Population dynamics of a modified predator-prey model with economic harvesting

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Abstract. The dynamical behaviors of a predator-prey model with commercial harvesting are studied in the present work. The model is developed from the Leslie predator-prey model with harvesting on predator, which is established by differential-algebra equations. The harvesting is considered from an economic perspective, and the impacts of the harvesting profit on the dynamics of our model are investigated. Firstly, basing on the parameterisation approach of differential-algebra system, the local stability of positive equilibrium point is studied. Further, by treating the harvesting profit as a bifurcation parameter, the Hopf bifurcation occurring at the equilibrium point is analyzed, and we find a qualitative change in the dynamics. Besides, the stability of centre is also considered. Some computer simulations using Matlab software are presented to support the analytical results. Lastly, we relate the results on mathematics and dynamics with the biology, and interpret these results in terms of ecosystem stability and destruction.

Keywords: predator-prey, differential-algebra, local stability, Hopf bifurcation, centre, harvesting profit.

MSC 2020: 34A09

1. Introduction

Predator-prey interactions are the fundamental blocks of any complex biological and ecological systems, as well as generalized competitive and cooperative systems [1]. As a result, the dynamic relationship between the populations of predators and preys is an important research theme in the areas of applied mathematics and theoretical ecology (see, [2, 3]). Actually, as with the dynamic theory of differential equations has been widely used in these research areas, in the past few years the dynamics of predator-prey system (usually formulated by differential equations) also has become an interesting subject in itself, since many complicated dynamical behaviors have been discovered in this subject, for instances, instability, stability switches, limit cycle, oscillations, various kinds of bifurcations, chaos, and so on [2-5]. Especially, in this work, by combining the dynamic theories of differential-algebra system and differential equations, we aim to present a complete dynamical analysis for a modified Leslie's predator-prey model with commercial harvesting, which takes the form of differential-algebra equations. The establishing process of our model is introduced as follows.

The fundamental model that we consider is the following predator-prey model introduced by Leslie [6], which is a system of nonlinear ordinary differential equations:

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

where $x(t)$ and $y(t)$ represent the densities of preys and predators at time $t \geq 0$, respectively; besides, the parameters r_1, a, r_2, and b are positive constants, which stand for the intrinsic growth rate of prey species, the catch rate at which the predator population kills its preys, the intrinsic growth rate of predator species, and the conversion rate of consumed preys into the newborns of predator species, respectively. For more details on the biological significance of model (1.1), refer to the literature [6, 7].

In reality, biological populations are often harvested to satisfy people's demands for material life [8, 9]. For predator-prey system, in order to avoid the extinction of prey population, harvesting of predator population is commonly practiced, which is effective in controlling the population size of predators. So we consider human harvesting effort $E(t)$ on the predator species in model (1.1), and then we have

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

Subsequently, the number of predators harvested by people is $E(t)y(t)$, which is regarded as the market supply here. We assume that the market is quite capable of absorbing all the catches. Referring to Refs. [10, 11], the selling price and market supply move in opposite directions, and harvesting cost also moves inversely to the population density of harvested population. In light of these rules, we let the unit selling price $\tilde{p}$ and the unit harvesting cost $\tilde{c}$ respectively be $p/[l + E(t)y(t)]$ and $c/y(t)$, where p, l and c are positive parameters, p/l is the maximum unit selling price, and c is the harvesting cost for unit population density of predators. And then, we can show that $\tilde{p} \to p/l$ as $E(t)y(t) \to 0$, and $\tilde{p} \to 0$ as $E(t)y(t) \to +\infty$, which indicate that the selling price will decrease when the supply $E(t)y(t)$ increases. Moreover, $\tilde{c} \to +\infty$ as $y(t) \to 0$, and $\tilde{c} \to 0$ as $y(t) \to +\infty$, which imply that the harvesting cost will increase when the population density of predators becomes small. It is easy to imagine that, when the predators are rare, people must make more effort to capture them. In this way, the total revenue from harvesting is $[p/(l+E(t)y(t))] \cdot E(t)y(t)$ and the total harvesting cost is $[c/y(t)] \cdot E(t)y(t)$. Consequently, the net economic revenue is $[p/(l + E(t)y(t))] \cdot E(t)y(t) - [c/y(t)] \cdot E(t)y(t)$. On the basis of model (1.2), so we can establish the following modified predator-prey model with economic harvesting, which is a differential-algebra system:

$$\begin{cases} \dot{x}(t) = x(t)\left(r_1 - ay(t)\right), \\ \dot{y}(t) = y(t)\left(r_2 - b\dfrac{y(t)}{x(t)} - E(t)\right), \\ \;0 = E(t)y(t)\left(\dfrac{p}{l + E(t)y(t)} - \dfrac{c}{y(t)}\right) - v, \end{cases} \tag{1.3}$$

where v denotes people's harvesting profit. In addition, when time $t = 0$, the initial values of system (1.3) should be positive. That is,

$$x(0) > 0,\;\; y(0) > 0,\;\; E(0) > 0. \tag{1.4}$$

In recent years, dynamical behaviors of harvested predator-prey models are reported in Refs. [46-50]. The literature [45] has investigated the nontrivial equilibrium solution and transcritical bifurcation of a three dimensional intraguild predator-prey model with Michaelis-Menten type of harvesting in predator. Besides, the stability of equilibria, limit cycle, saddle-node bifurcation and Bogdanov-Takens bifurcation in several predator-prey systems with nonlinear prey harvesting are discussed in Refs. [46, 47]. Das et al. [48] have studied the endangeredness, resilience and extinction of a predator-prey system under prey harvesting and predator harvesting, respectively. Kashyap et al. [49] have explored the coexistence, ecologically feasible steady states and local codimension one bifurcations of a predator-prey system with predator harvesting. Moreover, local and global stability at the interior equilibrium points of a harvested three species predator-prey model (prey, predator, and super predator) have been considered in Ref. [50]. Clearly, these harvested predator-prey models [46-50] are modelled by systems of differential equations. In contrast, our harvested predator-prey model (1.3) is established by differential-algebra equations. Compared with the familiar harvested predator-prey models expressed by differential equations, the superiority of our modified model (1.3) is that it not only involves population interactions in the harvested predator-prey system but also investigates the harvesting from an economic viewpoint. Some relevant modified models are presented in the publications [21, 24, 26, 29, 32]. By employing Rouche's theorem [22] as well as the centre manifold reduction methods [23, 25], Refs. [21, 24] have analyzed the existence of time-delay-induced Hopf bifurcation phenomena and the stability of bifurcating periodic orbits in delayed modified predator-prey models. Moreover, the authors [26, 29, 32] have discussed the local stability of equilibrium points and bifurcations (flip bifurcation and N-S bifurcation) in several discrete modified predator-prey models by applying the center manifold theory and the bifurcation theory of discrete systems in Refs. [27, 28, 30, 31]. Different from the literature [21, 24, 26, 29, 32], we will investigate the impact of the harvesting profit v on the dynamics (including the local stability of equilibrium point, Hopf bifurcation and stability of centre) in the modified predator-prey model (1.3), and then afterwards we propose an appropriate scope for the profit to guarantee the maintenance of long-term sustainable development of our biological system. Besides, it is notable that the relevant differential-algebra predator-prey models [21, 24, 26, 29, 32] are all established under the assumptions that the price $\tilde{p}$ and cost $\tilde{c}$ are constants, which results in that the harvesting variable $E(t)$ can be explicitly solved out from the algebra equation, and then the differential-algebra models can be easily reduced to the systems of differential equations. Apparently, our differential-algebra model (1.3) has overcome the shortages.

Furthermore, it is worth noting that there are many essential distinctions between differential-algebra system and the system of differential equations, see the literature [34-38] for more details. In the sense of index, the system of ordinary differential equations is a special case of differential-algebraic system, since the index of the former is zero, while the index of the latter is nonzero. Obviously, it is a leap from a zero index system to a nonzero index one. In fact, the dynamics of differential-algebra system is much more difficult to investigate than the corresponding system of differential equations (see, [35-37]). Hence, in a certain meaning, our work supplements and enhances the research in the previous publications [12-21, 24, 26, 29, 32, 45-50] on the dynamic analysis for predator-prey models.

We organize the rest of this paper as follows. In the next section, we deduce the Jacobian matrix of model (1.3) and investigate the corresponding characteristic equation, which give the local stability results for the equilibrium point. In Section 3, we study the Hopf bifurcation of our model in detail basing on the previous section. To complement Sections 2 and 3, the stability of the centre is further explored in Section 4. Moreover, some numerical simulations are presented in Section 5 to make the derived findings more complete. Finally, in Section 6 we discuss the theoretical results and summarize the research work of this article.

2. Stability analysis for equilibrium point

In this section, combining the parameterisation approach [39, 40] with Routh-Hurwitz stability criteria [2, 3], we study local stability of the equilibrium point of model (1.3). At first, we prove the positiveness of the solutions of model (1.3).

Lemma 2.1. *The trajectories of model* (1.3) *with initial values* (1.4) *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 (1.3), 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

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

Similarly, we can get

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

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

Lemma 2.1 suggests that only the positive equilibrium point of model (1.3) is required to be considered. If $X_0:=(x_0,y_0,E_0)^T$ is an equilibrium point of model (1.3), 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 means of solving this set of linear equations, model (1.3) has an equilibrium point:

$$X_0(v)=(x_0,y_0,E_0)^T=\left(\frac{by_0}{r_2-E_0},\frac{r_1}{a},E_0\right)^T,$$

where $E_0=\left\{(py_0-vy_0-cl)\pm\sqrt{(cl+vy_0-py_0)^2-4clvy_0}\right\}/2cy_0$.

To make such an equilibrium point X_0 is positive, in this paper we need to suppose that

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

On the basis of the theory of differential-algebra system [35-37], near the point of X_0, model (1.3) can be locally equivalent to

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

where the function f_3 satisfies $f_3(X_0)=0$. The explicit expression of f_3 is not required to be defined, refer to Eq. (A.5) in Appendix.

For the purpose of discussions, we denote

$$f(X)=\begin{pmatrix}f_1(X)\\ f_2(X)\\ f_3(X)\end{pmatrix}=\begin{pmatrix}x(t)\,(r_1-ay(t))\\ y(t)\left(r_2-b\dfrac{y(t)}{x(t)}-E(t)\right)\\ f_3(x(t),y(t),E(t))\end{pmatrix},$$

$$g(X)=E(t)y(t)\left(\frac{p}{l+E(t)y(t)}-\frac{c}{y(t)}\right)-v,\ \ X=(x(t),y(t),E(t))^T. \tag{2.3}$$

So, system (2.2) can be written as

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

In the following, we consider the parameterisation ψ [39, 40] for system (2.4):

$$X=\psi(Y)=X_0+U_0Y+V_0h(Y)\quad \text{and} \tag{2.5}$$

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

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. Consequently, by the parameterised system (A.5) in Appendix, the Taylor expansions of the parameterised system of system (2.2) at X_0 takes the form of

$$\dot{Y}=U_0^TD_Xf(X_0)D_Y\psi(0)Y+o(|Y|), \tag{2.7}$$

where D denotes the differential operator, and $D_Xf(X)$ represents the Jacobian matrix of function $f(X)$ regarding X. With respect to the derivation process of the formula (2.7), refer to Appendix. □

Summarizing the above analysis, we have the following results.

Theorem 2.1. *For model* (1.3),

(*i*) *if*

$$\left(\frac{by_0}{x_0}-\frac{plE_0y_0}{ply_0-c(l+E_0y_0)^2}\right)^2\geq\frac{4aby_0^2}{x_0},$$

then, when $by_0/x_0>plE_0y_0/[ply_0-c(l+E_0y_0)^2]$, *the equilibrium point* X_0 *is a stable node*; *when* $by_0/x_0<plE_0y_0/[ply_0-c(l+E_0y_0)^2]$, *the equilibrium point* X_0 *is an unstable node*;

(*ii*) *if*

$$\left(\frac{by_0}{x_0}-\frac{plE_0y_0}{ply_0-c(l+E_0y_0)^2}\right)^2<\frac{4aby_0^2}{x_0},$$

then, when $by_0/x_0>plE_0y_0/[ply_0-c(l+E_0y_0)^2]$, *the equilibrium point* X_0 *is a sink*; *when* $by_0/x_0<plE_0y_0/[ply_0-c(l+E_0y_0)^2]$, *the equilibrium point* X_0 *is a source.*

Proof. We can derive the following Jacobian matrix P of system (2.7) in view of Eqs. (2.7), (A.2) and (A.3) (in Appendix) that

$$\begin{aligned} \mathrm{P} &= \begin{pmatrix} D_{y_1} f_1(\psi(Y)) & D_{y_2} f_1(\psi(Y)) \\ D_{y_1} f_2(\psi(Y)) & D_{y_2} f_2(\psi(Y)) \end{pmatrix}\Bigg|_{Y=0} \\ &= U_0^T D_X f(X_0) D_Y \psi(0) = U_0^T D_X f(X_0) \begin{pmatrix} D_X g(X_0) \\ U_0^T \end{pmatrix}^{-1} \begin{pmatrix} 0 \\ I_2 \end{pmatrix} \\ &= \begin{pmatrix} D_x f_1(X_0) & D_y f_1(X_0) - \dfrac{plE_0 \cdot D_E f_1(X_0)}{ply_0 - c(l+E_0 y_0)^2} \\ D_x f_2(X_0) & D_y f_2(X_0) - \dfrac{plE_0 \cdot D_E f_2(X_0)}{ply_0 - c(l+E_0 y_0)^2} \end{pmatrix} \\ &= \begin{pmatrix} 0 & -ax_0 \\ \dfrac{by_0^2}{x_0^2} & -\dfrac{by_0}{x_0} + \dfrac{plE_0 y_0}{ply_0 - c(l+E_0 y_0)^2} \end{pmatrix}, \end{aligned} \tag{2.8}$$

where $D_X f_1(X_0) = \big(0, -ax_0, 0\big)$, $D_X f_2(X_0) = \big(by_0^2/x_0^2, -by_0/x_0, -y_0\big)$, $D_X g(X_0) = \big(0, plE_0/(l+E_0 y_0)^2, [ply_0 - c(l+E_0 y_0)^2]/(l+E_0 y_0)^2\big)$. Hence, from Eq. (2.8), the characteristic equation of matrix P is

$$\lambda^2 + \left(\frac{by_0}{x_0} - \frac{plE_0 y_0}{ply_0 - c(l+E_0 y_0)^2}\right)\lambda + \frac{aby_0^2}{x_0} = 0. \tag{2.9}$$

For case (i), if $by_0/x_0 > plE_0 y_0/[ply_0 - c(l+E_0 y_0)^2]$, then Eq. (2.9) has two negative real roots. Hence, X_0 is a stable node. Conversely, X_0 is an unstable node iff Eq. (2.9) has two positive real roots. For case (ii), if $by_0/x_0 > plE_0 y_0/[ply_0 - c(l+E_0 y_0)^2]$, then Eq. (2.9) has two complex roots which have negative real parts, and therefore X_0 is a sink. On the contrary, X_0 is a source iff the two complex roots of Eq. (2.9) have positive real parts. And then, in view of Eq. (2.9), we are easy to derive Theorem 2.1 on the grounds of Routh-Hurwitz stability criteria [2, 3]. □

Remark 2.1. *By analyzing the eigenvalues of characteristic equation* (2.9), *Hopf bifurcation can take place in model* (1.3) *under certain conditions, which will be discussed in the following section.*

3. Hopf bifurcation analysis

In this section, by choosing the economic profit v as a variable bifurcation parameter, we investigate the Hopf bifurcation in model (1.3) on the grounds of the Hopf bifurcation theorem developed by Guckenheimer and Holmes [33].

When $\Delta = \{by_0/x_0 - plE_0 y_0/[ply_0 - c(l+E_0 y_0)^2]\}^2 - 4aby_0^2/x_0 < 0$, it is clear that Eq. (2.9) has the following complex roots:

$$\lambda_{1,2}(v) := \alpha(v) \pm i\omega(v),$$

where $\alpha(v) = -(1/2)\{by_0/x_0 - plE_0y_0/[ply_0 - c(l+E_0y_0)^2]\}$, $\omega(v) = \{aby_0^2/x_0 - (1/4)[by_0/x_0 - plE_0y_0/(ply_0 - c(l+E_0y_0)^2)]^2\}^{1/2}$. Besides, in view of Eq. (2.9), the bifurcation value v_0 of variable v firstly needs to meet the equation

$$\frac{by_0}{x_0(v)} = \frac{plE_0(v)y_0}{ply_0 - c(l+E_0(v)y_0)^2}. \tag{3.1}$$

Further, in order to guarantee the existence of Hopf bifurcation in model (1.3), we assume that the following transversality conditions in the literatrue [33] are satisfied throughout this section:

$$\begin{aligned}\alpha(v_0) = 0,\ \alpha'(v_0) = \Bigg(&-\frac{b^2y_0^2}{x_0^2(r_2 - E_0(v_0))^2} - \frac{ply_0}{ply_0 - c(l+E_0(v_0)y_0)^2}\\ &-\frac{2pcly_0^2E_0(v_0)(l+E_0(v_0)y_0)}{[ply_0 - c(l+E_0(v_0)y_0)^2]^2}\Bigg)\cdot E_0'(v_0) \neq 0,\ \ \omega(v_0) := \omega_0 = \sqrt{\frac{ab}{x_0}}y_0 \neq 0,\end{aligned} \tag{3.2}$$

where $E_0'(v_0) = -\frac{1}{2c} \pm \frac{v_0y_0 - py_0 - cl}{2c\sqrt{(cl+v_0y_0-py_0)^2 - 4clv_0y_0}}$. So Hopf bifurcation takes place if the quantity v attains the critical value v_0.

To derive the detailed information about the Hopf bifurcation, in the light of the Hopf bifurcation theorem in Ref. [33], we need to make system (2.7) equivalent to the following normal form:

$$\begin{cases}\dot{y}_1 = -\omega_0y_2 + \frac{1}{2}a_{11}^1y_1^2 + a_{12}^1y_1y_2 + \frac{1}{2}a_{22}^1y_2^2 + \frac{1}{6}a_{111}^1y_1^3 + \frac{1}{2}a_{112}^1y_1^2y_2\\ \qquad +\frac{1}{2}a_{122}^1y_1y_2^2 + \frac{1}{6}a_{222}^1y_2^3 + o(|Y|^4)\ ,\\ \dot{y}_2 = \omega_0y_1 + \frac{1}{2}a_{11}^2y_1^2 + a_{12}^2y_1y_2 + \frac{1}{2}a_{22}^2y_2^2 + \frac{1}{6}a_{111}^2y_1^3 + \frac{1}{2}a_{112}^2y_1^2y_2\\ \qquad +\frac{1}{2}a_{122}^2y_1y_2^2 + \frac{1}{6}a_{222}^2y_2^3 + o(|Y|^4)\ .\end{cases} \tag{3.3}$$

Subsequently, we should first of all calculate the following third order Taylor series developments of system (2.7):

$$\begin{cases}\dot{y}_1 = f_{1y_1}(X_0)y_1 + f_{1y_2}(X_0)y_2 + \frac{1}{2}f_{1y_1y_1}(X_0)y_1^2 + f_{1y_1y_2}(X_0)y_1y_2\\ \qquad +\frac{1}{2}f_{1y_2y_2}(X_0)y_2^2 + \frac{1}{6}f_{1y_1y_1y_1}(X_0)y_1^3 + \frac{1}{2}f_{1y_1y_1y_2}(X_0)y_1^2y_2\\ \qquad +\frac{1}{2}f_{1y_1y_2y_2}(X_0)y_1y_2^2 + \frac{1}{6}f_{1y_2y_2y_2}(X_0)y_2^3 + o(|Y|^4),\\ \dot{y}_2 = f_{2y_1}(X_0)y_1 + f_{2y_2}(X_0)y_2 + \frac{1}{2}f_{2y_1y_1}(X_0)y_1^2 + f_{2y_1y_2}(X_0)y_1y_2\\ \qquad +\frac{1}{2}f_{2y_2y_2}(X_0)y_2^2 + \frac{1}{6}f_{2y_1y_1y_1}(X_0)y_1^3 + \frac{1}{2}f_{2y_1y_1y_2}(X_0)y_1^2y_2\\ \qquad +\frac{1}{2}f_{2y_1y_2y_2}(X_0)y_1y_2^2 + \frac{1}{6}f_{2y_2y_2y_2}(X_0)y_2^3 + o(|Y|^4).\end{cases} \tag{3.4}$$

The coefficients of (3.4) are calculated as follows. From Eq. (2.3), we have

$$D_X f_1(X) = (r_1 - ay,\ -ax,\ 0)\,,\ D_X f_2(X) = \left(\frac{by^2}{x^2},\ r_2 - \frac{2by}{x} - E,\ -y\right),$$

$$D_X g(X) = \left(0,\ \frac{plE}{(l+Ey)^2},\ \frac{ply - c(l+Ey)^2}{(l+Ey)^2}\right). \tag{3.5}$$

In view of Eqs. (A.2) and (A.3) in Appendix, we can derive

$$D_Y\psi(Y) = \begin{pmatrix} D_X g(X) \\ U_0^T \end{pmatrix}^{-1} \begin{pmatrix} 0 \\ I_2 \end{pmatrix} = \begin{pmatrix} 0 & \frac{plE}{(l+Ey)^2} & \frac{ply - c(l+Ey)^2}{(l+Ey)^2} \\ 1 & 0 & 0 \\ 0 & 1 & 0 \end{pmatrix}^{-1}$$

$$\times \begin{pmatrix} 0 & 0 \\ 1 & 0 \\ 0 & 1 \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ 0 & 1 \\ 0 & -\frac{plE}{ply - c(l+Ey)^2} \end{pmatrix} := \big(D_{y_1}\psi(Y),\ D_{y_2}\psi(Y)\big). \tag{3.6}$$

By Eqs. (2.7), (3.5) and (3.6), we get

$$\begin{aligned} f_{1y_1}(X) &= D_X f_1(X) D_{y_1}\psi(Y) = r_1 - ay, \\ f_{1y_2}(X) &= D_X f_1(X) D_{y_2}\psi(Y) = -ax, \\ f_{2y_1}(X) &= D_X f_2(X) D_{y_1}\psi(Y) = \frac{by^2}{x^2}, \\ f_{2y_2}(X) &= D_X f_2(X) D_{y_2}\psi(Y) = r_2 - \frac{2by}{x} - E + \frac{plEy}{ply - c(l+Ey)^2}. \end{aligned} \tag{3.7}$$

Substituting $X = X_0$ into Eq. (3.7), we obtain

$$\begin{aligned} &f_{1y_1}(X_0) = 0,\ \ f_{1y_2}(X_0) = -ax_0,\ \ f_{2y_1}(X_0) = \frac{by_0^2}{x_0^2}, \\ &f_{2y_2}(X_0) = -\frac{by_0}{x_0} + \frac{plE_0y_0}{ply_0 - c(l+E_0y_0)^2} = 0. \end{aligned} \tag{3.8}$$

By Eq. (3.7), we have

$$D_X f_{1y_1}(X) = (0, -a, 0), D_X f_{1y_2}(X) = (-a, 0, 0), D_X f_{2y_1}(X) = \left(-\frac{2by^2}{x^3}, \frac{2by}{x^2}, 0\right),$$

$$\begin{aligned} D_X f_{2y_2}(X) = \Bigg(&\frac{2by}{x^2},\ -\frac{2b}{x} + \frac{plE}{ply - c(l+Ey)^2} - \frac{p^2l^2Ey}{[ply - c(l+Ey)^2]^2} \\ &+ \frac{2pclE^2y(l+Ey)}{[ply - c(l+Ey)^2]^2}, -1 + \frac{ply}{ply - c(l+Ey)^2} + \frac{2pclEy^2(l+Ey)}{[ply - c(l+Ey)^2]^2}\Bigg). \end{aligned} \tag{3.9}$$

In view of Eqs. (2.7), (3.6) and (3.9), we obtain

$$
\begin{aligned}
&f_{1y_1y_1}(X)=D_X f_{1y_1}(X)D_{y_1}\psi(Y)=0, f_{1y_1y_2}(X)=D_X f_{1y_1}(X)D_{y_2}\psi(Y)=-a,\\
&f_{1y_2y_2}(X)=D_X f_{1y_2}(X)D_{y_2}\psi(Y)=0, f_{2y_1y_1}(X)=D_X f_{2y_1}(X)D_{y_1}\psi(Y)=-\frac{2by^2}{x^3},\\
&f_{2y_1y_2}(X)=D_X f_{2y_1}(X)D_{y_2}\psi(Y)=\frac{2by}{x^2},\\
&f_{2y_2y_2}(X)=D_X f_{2y_2}(X)D_{y_2}\psi(Y)=-\frac{2b}{x}+\frac{2plE}{ply-c(l+Ey)^2}\\
&\qquad -\frac{2p^2l^2Ey}{[ply-c(l+Ey)^2]^2}+\frac{2pclE^2y(l+Ey)}{[ply-c(l+Ey)^2]^2}-\frac{2p^2cl^2E^2y^2(l+Ey)}{[ply-c(l+Ey)^2]^3}.
\end{aligned}
\tag{3.10}
$$

Substituting $X = X_0$ into Eq. (3.10), which yields

$$
\begin{aligned}
&f_{1y_1y_1}(X_0)=0,\ \ f_{1y_1y_2}(X_0)=-a,\ \ f_{1y_2y_2}(X_0)=0,\\
&f_{2y_1y_1}(X_0)=-\frac{2by_0^2}{x_0^3},\ \ f_{2y_1y_2}(X_0)=\frac{2by_0}{x_0^2},\\
&f_{2y_2y_2}(X_0)=-\frac{2p^2l^2E_0y_0}{[ply_0-c(l+E_0y_0)^2]^2}+\frac{2pclE_0^2y_0(l+E_0y_0)}{[ply_0-c(l+E_0y_0)^2]^2}\\
&\qquad -\frac{2p^2cl^2E_0^2y_0^2(l+E_0y_0)}{[ply_0-c(l+E_0y_0)^2]^3}.
\end{aligned}
\tag{3.11}
$$

Besides, in view of Eqs. (3.6) and (3.10), we have

$$
\begin{aligned}
&D_X f_{1y_1y_1}(X_0)=D_X f_{1y_1y_2}(X_0)=D_X f_{1y_2y_2}(X_0)=(0,0,0),\\
&D_X f_{2y_1y_1}(X_0)=\left(\frac{6by_0^2}{x_0^4},-\frac{4by_0}{x_0^3},0\right),\ D_X f_{2y_1y_2}(X_0)=\left(-\frac{4by_0}{x_0^3},\frac{2b}{x_0^2},0\right),\\
&D_X f_{2y_2y_2}(X_0)=\left(\frac{2b}{x_0^2},\frac{2plE_0(3clE_0+4E_0^2y_0-2pl)}{[ply_0-c(l+E_0y_0)^2]^2}\right.\\
&\quad+\frac{2p^2l^2E_0y_0(2pl-9cE_0^2y_0)}{[ply_0-c(l+E_0y_0)^2]^3}+\frac{8pc^2lE_0^3y_0(l+E_0y_0)^2-16p^2cl^3E_0^2y_0}{[ply_0-c(l+E_0y_0)^2]^3}\\
&\quad+\frac{6p^2cl^2E_0^2y_0^2(l+E_0y_0)[pl-2cE_0(l+E_0y_0)]}{[ply_0-c(l+E_0y_0)^2]^4},\\
&\frac{2pl}{ply_0-c(l+E_0y_0)^2}+\frac{2ply_0[4clE_0+5cE_0^2y_0-pl]}{[ply_0-c(l+E_0y_0)^2]^2}+\frac{8pc^2lE_0^2y_0^2(l+E_0y_0)^2}{[ply_0-c(l+E_0y_0)^2]^3}\\
&\quad\left.-\frac{2p^2l^2E_0y_0^2(6cl+7cE_0y_0)}{[ply_0-c(l+E_0y_0)^2]^3}-\frac{12p^2c^2l^2E_0^2y_0^3(l+E_0y_0)^2}{[ply_0-c(l+E_0y_0)^2]^4}\right),\\
&D_Y\psi(0)=\begin{pmatrix}1 & 0\\ 0 & 1\\ 0 & -\dfrac{plE_0}{ply_0-c(l+E_0y_0)^2}\end{pmatrix}:=\big(D_{y_1}\psi(0),\ D_{y_2}\psi(0)\big).
\end{aligned}
\tag{3.12}
$$

Furthermore, Eqs. (2.7) and (3.12) can give that

$$
\begin{aligned}
&f_{1y_1y_1y_1}(X_0) = D_X f_{1y_1y_1}(X_0) D_{y_1}\psi(0) = 0,\\
&f_{1y_1y_1y_2}(X_0) = D_X f_{1y_1y_1}(X_0) D_{y_2}\psi(0) = 0,\\
&f_{1y_1y_2y_2}(X_0) = D_X f_{1y_1y_2}(X_0) D_{y_2}\psi(0) = 0,\\
&f_{1y_2y_2y_2}(X_0) = D_X f_{1y_2y_2}(X_0) D_{y_2}\psi(0) = 0,\\
&f_{2y_1y_1y_1}(X_0) = D_X f_{2y_1y_1}(X_0) D_{y_1}\psi(0) = \frac{6by_0^2}{x_0^4},\\
&f_{2y_1y_1y_2}(X_0) = D_X f_{2y_1y_1}(X_0) D_{y_2}\psi(0) = -\frac{4by_0}{x_0^3},\\
&f_{2y_1y_2y_2}(X_0) = D_X f_{2y_1y_2}(X_0) D_{y_2}\psi(0) = \frac{2b}{x_0^2},\\
&f_{2y_2y_2y_2}(X_0) = D_X f_{2y_2y_2}(X_0) D_{y_2}\psi(0) = \frac{2plE_0(3clE_0 + 4E_0^2 y_0 - 3pl)}{[ply_0 - c(l+E_0y_0)^2]^2}\\
&\qquad + \frac{2p^2l^2E_0y_0(3pl - 14cE_0^2y_0 - 12clE_0) + 8pc^2lE_0^3y_0(l+E_0y_0)^2}{[ply_0 - c(l+E_0y_0)^2]^3}\\
&\qquad + \frac{2p^2cl^2E_0^2y_0^2(l+E_0y_0)[3pl - 10cE_0(l+E_0y_0)]}{[ply_0 - c(l+E_0y_0)^2]^4}\\
&\qquad + \frac{2p^3l^3E_0^2y_0^2(6cl + 7cE_0y_0)}{[ply_0 - c(l+E_0y_0)^2]^4} + \frac{12p^3c^2l^3E_0^3y_0^3(l+E_0y_0)^2}{[ply_0 - c(l+E_0y_0)^2]^5}.
\end{aligned}
\tag{3.13}
$$

Substituting Eqs. (3.8), (3.11) and (3.13) into Taylor series developments (3.4), we derive

$$
\begin{cases}
\dot{y}_1 = -ax_0y_2 - ay_1y_2,\\
\dot{y}_2 = \dfrac{by_0^2}{x_0^2}y_1 - \dfrac{by_0^2}{x_0^3}y_1^2 + \dfrac{2by_0}{x_0^2}y_1y_2 + \dfrac{1}{2}f_{2y_2y_2}(X_0)y_2^2 + \dfrac{by_0^2}{x_0^4}y_1^3\\
\qquad -\dfrac{2by_0}{x_0^3}y_1^2y_2 + \dfrac{b}{x_0^2}y_1y_2^2 + \dfrac{1}{6}f_{2y_2y_2y_2}(X_0)y_2^3 + o(|Y|^4).
\end{cases}
\tag{3.14}
$$

In view of the required form (3.3), we need to make a matrix transformation — viz. $Y = \mathrm{T}Z$ for system (3.14), where $Z = (z_1, z_2)^T$, $\mathrm{T}_{2\times 2}$ is an invertible matrix and satisfies

$$
\mathrm{T}^{-1}\begin{pmatrix} 0 & -ax_0 \\ \dfrac{by_0^2}{x_0^2} & 0 \end{pmatrix}\mathrm{T} = \begin{pmatrix} 0 & -\omega_0 \\ \omega_0 & 0 \end{pmatrix}.
$$

By computing, we can get $\mathrm{T} = \begin{pmatrix} x_0^{\frac{3}{2}} & 0 \\ 0 & \sqrt{\dfrac{b}{a}}y_0 \end{pmatrix}$. For convenience, Z is denoted as Y. Accordingly, we obtain the normal form of system (3.14):

$$
(3.15)\quad \begin{cases} \dot{y}_1 = -\omega_0 y_2 - \sqrt{ab} y_0 y_1 y_2, \\ \dot{y}_2 = \omega_0 y_1 - \sqrt{ab} y_0 y_1^2 + \dfrac{2by_0}{\sqrt{x_0}} y_1 y_2 + \dfrac{y_0}{2}\sqrt{\dfrac{b}{a}} f_{2y_2y_2}(X_0) y_2^2 + \sqrt{abx_0} y_0 y_1^3 \\ \qquad -2by_0 y_1^2 y_2 + \dfrac{b^{\frac{3}{2}} y_0}{\sqrt{ax_0}} y_1 y_2^2 + \dfrac{by_0^2}{6a} f_{2y_2y_2y_2}(X_0) y_2^3 + o(|Y|^4). \end{cases}
$$

Summarizing the above analysis, we have the following Hopf bifurcation theorem.

Theorem 3.1. *For model* (1.3), *there exist a small neighborhood* Ω *of equilibrium point* $X_0(v)$ *as well as a small positive constant* γ.

Case I. If

$$y_0 f_{2y_2y_2y_2}(X_0) > 2 f_{2y_2y_2}(X_0),$$

then

(i) *when* $v_0 < v < v_0 + \gamma$, $X_0(v)$ *is unstable, which excludes the points in* Ω;

(ii) *when* $v_0 - \gamma < v < v_0$, *there exists a periodic orbit in* $\Omega \setminus \{X_0(v)\}$, *besides* $X_0(v)$ *is locally asymptotically stable, which attracts the points in* Ω;

Case II. If

$$y_0 f_{2y_2y_2y_2}(X_0) < 2 f_{2y_2y_2}(X_0),$$

then

(i) *when* $v_0 - \gamma < v < v_0$, $X_0(v)$ *is locally asymptotically stable, which attracts the points in* Ω;

(ii) *when* $v_0 < v < v_0 + \gamma$, *there exists a periodic orbit in* $\Omega \setminus \{X_0(v)\}$, *besides* $X_0(v)$ *is unstable, which excludes the points in* Ω.

Proof. In terms of the Hopf bifurcation theorem in the literature [33], we need to calculate the important quantity $16\varrho_0$ (see below), in view of the normal forms (3.3) and (3.15), we have

$$
\begin{aligned}
16\varrho_0 :=& \{a_{11}^1(a_{12}^1 - a_{11}^2) + a_{22}^2(a_{22}^1 - a_{12}^2) + (a_{12}^1 a_{22}^1 - a_{11}^2 a_{12}^2)\}/\omega_0 \\
&+ (a_{111}^1 + a_{122}^1 + a_{112}^2 + a_{222}^2) \\
=& \left\{ \sqrt{\frac{b}{a}} y_0 f_{2y_2y_2}(X_0) \left(0 - \frac{2by_0}{\sqrt{x_0}}\right) + 2\sqrt{ab} y_0 \cdot \frac{2by_0}{\sqrt{x_0}} \right\} \Bigg/ \left\{ \sqrt{\frac{ab}{x_0}} y_0 \right\} \\
&- 4by_0 + \frac{by_0^2}{a} f_{2y_2y_2y_2}(X_0) \\
=& -\frac{2by_0}{a} f_{2y_2y_2}(X_0) + \frac{by_0^2}{a} f_{2y_2y_2y_2}(X_0).
\end{aligned}
$$

Next, the two cases $16\varrho_0 > 0$ and $16\varrho_0 < 0$ need further discussion. Because the rest of the process is quite similar to Ref. [33], and therefore it is eliminated in this paper. □

4. Stability analysis for centre

In view of Eq. (2.9), when $by_0/x_0 = plE_0y_0/[ply_0 - c(l + E_0y_0)^2]$ (i.e., $v = v_0$), the eigenvalues of Eq. (2.9) are a pair of imaginary roots: $\pm i\sqrt{ab/x_0y_0}$. That is to say, the equilibrium point X_0 is a centre. Nevertheless, for $v = v_0$, Theorems 2.1 and 3.1 don't include the corresponding stability result. In this section, we study the stability of the centre.

Theorem 4.1. *When $v = v_0$,*

(*i*) *if*

$$y_0 f_{2y_2y_2y_2}(X_0) > 2f_{2y_2y_2}(X_0),$$

then the centre X_0 of model (1.3) *is unstable*;

(*ii*) *if*

$$y_0 f_{2y_2y_2y_2}(X_0) < 2f_{2y_2y_2}(X_0),$$

then the centre X_0 of model (1.3) *is stable.*

Proof. First of all, we need to make system (3.15) equivalent to the following form according to the formal series approach [33, 41, 42]:

$$\begin{cases} \dot{y}_1 = -y_2 + M_2(y_1, y_2) + M_3(y_1, y_2) + o(|Y|^4), \\ \dot{y}_2 = y_1 + N_2(y_1, y_2) + N_3(y_1, y_2) + o(|Y|^4), \end{cases} \tag{4.1}$$

where $M_i(y_1, y_2)$ and $N_i(y_1, y_2)$ denote the i^{th} degree homogeneous polynomials of y_1 and y_2.

On writing $\bar{t} = \omega_0 t$ in system (3.15), and in this section $\dot{Y}$ denotes the derivative of vector function Y regarding $\bar{t}$, then (3.15) is transformed into

$$\begin{cases} \dot{y}_1 = -y_2 - \dfrac{\sqrt{ab}y_0}{\omega_0} y_1 y_2, \\ \dot{y}_2 = y_1 - \dfrac{\sqrt{ab}y_0}{\omega_0} y_1^2 + \dfrac{2by_0}{\omega_0\sqrt{x_0}} y_1 y_2 + \dfrac{y_0}{2\omega_0}\sqrt{\dfrac{b}{a}} f_{2y_2y_2}(X_0) y_2^2 + \dfrac{\sqrt{abx_0}y_0}{\omega_0} y_1^3 \\ \qquad - \dfrac{2by_0}{\omega_0} y_1^2 y_2 + \dfrac{b^{\frac{3}{2}} y_0}{\omega_0\sqrt{ax_0}} y_1 y_2^2 + \dfrac{by_0^2}{6a\omega_0} f_{2y_2y_2y_2}(X_0) y_2^3 + o(|Y|^4). \end{cases} \tag{4.2}$$

Next, we consider the following formal series for the above system (4.2):

$$V(y_1, y_2) = y_1^2 + y_2^2 + \sum_{n=3}^{\infty} V_n(y_1, y_2),$$

where $V_n(y_1, y_2)$ denotes the n^{th} degree homogeneous polynomials of y_1 and y_2. We then have

$$\begin{aligned}\frac{\mathrm{d}V(y_1,y_2)}{\mathrm{d}\bar{t}}\bigg|_{(4.2)} &= \frac{\partial V(y_1,y_2)}{\partial y_1}\cdot \dot{y}_1 + \frac{\partial V(y_1,y_2)}{\partial y_2}\cdot \dot{y}_2\\ &= \left(2y_1+\sum_{n=3}^{\infty}\frac{\partial V_j(y_1,y_2)}{\partial y_1}\right)\left(-y_2-\frac{\sqrt{ab}y_0}{\omega_0}y_1y_2\right)+\left(2y_2+\sum_{n=3}^{\infty}\frac{\partial V_j(y_1,y_2)}{\partial y_2}\right)\\ &\times\left(y_1-\frac{\sqrt{ab}y_0}{\omega_0}y_1^2+\frac{2by_0}{\omega_0\sqrt{x_0}}y_1y_2+\frac{y_0}{2\omega_0}\sqrt{\frac{b}{a}}f_{2y_2y_2}(X_0)y_2^2\right.\\ &\left.+\frac{\sqrt{abx_0}y_0}{\omega_0}y_1^3-\frac{2by_0}{\omega_0}y_1^2y_2+\frac{b^{\frac{3}{2}}y_0}{\omega_0\sqrt{ax_0}}y_1y_2^2+\frac{by_0^2}{6a\omega_0}f_{2y_2y_2y_2}(X_0)y_2^3+\cdots\right).\end{aligned}\tag{4.3}$$

Setting the 3^{th} degree homogeneous polynomial in Eq. (4.3) to 0, we obtain

$$\begin{aligned}&y_1\frac{\partial V_3(y_1,y_2)}{\partial y_2}-y_2\frac{\partial V_3(y_1,y_2)}{\partial y_1}\\ &=\frac{4\sqrt{ab}y_0}{\omega_0}y_1^2y_2-\frac{4by_0}{\omega_0\sqrt{x_0}}y_1y_2^2-\frac{y_0}{\omega_0}\sqrt{\frac{b}{a}}f_{2y_2y_2}(X_0)y_2^3.\end{aligned}\tag{4.4}$$

Let $y_1 = r\cos\theta$, $y_2 = r\sin\theta$, then by chain rule we can get

$$y_1\frac{\partial V_n(y_1,y_2)}{\partial y_2}-y_2\frac{\partial V_n(y_1,y_2)}{\partial y_1}=\frac{\partial V_n(y_1,y_2)}{\partial\theta}=r^n\cdot\frac{\mathrm{d}V_n(\cos\theta,\sin\theta)}{\mathrm{d}\theta}.\tag{4.5}$$

In view of Eqs. (4.4) and (4.5), we have

$$\begin{aligned}\frac{\mathrm{d}V_3(\cos\theta,\sin\theta)}{\mathrm{d}\theta}=&\frac{4\sqrt{ab}y_0}{\omega_0}\cos^2\theta\sin\theta-\frac{4by_0}{\omega_0\sqrt{x_0}}\cos\theta\sin^2\theta\\ &-\frac{y_0}{\omega_0}\sqrt{\frac{b}{a}}f_{2y_2y_2}(X_0)\sin^3\theta\\ :=&-H_3(\cos\theta,\sin\theta)=\frac{\sigma_0}{2}+\sum_{\delta=1}^{\infty}(a_\delta\cos\delta\theta+b_\delta\sin\delta\theta),\end{aligned}\tag{4.6}$$

where $(\sigma_0/2)+\sum_{\delta=1}^{\infty}(a_\delta\cos\delta\theta+b_\delta\sin\delta\theta)$ is the Fourier series of H_3. Such a $V_3(\cos\theta,\sin\theta)$ exists if and only if $\sigma_0 = 0$, viz., $\int_0^{2\pi}H_3(\cos\theta,\sin\theta)\,\mathrm{d}\theta = 0$. Indeed,

$$\int_0^{2\pi}\left\{\frac{4\sqrt{ab}y_0}{\omega_0}\cos^2\theta\sin\theta-\frac{4by_0}{\omega_0\sqrt{x_0}}\cos\theta\sin^2\theta-\frac{y_0}{\omega_0}\sqrt{\frac{b}{a}}f_{2y_2y_2}(X_0)\sin^3\theta\right\}\mathrm{d}\theta=0.$$

Hence, $V_3(y_1, y_2)$ exists, and by Eq. (4.6) we derive

$$\begin{aligned}V_3(y_1,y_2)=&\left(\frac{2y_0}{3\omega_0}\sqrt{\frac{b}{a}}f_{2y_2y_2}(X_0)-\frac{4\sqrt{ab}y_0}{3\omega_0}\right)y_1^3\\ &+\frac{y_0}{\omega_0}\sqrt{\frac{b}{a}}f_{2y_2y_2}(X_0)y_1y_2^2-\frac{4by_0}{3\omega_0\sqrt{x_0}}y_2^3.\end{aligned}\tag{4.7}$$

Again, setting 4^{th} degree homogeneous polynomial in Eq. (4.3) to 0, which yields

$$
\begin{aligned}
y_1\frac{\partial V_4(y_1,y_2)}{\partial y_2}-y_2\frac{\partial V_4(y_1,y_2)}{\partial y_1}&=-\frac{2\sqrt{abx_0}y_0}{\omega_0}y_1^3y_2+\frac{4by_0}{\omega_0}y_1^2y_2^2\\
&-\frac{2b^{\frac{3}{2}}y_0}{\omega_0\sqrt{ax_0}}y_1y_2^3-\frac{by_0^2}{3a\omega_0}f_{2y_2y_2y_2}(X_0)y_2^4+\frac{\sqrt{ab}y_0}{\omega_0}y_1y_2\cdot\frac{\partial V_3(y_1,y_2)}{\partial y_1}\\
&+\left(\frac{\sqrt{ab}y_0}{\omega_0}y_1^2-\frac{2by_0}{\omega_0\sqrt{x_0}}y_1y_2-\frac{y_0}{2\omega_0}\sqrt{\frac{b}{a}}f_{2y_2y_2}(X_0)y_2^2\right)\cdot\frac{\partial V_3(y_1,y_2)}{\partial y_2}.
\end{aligned}\tag{4.8}
$$

Furthermore, setting $y_1=r\cos\theta$, $y_2=r\sin\theta$ in Eq. (4.8), which leads to

$$
\begin{aligned}
\frac{\mathrm{d}V_4(\cos\theta,\sin\theta)}{\mathrm{d}\theta}&=\left(-\frac{2\sqrt{abx_0}y_0}{\omega_0}+\frac{2by_0^2}{\omega_0^2}f_{2y_2y_2}(X_0)-\frac{4aby_0}{\omega_0^2}+\frac{2by_0^2}{\omega_0^2}\right)\cos^3\theta\sin\theta\\
&+\left(\frac{4by_0}{\omega_0}-\frac{4b\sqrt{ab}y_0^2}{\omega_0^2\sqrt{x_0}}-\frac{4by_0^2}{\omega_0^2\sqrt{x_0}}\sqrt{\frac{b}{a}}f_{2y_2y_2}(X_0)\right)\cos^2\theta\sin^2\theta\\
&+\left(\frac{by_0^2}{\omega_0^2}f_{2y_2y_2}(X_0)-\frac{2b^{\frac{3}{2}}y_0}{\omega_0\sqrt{ax_0}}+\frac{8b^2y_0^2}{\omega_0^2x_0}-\frac{by_0^2}{a\omega_0^2}\left(f_{2y_2y_2}(X_0)\right)^2\right)\cos\theta\sin^3\theta\\
&+\left(\frac{2by_0^2}{\omega_0^2\sqrt{x_0}}\sqrt{\frac{b}{a}}f_{2y_2y_2}(X_0)-\frac{by_0^2}{3a\omega_0}f_{2y_2y_2y_2}(X_0)\right)\sin^4\theta\\
&:=-H_4(\cos\theta,\sin\theta).
\end{aligned}
$$

Similarly, such a $V_4(\cos\theta,\sin\theta)$ exists if and only if $\int_0^{2\pi}H_4(\cos\theta,\sin\theta)\mathrm{d}\theta=0$. But,

$$
\begin{aligned}
&\int_0^{2\pi}H_4(\cos\theta,\sin\theta)\mathrm{d}\theta\\
&=-\frac{by_0\pi}{\omega_0}+\frac{b\sqrt{ab}y_0^2\pi}{\omega_0^2\sqrt{x_0}}-\frac{by_0^2\pi}{2\omega_0^2\sqrt{x_0}}\sqrt{\frac{b}{a}}f_{2y_2y_2}(X_0)+\frac{by_0^2\pi}{4a\omega_0}f_{2y_2y_2y_2}(X_0)\neq 0.
\end{aligned}
$$

There upon we should amend $V_4(\cos\theta,\sin\theta)$ such that

$$
\frac{\mathrm{d}V_4(\cos\theta,\sin\theta)}{\mathrm{d}\theta}=-H_4(\cos\theta,\sin\theta)+\aleph_4:=-\widetilde{H}_4(\cos\theta,\sin\theta),
$$

where $\aleph_4=\frac{1}{2\pi}\int_0^{2\pi}H_4(\cos\theta,\sin\theta)\mathrm{d}\theta=-\frac{by_0}{2\omega_0}+\frac{b\sqrt{ab}y_0^2}{2\omega_0^2\sqrt{x_0}}-\frac{by_0^2}{4\omega_0^2\sqrt{x_0}}\sqrt{\frac{b}{a}}f_{2y_2y_2}(X_0)$ $+\frac{by_0^2}{8a\omega_0}f_{2y_2y_2y_2}(X_0)$. Substituting $\omega_0=\sqrt{ab/x_0}y_0$ into $\aleph_4$, which yields $\aleph_4=\frac{1}{2a}(\frac{y_0}{2}f_{2y_2y_2y_2}(X_0)-f_{2y_2y_2}(X_0))\neq 0$. Clearly, $\int_0^{2\pi}\widetilde{H}_4(\cos\theta,\sin\theta)\mathrm{d}\theta=0$, therefore the amended $V_4(\cos\theta,\sin\theta)$ exists.

We now construct the Lyapunov function $V(y_1,y_2)=y_1^2+y_2^2+V_3(y_1,y_2)+V_4(y_1,y_2)$ for system (4.2), and further we have

$$
\left.\frac{\mathrm{d}V(y_1,y_2)}{\mathrm{d}\bar{t}}\right|_{(4.2)}=\aleph_4(y_1^2+y_2^2)^2+o\left((y_1^2+y_2^2)^2\right).
$$

If $\aleph_4 > 0$ (viz., $y_0 f_{2y_2y_2y_2}(X_0) > 2f_{2y_2y_2}(X_0)$), then the equilibrium point $(0,0)^T$ of system (4.2) is unstable, consequently the centre X_0 is unstable. On the contrary, if $\aleph_4 < 0$ (viz., $y_0 f_{2y_2y_2y_2}(X_0) < 2f_{2y_2y_2}(X_0)$), then the equilibrium point $(0,0)^T$ of system (4.2) is stable, hence the centre X_0 is stable. □

Remark 4.1. Due to $\int_0^{2\pi} H_{2\mu-1}(\cos\theta, \sin\theta)\mathrm{d}\theta = 0$, $\mu = 2, 3, \cdots$, so if $\int_0^{2\pi} H_4(\cos\theta, \sin\theta)\mathrm{d}\theta = 0$, then we should find the minimum positive integer ϑ such that $\int_0^{2\pi} H_{2\vartheta}(\cos\theta, \sin\theta)\mathrm{d}\theta \neq 0$, and then afterwards, amending the corresponding function $V_{2\vartheta}(\cos\theta, \sin\theta)$ similar to $V_4(\cos\theta, \sin\theta)$.

5. Numerical simulations

In this section, we perform several Matlab simulations to complement the analytical results above.

As an example, we consider the harvested predator-prey model (1.3) with the coefficients $r_1 = 2,\ a = 1,\ r_2 = \frac{3}{4},\ b = 1,\ p = 1,\ l = 1,\ c = \frac{4}{9}$. Then by the analysis in section 2, we can find that model (1.3) has a positive equilibrium point $X_0 = (4, 2, 0.25)$ and the bifurcation value $v_0 = 2/9$. We can check that model (1.3) satisfies the requirement (2.1), the transversality conditions for Hopf bifurcation in (3.2), as well as the condition of case (i) in Theorems 3.1 and 4.1.

In accordance with Theorems 3.1 and 4.1 (on choosing $\gamma = 0.002$), we present four groups of numerical simulations as follows:

(i) The equilibrium point X_0 is locally asymptotically stable when $v = 0.2205 < v_0$, which is verified as shown in Fig. 1. In this case, the prey species, predator species and economic harvesting are in a stable state, so the ecological balance can be maintained.

(ii) A Hopf-bifurcating periodic orbit bifurcates from the equilibrium point X_0 when $v = 0.222222 < v_0$, which is verified as shown in Fig. 2. The emergence of the periodic orbit would generate small-amplitude population oscillations in our ecosystem.

(iii) The centre X_0 is unstable when v equals to $v_0 = 2/9$, which is verified as shown in Fig. 3. Unstable center means that the aforementioned population oscillations are growing as time t goes on, i.e., the prey species, predator species and economic harvesting can't coexist in an oscillatory mode.

(iv) The equilibrium point X_0 is unstable when $v = 0.223 > v_0$, which is verified as shown in Fig. 4. At this moment, the biological populations and harvesting effort are unstable, which can result in ecological unbalance.

From Figs. 1-4, it is clear that our harvested predator-prey model can exhibit a Hopf bifurcation as the increase of the harvesting profit v, which can cause potentially dramatic variations in the dynamical behaviors of the population model. Hence, the Hopf bifurcation is biologically important.

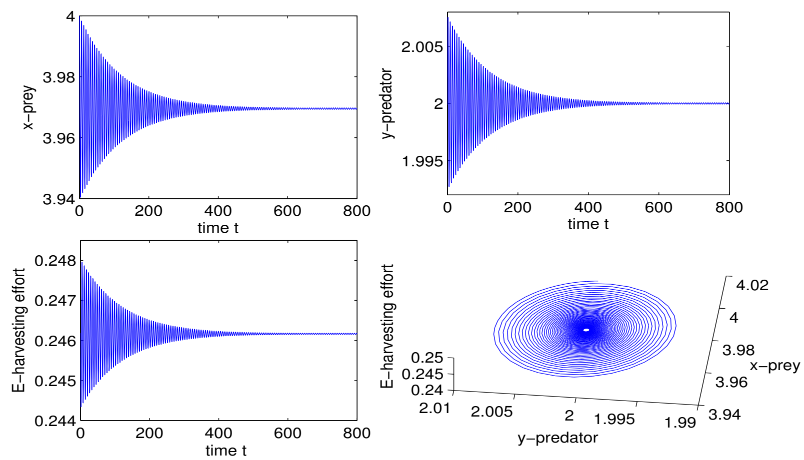

Figure 1: For the parameters of model (1.3) with the values $r_1 = 2$, $a = 1$, $r_2 = \frac{3}{4}$, $b = 1$, $p = 1$, $l = 1$, $c = \frac{4}{9}$, $x(0) = 3.9999$, $y(0) = 1.9999$, $E(0) = 0.2499$, numerical simulations show that the equilibrium point $X_0 = (4, 2, 0.25)$ of model (1.3) is locally asymptotically stable when $v = 0.2205 < v_0 = 2/9$.

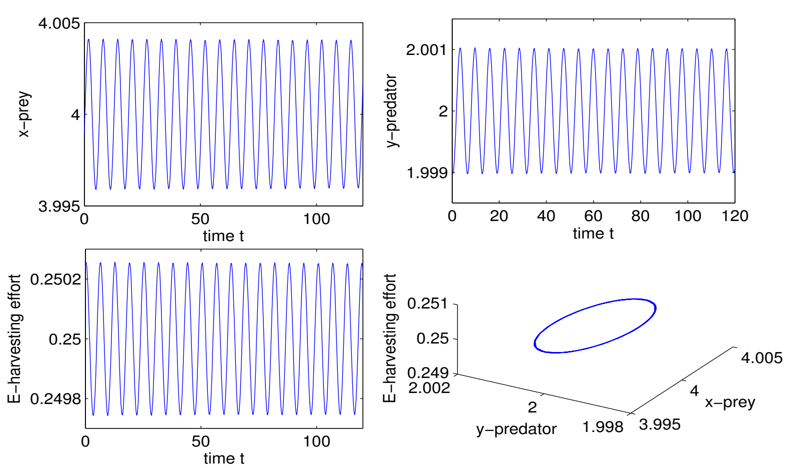

Figure 2: For the parameters of model (1.3) with the values $r_1 = 2$, $a = 1$, $r_2 = \frac{3}{4}$, $b = 1$, $p = 1$, $l = 1$, $c = \frac{4}{9}$, $x(0) = 3.999$, $y(0) = 1.999$, $E(0) = 0.249$, numerical simulations show that a periodic orbit bifurcates from the equilibrium point $X_0 = (4, 2, 0.25)$ of model (1.3) when $v = 0.222222 < v_0 = 2/9$.

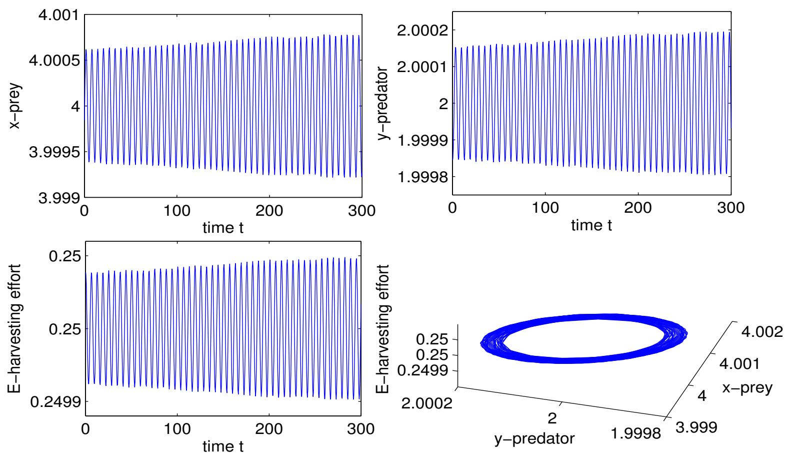

Figure 3: For the parameters of model (1.3) with the values $r_1 = 2$, $a = 1$, $r_2 = \frac{3}{4}$, $b = 1$, $p = 1$, $l = 1$, $c = \frac{4}{9}$, $x(0) = 3.99984$, $y(0) = 1.99985$, $E(0) = 0.24986$, numerical simulations show that the equilibrium point $X_0 = (4, 2, 0.25)$ of model (1.3) is an unstable centre when v equals to the bifurcation value $v_0 = 2/9$.

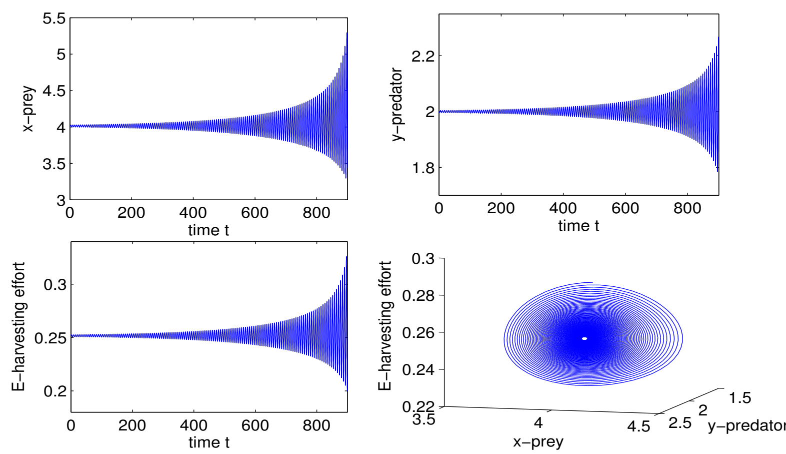

Figure 4: For the parameters of model (1.3) with the values $r_1 = 2$, $a = 1$, $r_2 = \frac{3}{4}$, $b = 1$, $p = 1$, $l = 1$, $c = \frac{4}{9}$, $x(0) = 3.9999$, $y(0) = 1.9999$, $E(0) = 0.2499$, numerical simulations show that the equilibrium point $X_0 = (4, 2, 0.25)$ of model (1.3) is unstable when $v = 0.223 > v_0 = 2/9$.

6. Concluding remarks

The present paper has studied the dynamics of a predator-prey model with external harvesting for predators. The original predator-prey model (1.1) proposed by Leslie is described by two differential equations, which has been reasonably modified as the differential-algebra predator-prey system (1.3) on the basis of the consideration of expressing the harvesting profit. The asymptotic stability of the modified predator-prey model (1.3) is investigated here, which reveals that the population model can be asymptotically stable under certain condition. In such a circumstance, the prey population, predator population and human harvesting are able to coexist in harmony. For the benefit of maintaining the ecological balance, the rational range of the harvesting profit v of human beings should be the interval $(0, v_0)$. It means that people can't exploit the biological resource too heavy. Otherwise, the ecological balance would be in danger of being damaged, and then people will completely loss their productivity eventually.

Besides, it is interesting to note that the parameterisation used in section 2 can reduce our model (1.3) described by differential-algebra equations to the system (3.14) of differential equations, which has a significant effect in this study. Refs. [34-37] suggest that Differential-Algebraic Equations have widespread applications in constrained dynamical systems, so we expect that the parameterisation can be employed to analyze the dynamics of more complex constrained systems in biology and engineering.

Finally, Refs. [43, 44] show that the impact of delays on the dynamics of a system is an interesting problem. Thus, further studies on the stability and bifurcations of differential-algebra population model (1.3) with delays can be considered.

Acknowledgements

I would like to thank the two anonymous expert referees and the editor for their careful reading and valuable comments, which greatly improve the quality of the original manuscript. Besides, I would also like to thank the data modeling and intelligent optimization team of Jiangxi University of Finance and Economics for its support and assistance.

This work is supported by the Science and Technology Project founded by the Education Department of Jiangxi Province (Grant No. GJJ210512), and the National Natural Science Foundation of China (Grant No. 72161017).

Appendix

Here we deduce the formula (2.7). Substituting $X = \psi(Y)$ into system (2.4), we have

$$D_Y\psi(Y)\dot{Y} = f(\psi(Y)), \tag{A.1}$$

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

$$U_0^T D_Y \psi(Y) = I_2. \tag{A.2}$$

Differentiating Eq. (2.6) regarding Y, which yields

$$D_X g(X) D_Y \psi(Y) = 0. \tag{A.3}$$

By Eqs. (A.1)-(A.3), we get

$$\begin{pmatrix} D_X g(X) \\ U_0^T \end{pmatrix}^{-1} \begin{pmatrix} 0 \\ I_2 \end{pmatrix} \dot{Y}(t) = f(\psi(Y)). \tag{A.4}$$

Further, Eqs. (A.1), (A.3) and (A.4) suggest that system (2.4) can be locally equivalent to

$$\dot{Y} = U_0^T f(\psi(Y)), \tag{A.5}$$

which shows that X_0 corresponds to $Y = 0$ of system (A.5).

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Accepted: August 23, 2023