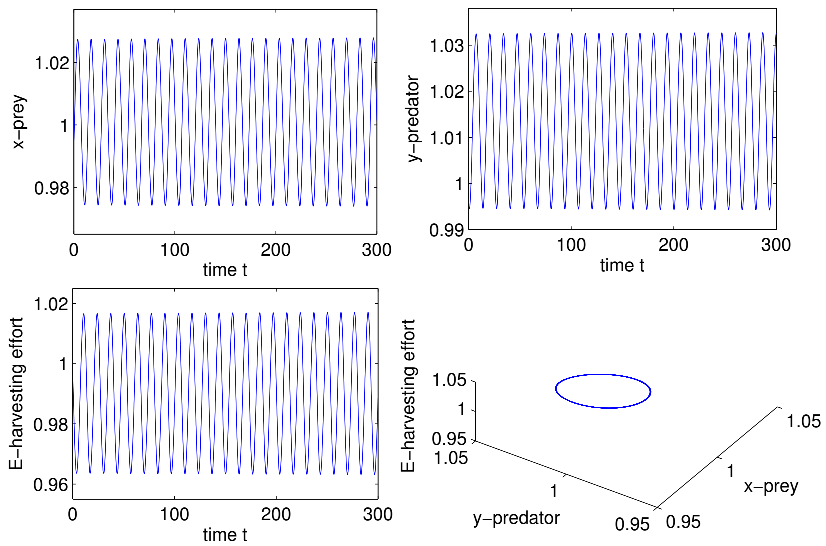

Figure 3. Matlab simulations show that periodic orbits bifurcate from the interior equilibrium $X_*(1, 1, 1)$ of the numerical example (4.1) when the gestation delay $\tau = \tau_0^+ = 0.5023$ and the initial values $(x(\theta), y(0), E(0)) = (0.995, 0.995, 0.995)$, $\theta \in [-\tau, 0]$.

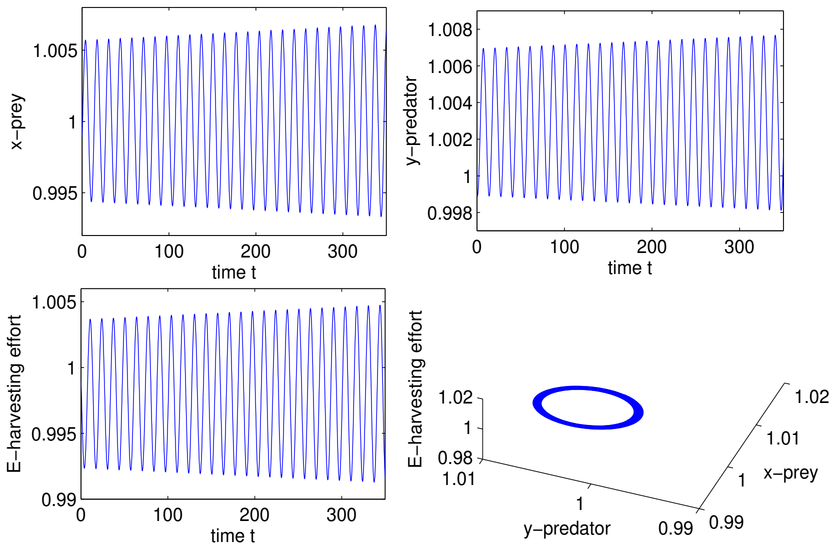

Figure 4. Matlab simulations show that the periodic orbits bifurcating from the interior equilibrium $X_*(1, 1, 1)$ of the numerical example (4.1) are unstable and increase when the gestation delay $\tau = 0.5025 > \tau_0^+$ and the initial values $(x(\theta), y(0), E(0)) = (0.999, 0.999, 0.999)$, $\theta \in [-\tau, 0]$.

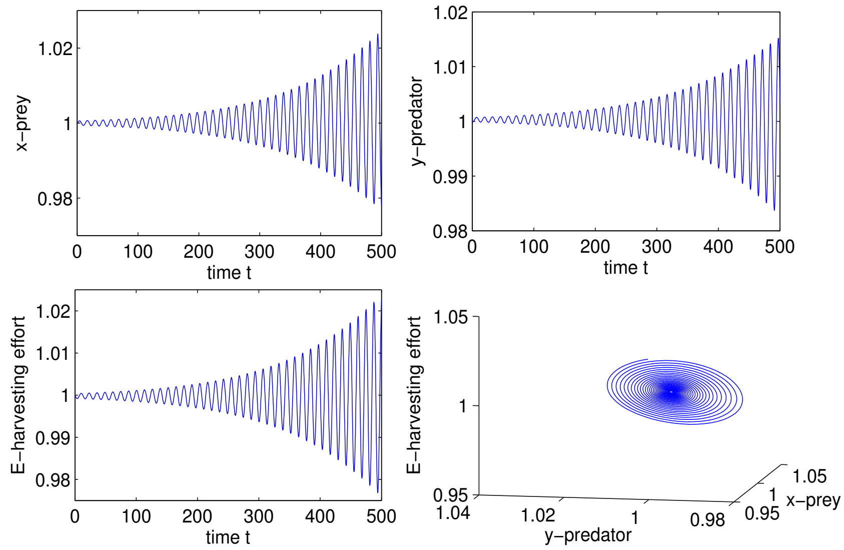

Figure 5. Matlab simulations show that the interior equilibrium $X_*(1, 1, 1)$ of the numerical example (4.1) is unstable when the gestation delay $\tau = 0.54 > \tau_0^+$ and the initial values $(x(\theta), y(0), E(0)) = (0.9999, 0.9999, 0.9999)$, $\theta \in [-\tau, 0]$.

5. Discussion

In this work, under the variations of the gestation delay of prey population, we have carefully studied the dynamical behaviors of a delayed differential-algebra predator-prey system with Holling type IV functional response and a rational nonlinear harvesting rate. In order to maintain the sustainable development of the biological populations, we are concerned with the coexistence conditions (in stable state and oscillatory stable state) of preys, predators, and the harvesting effort in biosystem (1.5).

In Section 2, some sufficient conditions about the existence of Hopf bifurcations in predator-prey system (1.5) are obtained. It can be observed from the analytical results of Theorem 2.1 that the local asymptotic stability or instability of the interior equilibrium depends upon the magnitude of the gestation delay, which could drive a stable co-existing equilibrium to an unstable one, and the stability of the equilibrium could be destabilized through Hopf bifurcations. That is, under certain conditions, small changes of the delay may results in significant changes to the asymptotic behaviors of our biosystem. This conclusion is in accordance with the actual conditions, and we can imagine that the sizes of biological populations in system (1.5) and the number of harvested preys can potentially be affected by the magnitude of the gestation delay of prey population.

For predator-prey system (1.5), when the gestation delay passes through each of its threshold values, the biosystem begins to oscillate, and as a result, stability switches and Hopf bifurcations occur. The appearance of bifurcating periodic orbits in biosystem (1.5) indicates that the population densities of predator and prey, and the harvesting effort would exhibit coherent small amplitude oscillations near the interior equilibrium. Then, a question naturally arises regarding whether the biological populations and the harvesting effort can coexist in an oscillatory mode when the gestation delay attains the threshold values. From a biological point of view, the oscillatory co-existence of the three requires that the bifurcating periodic orbits are stable, while unstable bifurcating period orbits mean that the populations of predators and preys, as well as the harvesting effort will be in an unstable oscillatory state, which may lead to ecological imbalance and the extinction of prey and predator species when the biosystem is slightly disturbed by the outside world. Therefore, further studies on the stability of the Hopf-bifurcating periodic orbits are presented in Section 3, and the analytical expressions for determining the natures, including direction, stability, and period of the periodic orbits have been rigorously established in this section.

On the basis of our research, we provide some directions for further investigations:

(i) The non-constant periodic orbits arising through Hopf bifurcations are local here, viz. they remain valid only in the small neighborhoods of the threshold values. Further, the global continuation of local Hopf-bifurcating periodic orbits, as well as the direction and stability of the global Hopf bifurcation can be studied using the global Hopf bifurcation theorem in [37].

(ii) The results in [38] suggest that periodic variations are often encountered in reality, such as food supplies, mating habits, seasonal affects of weather, and so on. Hence, the dynamics of a periodic differential-algebra predator-prey system with time delay can be considered.

(iii) The dynamics of differential-algebra predator-prey systems with other realistic harvesting policies [16] (such as seasonal or rotational harvesting, and threshold harvesting) can be investigated. In addition, the age-structure of a population is also important for population dynamics [39,40]. Hence, age-structure can be introduced into our model, which would make the model more realistic.

6. Conclusions

In this paper, we propose a predator-prey model with gestation delay of prey and nonlinear harvesting, which is described by delayed differential-algebra equations (1.5) due to the harvesting effort being formulated by an algebra equation. Our model is more complicated than the common predator-prey models with delay and harvesting, which are established by delayed differential equations, and the differential-algebra system model provides a potentially feasible way to study the impact of the varying of harvesting revenue on population dynamics. Thus, the formulation of differential-algebra equations would be helpful for understanding the complex dynamics of predator-prey models with delay and harvesting. Our research shows that the gestation delay has potential radical effects on the dynamics of predator-prey system (1.5). As the delay slightly increases through a sequence of threshold values, an interesting dynamical phenomenon would occur, i.e., the stability of interior equilibrium can change finite times from stable to unstable to stable and becomes unstable eventually, which could cause stability switches of the positive steady-state. During the stability switches, families of Hopf-bifurcating periodic orbits would arise from the interior equilibrium and induce population oscillations in the biosystem.

Besides, the parameterisation method plays a significant role in making the delayed differential-algebra system (1.5) locally equivalent to the system of delayed differential equations (3.1). By analyzing system (3.1), the qualitative methods on differential equations, such as Routh-Hurwitz criterion [1, 2], bifurcation results for delayed differential equations [28], center manifold reduction [29], and Rouche's theorem [36] can be applied to delayed differential-algebra system (1.5) indirectly. Thus, this is an effective way to study the dynamics of differential-algebra systems.

Use of AI tools declaration

The author declare he has not used Artificial Intelligence (AI) tools in the creation of this article.

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Conflict of interest

The author declare there is no conflict of interest.

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Appendix

Appendix A

Since the parameterisation method proposed in [30] is written in Chinese, we state the method as follows:

Consider the differential-algebra equations (hereafter referred to as DAEs):

$$\begin{cases} \dot{\overline{X}}(t) = f(\overline{X}(t)), \\ 0 = g(\overline{X}(t)), \end{cases} \tag{A.1}$$

where $f : \mathrm{R}^n \to \mathrm{R}^n$, $g : \mathrm{R}^n \to \mathrm{R}^u$ $(u < n)$, f and g are continuously differentiable functions, $\overline{X}(t) = (\overline{x}_1(t), \overline{x}_2(t), \cdots, \overline{x}_n(t))^T \in \mathrm{R}^n$, $f = (f_1, f_2, \cdots, f_n)^T$, $g = (g_1, g_2, \cdots, g_u)^T$.

Suppose that $\overline{X}_0$ is an equilibrium of DAEs (A.1). If DAEs (A.1) satisfies that rank $D_{\overline{X}}g(\overline{X}_0) = u$ and $D_{\overline{X}}g(\overline{X}_0) = (\,0, P\,)_{u\times n}$, where the determinant of matrix $P_{u\times u}$ is non-zero, then we can use the following parameterisation for DAEs (A.1):

$$\overline{X}(t) = \psi(Y(t)) = \overline{X}_0 + U_0 Y(t) + V_0 h(Y(t)), \tag{A.2}$$

$$g(\psi(Y(t))) = 0, \tag{A.3}$$

where $U_0 = \begin{pmatrix} I_{(n-u)} \\ 0 \end{pmatrix}_{n\times(n-u)}$, $V_0 = \begin{pmatrix} 0 \\ I_u \end{pmatrix}_{n\times u}$, $Y(t) = (y_1(t), y_2(t), \cdots, y_{(n-u)}(t))^T \in \mathrm{R}^{(n-u)}$, $h(Y)$ is a smooth mapping from $\mathrm{R}^{(n-u)}$ into R^u. Substituting $\overline{X}(t) = \psi(Y(t))$ into the differential equations of DAEs (A.1), one has

$$D_Y\psi(Y(t))\dot{Y}(t) = f(\psi(Y(t))). \tag{A.4}$$

Differentiating both sides of Eq (A.2) with respect to Y, and multiplying U_0^T with both sides of the differentiated equation, we derive

$$U_0^T D_Y \psi(Y(t)) = I_{(n-u)}. \tag{A.5}$$

Differentiating both sides of Eq (A.3) with respect to Y yields

$$D_{\overline{X}} g(\overline{X}(t)) D_Y \psi(Y(t)) = 0. \tag{A.6}$$

Equations (A.5) and (A.6) lead to

$$D_Y \psi(Y(t)) = \begin{pmatrix} D_{\overline{X}} g(\overline{X}(t)) \\ U_0^T \end{pmatrix}^{-1} \begin{pmatrix} 0 \\ I_{(n-u)} \end{pmatrix}. \tag{A.7}$$

Substituting Eq (A.7) into Eq (A.4), we gain

$$\begin{pmatrix} D_{\overline{X}} g(\overline{X}(t)) \\ U_0^T \end{pmatrix}^{-1} \begin{pmatrix} 0 \\ I_{(n-u)} \end{pmatrix} \dot{Y}(t) = f(\psi(Y(t))). \tag{A.8}$$

It follows from Eqs (A.4), (A.6), and (A.8) that

$$\begin{pmatrix} 0 \\ I_{(n-u)} \end{pmatrix} \dot{Y}(t) = \begin{pmatrix} D_{\overline{X}} g(\overline{X}(t)) f(\psi(Y(t))) \\ U_0^T f(\psi(Y(t))) \end{pmatrix} = \begin{pmatrix} 0 \\ U_0^T f(\psi(Y(t))) \end{pmatrix},$$

which indicates that DAEs (A.1) is locally equivalent to the parameterised system

$$\dot{Y}(t) = U_0^T f(\psi(Y(t))). \tag{A.9}$$

Appendix B

The second order Taylor series developments of parameterised system (2.4) at point $\overline{X}_0$ has the form

$$\begin{cases} \dot{y}_1 = f_{1y_1}(\overline{X}_0) y_1 + f_{1y_2}(\overline{X}_0) y_2 + \dfrac{1}{2} f_{1y_1y_1}(\overline{X}_0) y_1^2 + f_{1y_1y_2}(\overline{X}_0) y_1 y_2 \\ \qquad + \dfrac{1}{2} f_{1y_2y_2}(\overline{X}_0) y_2^2 + o(|Y|^3), \\ \dot{y}_2 = f_{2y_1}(\overline{X}_0) y_1 + f_{2y_2}(\overline{X}_0) y_2 + \dfrac{1}{2} f_{2y_1y_1}(\overline{X}_0) y_1^2 + f_{2y_1y_2}(\overline{X}_0) y_1 y_2 \\ \qquad + \dfrac{1}{2} f_{2y_2y_2}(\overline{X}_0) y_2^2 + o(|Y|^3). \end{cases} \tag{B.1}$$

In the following, we calculate the coefficients of the above Taylor series developments (B.1).

In view of Eq (2.3), we can compute that

$$\begin{aligned} D_{\overline{X}} f_1(\overline{X}) = \Big(& r - \frac{x(t-\tau)}{K} - \frac{y}{a+x^2} + \frac{pE_0 x}{(1+mx_0)[(p-cm)x_0 - c](1+mx)} \\ & - \frac{\overline{E}}{1+mx} - \frac{e^{-\lambda\tau} x}{K} + \frac{2x^2 y}{(a+x^2)^2} + \frac{pE_0 x}{(1+mx_0)[(p-cm)x_0 - c](1+mx)^2} \\ & + \frac{mx\overline{E}}{(1+mx)^2}, -\frac{x}{a+x^2}, -\frac{x}{1+mx} \Big), \end{aligned}$$

$$D_{\overline{X}}f_2(\overline{X}) = \left(\frac{\mu y(a-x^2)}{(a+x^2)^2},\ \frac{\mu x}{a+x^2} - D,\ 0\right),$$
$$D_{\overline{X}}g(\overline{X}) = \Big(\frac{p\overline{E}}{(1+mx)^2} - \frac{p^2E_0x}{(1+mx_0)[(p-cm)x_0-c](1+mx)^2}$$
$$- \frac{pE_0[(p-cm)x-c]}{(1+mx_0)[(p-cm)x_0-c](1+mx)},\ 0\,,\ \frac{(p-cm)x-c}{1+mx}\Big). \tag{B.2}$$

From Eq (A.8) in Appendix A, we have

$$D_Y\psi(Y) = \left(D_{y_1}\psi(Y),\ D_{y_2}\psi(Y)\right)$$
$$= \begin{pmatrix} D_{\overline{X}}g(\overline{X}) \\ U_0^T \end{pmatrix}^{-1} \begin{pmatrix} 0 \\ I_2 \end{pmatrix} = \begin{pmatrix} \Theta(\overline{X}) & 0 & \frac{(p-cm)x-c}{1+mx} \\ 1 & 0 & 0 \\ 0 & 1 & 0 \end{pmatrix}^{-1} \begin{pmatrix} 0 & 0 \\ 1 & 0 \\ 0 & 1 \end{pmatrix}$$
$$= \begin{pmatrix} 0 & 1 & 0 \\ 0 & 0 & 1 \\ \frac{1+mx}{(p-cm)x-c} & -\frac{(1+mx)\Theta(\overline{X})}{(p-cm)x-c} & 0 \end{pmatrix} \begin{pmatrix} 0 & 0 \\ 1 & 0 \\ 0 & 1 \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ 0 & 1 \\ -\frac{(1+mx)\Theta(\overline{X})}{(p-cm)x-c} & 0 \end{pmatrix}, \tag{B.3}$$

where

$$\Theta(\overline{X}) = \frac{p\overline{E}}{(1+mx)^2} - \frac{p^2E_0x}{(1+mx_0)[(p-cm)x_0-c](1+mx)^2}$$
$$- \frac{pE_0[(p-cm)x-c]}{(1+mx_0)[(p-cm)x_0-c](1+mx)}.$$

By Eqs (2.4), (B.2) and (B.3), we get

$$f_{1y_1}(\overline{X}) = D_{\overline{X}}f_1(\overline{X})D_{y_1}\psi(Y) = r - \frac{x(t-\tau)}{K} - \frac{y}{a+x^2} + \frac{pE_0x}{(1+mx_0)[(p-cm)x_0-c](1+mx)}$$
$$- \frac{\overline{E}}{1+mx} - \frac{e^{-\lambda\tau}x}{K} + \frac{2x^2y}{(a+x^2)^2}$$
$$+ \frac{pE_0x}{(1+mx_0)[(p-cm)x_0-c](1+mx)^2} + \frac{mx\overline{E}}{(1+mx)^2}$$
$$- \frac{x}{(p-cm)x-c}\Big\{\frac{p^2E_0x}{(1+mx_0)[(p-cm)x_0-c](1+mx)^2}$$
$$+ \frac{pE_0[(p-cm)x-c]}{(1+mx_0)[(p-cm)x_0-c](1+mx)} - \frac{p\overline{E}}{(1+mx)^2}\Big\},$$
$$f_{1y_2}(\overline{X}) = D_{\overline{X}}f_1(\overline{X})D_{y_2}\psi(Y) = -\frac{x}{a+x^2},$$
$$f_{2y_1}(\overline{X}) = D_{\overline{X}}f_2(\overline{X})D_{y_1}\psi(Y) = \frac{\mu y(a-x^2)}{(a+x^2)^2},$$
$$f_{2y_2}(\overline{X}) = D_{\overline{X}}f_2(\overline{X})D_{y_2}\psi(Y) = \frac{\mu x}{a+x^2} - D. \tag{B.4}$$

Substituting $\overline{X}_0$ into Eq (B.4), we gain

$$f_{1y_1}(\overline{X}_0) = -\frac{e^{-\lambda\tau}}{K}x_0 + \frac{2x_0^2 y_0}{(a+x_0^2)^2} + \frac{mx_0E_0}{(1+mx_0)^2} + \frac{px_0E_0}{(1+mx_0)^2[(p-cm)x_0-c]},$$
$$f_{1y_2}(\overline{X}_0) = -\frac{x_0}{a+x_0^2},\ \ f_{2y_1}(\overline{X}_0) = \frac{\mu y_0(a-x_0^2)}{(a+x_0^2)^2},\ \ f_{2y_2}(\overline{X}_0) = 0. \tag{B.5}$$

From Eq (B.4), we can calculate

$$\begin{aligned}
D_{\overline{X}}f_{1y_1}(\overline{X}) =& \Bigg(-\frac{2e^{-\lambda\tau}}{K} + \frac{2xy}{(a+x^2)^2} + \frac{pE_0}{(1+mx_0)[(p-cm)x_0-c](1+mx)^2} \\
&+ \frac{m\overline{E}}{(1+mx)^2} + \frac{4xy}{(a+x^2)^2} - \frac{8x^3y}{(a+x^2)^3} + \frac{pE_0}{(1+mx_0)[(p-cm)x_0-c]} \\
&\times\left(\frac{1}{(1+mx)^2} - \frac{2mx}{(1+mx)^3}\right) + \frac{m\overline{E}}{(1+mx)^2} - \frac{2m^2x\overline{E}}{(1+mx)^3} + \frac{c}{[(p-cm)x-c]^2} \\
&\times\left(\frac{p^2E_0x}{(1+mx_0)[(p-cm)x_0-c](1+mx)^2} + \frac{pE_0[(p-cm)x-c]}{(1+mx_0)[(p-cm)x_0-c](1+mx)}\right. \\
&\left.-\frac{p\overline{E}}{(1+mx)^2}\right) - \frac{x}{(p-cm)x-c}\left[\frac{p^2E_0}{(1+mx_0)[(p-cm)x_0-c]}\right. \\
&\times\left(\frac{1}{(1+mx)^2} - \frac{2mx}{(1+mx)^3}\right) + \frac{pE_0}{(1+mx_0)[(p-cm)x_0-c]} \\
&\left.\times\left(\frac{p-cm}{1+mx} - \frac{m[(p-cm)x-c]}{(1+mx)^2}\right) + \frac{2pm\overline{E}}{(1+mx)^3}\right], \\
&-\frac{1}{a+x^2} + \frac{2x^2}{(a+x^2)^2},\ -\frac{1}{1+mx} + \frac{mx}{(1+mx)^2} + \frac{px}{(1+mx)^2[(p-cm)x-c]}\Bigg), \\
D_{\overline{X}}f_{1y_2}(\overline{X}) =& \left(\frac{x^2-a}{(a+x)^2},\ 0,\ 0\right), \\
D_{\overline{X}}f_{2y_1}(\overline{X}) =& \left(-\frac{2\mu xy}{(a+x^2)^2} - \frac{4\mu xy(a-x^2)}{(a+x^2)^3},\ \frac{\mu(a-x^2)}{(a+x^2)^2},\ 0\right), \\
D_{\overline{X}}f_{2y_2}(\overline{X}) =& \left(\frac{\mu(a-x^2)}{(a+x^2)^2},\ 0,\ 0\right).
\end{aligned} \tag{B.6}$$

Substituting $\overline{X}_0$ into Eqs (B.3) and (B.6), we obtain

$$\begin{aligned}
D_{\overline{X}}f_{1y_1}(\overline{X}_0) = \Bigg(& -\frac{2e^{-\lambda\tau}}{K} + \frac{2x_0y_0(3a-x_0^2)}{(a+x_0^2)^3} + \frac{2mE_0}{(1+mx_0)^3} \\
& - \frac{px_0E_0(p-cm)}{(1+mx_0)^2[(p-cm)x_0-c]^2} + \frac{pE_0(2-mx_0)}{(1+mx_0)^3[(p-cm)x_0-c]} \\
& - \frac{p^2x_0E_0}{(1+mx_0)^3[(p-cm)x_0-c]^2},\ -\frac{1}{a+x_0^2} + \frac{2x_0^2}{(a+x_0^2)^2}, \\
& - \frac{1}{1+mx_0} + \frac{mx_0}{(1+mx_0)^2} + \frac{px_0}{(1+mx_0)^2[(p-cm)x_0-c]}\Bigg),
\end{aligned}$$

$$D_{\overline{X}} f_{1y_2}(\overline{X}_0) = \left(\frac{x_0^2 - a}{(a + x_0)^2}, 0, 0\right),$$

$$D_{\overline{X}} f_{2y_1}(\overline{X}_0) = \left(-\frac{2\mu x_0 y_0}{(a + x_0^2)^2} - \frac{4\mu x_0 y_0 (a - x_0^2)}{(a + x_0^2)^3}, \frac{\mu(a - x_0^2)}{(a + x_0^2)^2}, 0\right),$$

$$D_{\overline{X}} f_{2y_2}(\overline{X}_0) = \left(\frac{\mu(a - x_0^2)}{(a + x_0^2)^2}, 0, 0\right),$$

$$D_Y \psi(0) = \left(D_{y_1}\psi(0),\ D_{y_2}\psi(0)\right) = \begin{pmatrix} 1 & 0 \\ 0 & 1 \\ -\dfrac{(1 + mx)\Theta(\overline{X}_0)}{(p - cm)x - c} & 0 \end{pmatrix}$$

$$= \begin{pmatrix} 1 & 0 \\ 0 & 1 \\ \dfrac{p\overline{E}_0}{(1 + mx_0)^2} - \dfrac{p^2 x_0 E_0}{(1 + mx_0)^3[(p - cm)x_0 - c]} - \dfrac{pE_0}{(1 + mx_0)^2} & 0 \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ 0 & 1 \\ 0 & 0 \end{pmatrix}. \tag{B.7}$$

From Eqs (2.4) and (B.7), we derive

$$\begin{aligned}
f_{1y_1y_1}(\overline{X}_0) &= D_{\overline{X}} f_{1y_1}(\overline{X}_0) D_{y_1}\psi(0) \\
&= -\frac{2e^{-\lambda\tau}}{K} + \frac{2x_0 y_0 (3a - x_0^2)}{(a + x_0^2)^3} + \frac{2mE_0}{(1 + mx_0)^3} \\
&\quad - \frac{px_0 E_0 (p - cm)}{(1 + mx_0)^2[(p - cm)x_0 - c]^2} + \frac{pE_0(2 - mx_0)}{(1 + mx_0)^3[(p - cm)x_0 - c]} \\
&\quad - \frac{p^2 x_0 E_0}{(1 + mx_0)^3[(p - cm)x_0 - c]^2}, \\
f_{1y_1y_2}(\overline{X}_0) &= D_{\overline{X}} f_{1y_1}(\overline{X}_0) D_{y_2}\psi(0) = \frac{x_0^2 - a}{(a + x_0^2)^2}, \\
f_{1y_2y_2}(\overline{X}_0) &= D_{\overline{X}} f_{1y_2}(\overline{X}_0) D_{y_2}\psi(0) = 0, \\
f_{2y_1y_1}(\overline{X}_0) &= D_{\overline{X}} f_{2y_1}(\overline{X}_0) D_{y_1}\psi(0) = \frac{2\mu x_0 y_0 (x_0^2 - 3a)}{(a + x_0^2)^3}, \\
f_{2y_1y_2}(\overline{X}_0) &= D_{\overline{X}} f_{2y_1}(\overline{X}_0) D_{y_2}\psi(0) = \frac{\mu(a - x_0^2)}{(a + x_0^2)^2}, \\
f_{2y_2y_2}(\overline{X}_0) &= D_{\overline{X}} f_{2y_2}(\overline{X}_0) D_{y_2}\psi(0) = 0\,.
\end{aligned} \tag{B.8}$$

Substituting coefficients (B.5) and (B.8) into the Taylor series developments (B.1), we can obtain Eq (3.1).