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Nonlinear Dynamical Behaviour in a Predator-Prey Model with Harvesting

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Abstract. We investigate the stability and periodic orbits of a predator-prey model with harvesting. The model has a biologically-meaningful interior, an attractor undergoing damped oscillations, and can become destabilised to produce periodic orbits via a Hopf bifurcation. Some sufficient conditions for the existence of the Hopf bifurcation are established, and a stability analysis for the periodic solutions using a Lyapunov function is presented. Finally, some computer simulations illustrate our theoretical results.

AMS subject classifications: 92D25

Key words: Predator-prey system, Holling type IV functional response, periodic solution, bifurcation, Lyapunov function.

1. Introduction

The governing equations in the Kolmogorov predator-prey model are

$$\begin{cases} \dot{x} = xF(x,y)\,, \\ \dot{y} = yG(x,y)\,, \end{cases} \tag{1.1}$$

where $x(t)$ and $y(t)$ respectively denote the prey and predator populations at time t [1]. The functions $F(x,y)$ and $G(x,y)$ denote the respective per capita growth rates of the two species, and it is assumed that $\mathrm{d}F(x,y)/\mathrm{d}y < 0$ and $\mathrm{d}G(x,y)/\mathrm{d}x > 0$.

On the basis of model (1.1), Yodzis [2] proposed the corresponding generalised predator-prey model

$$\begin{cases} \dot{x} = xf(x) - yH(x,y)\,, \\ \dot{y} = yG(x,y)\,, \end{cases} \tag{1.2}$$

where $f(x)$ is the intrinsic growth rate of the prey and $H(x,y)$ is the predator response function. In this article, we assume $f(x) = r(1-x/K)$ such that the prey population grows

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logistically in the absence of predators, with the positive constants r and K denoting the maximal prey growth rate and carrying capacity, respectively. We also adopt the generalised Holling type IV response function $H(x,y) = my/(ax^2 + b_1x + 1)$ in Refs. [3,4] to describe "inhibition" in microbial dynamics and "group defence" in population dynamics, where the positive constants m and a respectively denote the capture rate and half-saturation constant, and the positive constant b_1 is such that the denominator of predator-prey model (1.2) does not vanish for nonnegative x. Finally, we choose the Lotka-Volterra type growth rate $G(x,y) = -k_1 + d_1x$, with the positive constants k_1 and d_1 respectively representing the predator mortality rate and maximal predator growth rate [4]. Consequently, the specific predator-prey model we consider is

$$\begin{cases} \dot{x} = x\left(r - \dfrac{r}{K}x - \dfrac{my}{ax^2 + b_1x + 1}\right), \\ \dot{y} = y\left(-k_1 + d_1x\right). \end{cases} \tag{1.3}$$

On scaling the variables x, y, t and the parameters such that

$$\bar{t} = rt\,, \quad \bar{x} = \frac{x}{K}\,, \quad \bar{y} = \frac{my}{rK^2}\,, \quad b = \frac{b_1}{K}\,, \quad c = \frac{1}{K^2}\,, \quad k = \frac{k_1}{r}, \quad d = \frac{d_1K}{r}\,,$$

and then omitting the bars, our model (1.3) becomes

$$\begin{cases} \dot{x} = x\left(1 - x - \dfrac{y}{ax^2 + bx + c}\right), \\ \dot{y} = y\left(-k + dx\right). \end{cases} \tag{1.4}$$

According to the economic principle of Gordon [5], we have the algebraic equation [6-9]

$$E(t)\big(px(t) - n\big) = v, \tag{1.5}$$

where $E(t)$ is the harvesting effort for the prey, v represents the economic profit, and the positive constants p and n respectively denote the harvesting reward and harvesting cost. Combining Eqs. (1.4) and (1.5), we obtain the following modified predator-prey model with the generalised Holling type IV response function:

$$\begin{cases} \dot{x} = x\left(1 - x - \dfrac{y}{ax^2 + bx + c} - E\right), \\ \dot{y} = y\left(-k + dx\right), \\ 0 = E\left(px - n\right) - v\,, \end{cases} \tag{1.6}$$

where the harvesting E is considered as a variable in this article.

We proceed to investigate the dependence of the dynamics of the model (1.6) on the economic profit, by treating v as the variable bifurcation parameter. Our work therefore complements the research undertaken in Refs. [6-9]., where related models are formulated and various issues including singularity induced bifurcation, flip bifurcation, saddle-node

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bifurcation, Neimark-Sacker bifurcation, chaotic behaviour and state feedback control have been discussed. In Refs. [10-15] there are predator-prey models represented by systems of differential equations, whereas the governing equations (1.6) we consider constitute a differential-algebraic system. In Section 2, the local parameterisation method [16] and the normal form method [17] are used to investigate the Hopf bifurcation phenomenon. In particular, we find that periodic orbits arise from the equilibrium point when the parameter v attains the bifurcation value, and in Section 3 we use the formal series method [18] to study the stability of the periodic solutions, Relevant numerical simulations are then presented in Section 4, and our concluding remarks are made in Section 5.

2. Stability of Equilibrium Point and Existence of Hopf Bifurcation

We characterise the solution to the differential-algebraic system (1.6) by the vector $X=(x,y,E)^T$, and conveniently write

$$f(X)=\begin{pmatrix} f_1(X) \\ f_2(X) \end{pmatrix}=\begin{pmatrix} x\left(1-x-\dfrac{y}{ax^2+bx+c}-E\right) \\ y\,(-k+dx) \end{pmatrix},$$
$$g(X)=E(px-n)-v\,.$$

The equilibrium point for Eqs. (1.6) is

$$X_0=(x_0,y_0,E_0)^T=(x_0,(ax_0^2+bx_0+c)(1-x_0-E_0),E_0)^T,$$

where $x_0=k/d$ and $E_0=v/(px_0-n)$; and to ensure that all entries in X_0 are positive (for the biological model to be realistic) we require

$$v>0\,,\qquad px_0-n>0\,,\qquad x_0+E_0<1\,. \tag{2.1}$$

Under the linear transformation $X=Q\overline{X}$ where $\overline{X}=(x,y,\overline{E})^T$ and

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

we can first rewrite Eqs. (1.6) as

$$\begin{cases} \dot{x}=x\left(1-x-\dfrac{y}{ax^2+bx+c}+\dfrac{pE_0}{px_0-n}x-\overline{E}\right), \\ \dot{y}=y\,(-k+dx)\,, \\ 0=\left(-\dfrac{pE_0}{px_0-n}x+\overline{E}\right)(px-n)-v\,, \end{cases} \tag{2.2}$$

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and in accord with the above denote

$$f(\overline{X}) = \begin{pmatrix} f_1(\overline{X}) \\ f_2(\overline{X}) \end{pmatrix} = \begin{pmatrix} x\left(1 - x - \dfrac{y}{ax^2+bx+c} + \dfrac{pE_0}{px_0 - n}x - \overline{E}\right) \\ y(-k + dx) \end{pmatrix},$$
$$g(\overline{X}) = \left(-\frac{pE_0}{px_0 - n}x + \overline{E}\right)(px - n) - v\,. \tag{2.3}$$

The equilibrium point from Eqs. (2.2) is

$$\overline{X}_0 = (x_0, y_0, \overline{E}_0)^T = \left(x_0, y_0, E_0\big(1 + px_0/(px_0 - n)\big)\right)^T.$$

Furthermore, we can calculate that

$$D_{\overline{X}} g(\overline{X}_0) = (0, 0, px_0 - n)\,,$$

where D denotes the differential operator, and $D_{\overline{X}} g$ denotes the matrix of partial derivatives of the components of g with respect to $\overline{X}$ that has rank 1. It is readily verified that the transformed system (2.2) satisfies the conditions for local parameterisation in Ref. [16] briefly introduced in Appendix A, with $n = 3$ and $m = 1$ here. However, it is notable that the original system (1.6) does not meet these conditions, since $D_X g(X_0) = (pE_0, 0, px_0 - n)$ such that rank $D_X g(X_0) = 2$ under assumption (2.1). For Eqs. (2.2) we introduce the local parameterisation

$$\overline{X} = \psi(Y) = \overline{X}_0 + U_0 Y + V_0 h(Y), \qquad g\big(\psi(Y)\big) = 0\,,$$

where $U_0 = \begin{pmatrix} 1 & 0 \\ 0 & 1 \\ 0 & 0 \end{pmatrix}$, $V_0 = \begin{pmatrix} 0 \\ 0 \\ 1 \end{pmatrix}$, $Y = (y_1, y_2)^T \in R^2$ and $h : R^2 \to R$ is a smooth mapping.

Then the parameterised system corresponding to Eqs. (2.2) can be expressed as

$$\begin{cases} \dot{y}_1 = f_1\big(\psi(Y)\big), \\ \dot{y}_2 = f_2\big(\psi(Y)\big), \end{cases} \tag{2.4}$$

with the Jacobian matrix at $\overline{X}_0$:

$$\begin{pmatrix} D_{\overline{X}} f_1(\overline{X}_0) \\ D_{\overline{X}} f_2(\overline{X}_0) \end{pmatrix} \begin{pmatrix} D_{\overline{X}} g(\overline{X}_0) \\ U_0^T \end{pmatrix}^{-1} \begin{pmatrix} 0 \\ I_2 \end{pmatrix}$$
$$= \begin{pmatrix} -x_0 + \dfrac{x_0 y_0 (2ax_0 + b)}{(ax_0^2 + bx_0 + c)^2} + \dfrac{px_0 E_0}{px_0 - n} & -\dfrac{x_0}{ax_0^2 + bx_0 + c} \\ dy_0 & 0 \end{pmatrix}.$$

Given this Jacobian matrix, it is readily shown that the characteristic equation of the linearised system obtained from (2.4) has the form

$$\lambda^2 + a_1(v)\lambda + a_2(v) = 0\,, \tag{2.5}$$

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where

$$a_1(\nu)=x_0-\frac{x_0y_0(2ax_0+b)}{(ax_0^2+bx_0+c)^2}-\frac{px_0E_0}{px_0-n},\qquad a_2(\nu)=\frac{dx_0y_0}{ax_0^2+bx_0+c}.$$

In Eq. (2.5), by letting $a_1(\nu)=0$ we obtain the bifurcation value

$$\nu_0=\frac{(px_0-n)^2\left[(2ax_0+b)(1-x_0)-(ax_0^2+bx_0+c)\right]}{(2ax_0+b)(px_0-n)-p(ax_0^2+bx_0+c)}.$$

Indeed, when $\Delta=a_1^2(\nu)-4a_2(\nu)<0$ the characteristic equation (2.5) has a pair of conjugate complex roots — viz.

$$\lambda_{1,2}=-\frac{1}{2}a_1(\nu)\pm i\sqrt{a_2(\nu)-\frac{a_1^2(\nu)}{4}}:=\alpha(\nu)\pm i\omega(\nu),$$

where

$$\begin{aligned}\alpha(\nu)=&-\frac{1}{2}\Bigg\{x_0-\frac{x_0(2ax_0+b)(1-x_0)}{ax_0^2+bx_0+c}\\&+\frac{\left[x_0(2ax_0+b)(px_0-n)-px_0(ax_0^2+bx_0+c)\right]\nu}{(ax_0^2+bx_0+c)(px_0-n)^2}\Bigg\},\\ \omega(\nu)=&\sqrt{\frac{dx_0y_0}{ax_0^2+bx_0+c}-\left(\frac{x_0}{2}-\frac{x_0y_0(2ax_0+b)}{2(ax_0^2+bx_0+c)^2}-\frac{px_0\nu}{2(px_0-n)^2}\right)^2}.\end{aligned}$$

If we assume that

$$x_0(2ax_0+b)(px_0-n)\neq px_0(ax_0^2+bx_0+c),\tag{2.6}$$

then

$$\begin{aligned}&\alpha(\nu_0)=0,\qquad \alpha'(\nu_0)=\frac{px_0(ax_0^2+bx_0+c)-x_0(2ax_0+b)(px_0-n)}{2(ax_0^2+bx_0+c)(px_0-n)^2}\neq 0,\\ &\omega(\nu_0)=\sqrt{\frac{dx_0y_0}{ax_0^2+bx_0+c}}\neq 0,\end{aligned}$$

which implies that a Hopf bifurcation occurs at the bifurcation value $\nu=\nu_0$.

In order to investigate the Hopf bifurcation according to Ref. [17], when $\nu=\nu_0$ and $\overline{X}=\overline{X}_0$ we should render the normal form of system (2.2) as follows:

$$\begin{cases}\dot{y}_1=-\omega(\nu_0)y_2+\frac{1}{2}a_{11}^1y_1^2+a_{12}^1y_1y_2+\frac{1}{2}a_{22}^1y_2^2+\frac{1}{6}a_{111}^1y_1^3+\frac{1}{2}a_{112}^1y_1^2y_2\\ \qquad+\frac{1}{2}a_{122}^1y_1y_2^2+\frac{1}{6}a_{222}^1y_2^3+o(|Y|^4),\\ \dot{y}_2=\omega(\nu_0)y_1+\frac{1}{2}a_{11}^2y_1^2+a_{12}^2y_1y_2+\frac{1}{2}a_{22}^2y_2^2+\frac{1}{6}a_{111}^2y_1^3+\frac{1}{2}a_{112}^2y_1^2y_2\\ \qquad+\frac{1}{2}a_{122}^2y_1y_2^2+\frac{1}{6}a_{222}^2y_2^3+o(|Y|^4).\end{cases}\tag{2.7}$$

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On the other hand, the Taylor series developments of the parameterised system (2.4) with $\overline{X} = \overline{X}_0$ takes the form

$$\begin{cases} \dot{y}_1 = f_{1y_1}(\overline{X}_0)y_1 + f_{1y_2}(\overline{X}_0)y_2 + \frac{1}{2}f_{1y_1y_1}(\overline{X}_0)y_1^2 + f_{1y_1y_2}(\overline{X}_0)y_1y_2 \\ \qquad + \frac{1}{2}f_{1y_2y_2}(\overline{X}_0)y_2^2 + \frac{1}{6}f_{1y_1y_1y_1}(\overline{X}_0)y_1^3 + \frac{1}{2}f_{1y_1y_1y_2}(\overline{X}_0)y_1^2y_2 \\ \qquad + \frac{1}{2}f_{1y_1y_2y_2}(\overline{X}_0)y_1y_2^2 + \frac{1}{6}f_{1y_2y_2y_2}(\overline{X}_0)y_2^3 + o(|Y|^4)\,, \\ \dot{y}_2 = f_{2y_1}(\overline{X}_0)y_1 + f_{2y_2}(\overline{X}_0)y_2 + \frac{1}{2}f_{2y_1y_1}(\overline{X}_0)y_1^2 + f_{2y_1y_2}(\overline{X}_0)y_1y_2 \\ \qquad + \frac{1}{2}f_{2y_2y_2}(\overline{X}_0)y_2^2 + \frac{1}{6}f_{2y_1y_1y_1}(\overline{X}_0)y_1^3 + \frac{1}{2}f_{2y_1y_1y_2}(\overline{X}_0)y_1^2y_2 \\ \qquad + \frac{1}{2}f_{2y_1y_2y_2}(\overline{X}_0)y_1y_2^2 + \frac{1}{6}f_{2y_2y_2y_2}(\overline{X}_0)y_2^3 + o(|Y|^4)\,. \end{cases} \tag{2.8}$$

On calculating the coefficients in the system (2.8), we obtain the following parameterised system corresponding to Eqs. (2.2) with $\overline{X} = \overline{X}_0$ (cf. Appendix B):

$$\begin{cases} \dot{y}_1 = -\dfrac{x_0}{ax_0^2+bx_0+c}y_2 + \Big(\dfrac{ax_0y_0}{(ax_0^2+bx_0+c)^2} - \dfrac{x_0y_0(2ax_0+b)^2}{(ax_0^2+bx_0+c)^3} \\ \qquad - \dfrac{p^2x_0E_0}{(px_0-n)^2}\Big)y_1^2 + \dfrac{ax_0^2-c}{(ax_0^2+bx_0+c)^2}y_1y_2 + \Big(\dfrac{ay_0}{(ax_0^2+bx_0+c)^2} \\ \qquad - \dfrac{y_0(2ax_0+b)(4ax_0+b)}{(ax_0^2+bx_0+c)^3} + \dfrac{x_0y_0(2ax_0+b)^3}{(ax_0^2+bx_0+c)^4} + \dfrac{p^2nE_0}{(px_0-n)^3}\Big)y_1^3 \\ \qquad + \Big(\dfrac{3ax_0+b}{(ax_0^2+bx_0+c)^2} - \dfrac{x_0(2ax_0+b)^2}{(ax_0^2+bx_0+c)^3}\Big)y_1^2y_2 + o(|Y|^4)\,, \\ \dot{y}_2 = dy_0y_1 + dy_1y_2\,. \end{cases} \tag{2.9}$$

For comparison with the normal form (2.7), we now normalise system (2.9) with a non-singular matrix transformation $Y = PU$, where $P = \begin{pmatrix} \sqrt{x_0} & 0 \\ 0 & \sqrt{dy_0(ax_0^2+bx_0+c)} \end{pmatrix}$ and $U = (u_1, u_2)^T$. For convenience, we still use Y to express U to derive the normal form

$$\begin{cases} \dot{y}_1 = -\omega(\nu_0)y_2 + \Big(\dfrac{a\sqrt{x_0}y_0}{(ax_0^2+bx_0+c)^2} - \dfrac{\sqrt{x_0}y_0(2ax_0+b)^2}{(ax_0^2+bx_0+c)^3} - \dfrac{p^2\sqrt{x_0}E_0}{(px_0-n)^2}\Big)y_1^2 \\ \qquad + \dfrac{(ax_0^2-c)\sqrt{dy_0}}{(ax_0^2+bx_0+c)^{\frac{3}{2}}}y_1y_2 + \Big(\dfrac{ax_0y_0}{(ax_0^2+bx_0+c)^2} - \dfrac{x_0y_0(2ax_0+b)(4ax_0+b)}{(ax_0^2+bx_0+c)^3} \\ \qquad + \dfrac{x_0^2y_0(2ax_0+b)^3}{(ax_0^2+bx_0+c)^4} + \dfrac{p^2nx_0E_0}{(px_0-n)^3}\Big)y_1^3 \\ \qquad + \Big(\dfrac{(3ax_0+b)\sqrt{dx_0y_0}}{(ax_0^2+bx_0+c)^{\frac{3}{2}}} - \dfrac{x_0^{\frac{3}{2}}(2ax_0+b)^2\sqrt{dy_0}}{(ax_0^2+bx_0+c)^{\frac{5}{2}}}\Big)y_1^2y_2 + o(|Y|^4)\,, \\ \dot{y}_2 = \omega(\nu_0)y_1 + d\sqrt{x_0}y_1y_2\,. \end{cases} \tag{2.10}$$

Summarizing the previous theoretical analysis, we arrive at the following theorem.

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Theorem 2.1. *For the predator-prey model* (1.6)*, there exist two sufficiently small neighbourhoods O and P of X_0, and a constant ε where $0 < \varepsilon \ll 1$ and $O \subset P$ are such that:*
(I) if

$$\frac{ay_0(ax_0^2-c)}{(ax_0^2+bx_0+c)^3}+\frac{3ax_0y_0}{(ax_0^2+bx_0+c)^2}+\frac{3x_0^2y_0(2ax_0+b)^3}{(ax_0^2+bx_0+c)^4}+\frac{3p^2nx_0E_0}{(px_0-n)^3}$$
$$>\frac{3x_0y_0(2ax_0+b)(4ax_0+b)}{(ax_0^2+bx_0+c)^3}+\frac{y_0(2ax_0+b)^2(ax_0^2-c)}{(ax_0^2+bx_0+c)^4}+\frac{p^2E_0(ax_0^2-c)}{(ax_0^2+bx_0+c)(px_0-n)^2},$$

then
(1) when $v_0 < v < v_0+\varepsilon$, the equilibrium point X_0 is unstable;
(2) when $v_0-\varepsilon < v < v_0$, the equilibrium point X_0 is locally asymptotically stable, and there exists at least one periodic solution in $\overline{O}$ that repels all the points in $\overline{O}\setminus\{X_0\}$, then there also exists one periodic solution that repels all the points in $P\setminus\overline{O}$; and
(II) if

$$\frac{ay_0(ax_0^2-c)}{(ax_0^2+bx_0+c)^3}+\frac{3ax_0y_0}{(ax_0^2+bx_0+c)^2}+\frac{3x_0^2y_0(2ax_0+b)^3}{(ax_0^2+bx_0+c)^4}+\frac{3p^2nx_0E_0}{(px_0-n)^3}$$
$$<\frac{3x_0y_0(2ax_0+b)(4ax_0+b)}{(ax_0^2+bx_0+c)^3}+\frac{y_0(2ax_0+b)^2(ax_0^2-c)}{(ax_0^2+bx_0+c)^4}+\frac{p^2E_0(ax_0^2-c)}{(ax_0^2+bx_0+c)(px_0-n)^2},$$

then
(1) when $v_0-\varepsilon < v < v_0$, the equilibrium point X_0 is locally asymptotically stable;
(2) when $v_0 < v < v_0+\varepsilon$, the equilibrium point X_0 is unstable, and there exists at least one periodic solution in $\overline{O}$ that absorbs all the points in $\overline{O}\setminus\{X_0\}$, then there also exists one periodic solution that absorbs all the points in $P\setminus\overline{O}$.

Proof. By comparing the coefficients of Eqs. (2.7) and (2.10), we calculate the value $16\boldsymbol{a}$ defined in Ref. [17] as follows:

$$\begin{aligned}16\boldsymbol{a} &:= \{a_{11}^1(a_{12}^1-a_{11}^2)+a_{22}^2(a_{22}^1-a_{12}^2)+(a_{12}^1a_{22}^1-a_{11}^2a_{12}^2)\}/\omega(v_0)\\ &\quad+(a_{111}^1+a_{122}^1+a_{112}^2+a_{222}^2)\\ &=\frac{2(ax_0^2-c)\sqrt{dy_0}}{\omega(v_0)(ax_0^2+bx_0+c)^{\frac{3}{2}}}\left(\frac{a\sqrt{x_0}y_0}{(ax_0^2+bx_0+c)^2}-\frac{\sqrt{x_0}y_0(2ax_0+b)^2}{(ax_0^2+bx_0+c)^3}-\frac{p^2\sqrt{x_0}E_0}{(px_0-n)^2}\right)\\ &\quad+\frac{6ax_0y_0}{(ax_0^2+bx_0+c)^2}-\frac{6x_0y_0(2ax_0+b)(4ax_0+b)}{(ax_0^2+bx_0+c)^3}+\frac{6x_0^2y_0(2ax_0+b)^3}{(ax_0^2+bx_0+c)^4}+\frac{6p^2nx_0E_0}{(px_0-n)^3},\end{aligned}$$

with two cases $\boldsymbol{a} > 0$ and $\boldsymbol{a} < 0$ to consider according to the Hopf bifurcation theorem in Ref. [17]. The procedure is quite similar to the proof of the Hopf bifurcation theorem [17], so omitted here. □

Remark 2.1. When $\mathbf{a} = 0$, a degenerate Hopf bifurcation occurs in our modified predator-prey model (1.6).

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3. Stability of Bifurcating Periodic Solutions

From the above analysis, we know that there are periodic solutions bifurcating from the equilibrium point X_0 when the bifurcation parameter $v = v_0$. In this section, the stability of the bifurcating periodic solutions is investigated using the formal series method discussed in Ref. [18].

Theorem 3.1. *For the predator-prey model* (1.6) *with* $v = v_0$*:*
(I) if

$$\frac{ay_0(ax_0^2-c)}{(ax_0^2+bx_0+c)^3}+\frac{3ax_0y_0}{(ax_0^2+bx_0+c)^2}+\frac{3x_0^2y_0(2ax_0+b)^3}{(ax_0^2+bx_0+c)^4}+\frac{3p^2nx_0E_0}{(px_0-n)^3}$$
$$>\frac{3x_0y_0(2ax_0+b)(4ax_0+b)}{(ax_0^2+bx_0+c)^3}+\frac{y_0(2ax_0+b)^2(ax_0^2-c)}{(ax_0^2+bx_0+c)^4}+\frac{p^2E_0(ax_0^2-c)}{(ax_0^2+bx_0+c)(px_0-n)^2},$$

then the bifurcating periodic solutions are unstable;
(II) if

$$\frac{ay_0(ax_0^2-c)}{(ax_0^2+bx_0+c)^3}+\frac{3ax_0y_0}{(ax_0^2+bx_0+c)^2}+\frac{3x_0^2y_0(2ax_0+b)^3}{(ax_0^2+bx_0+c)^4}+\frac{3p^2nx_0E_0}{(px_0-n)^3}$$
$$<\frac{3x_0y_0(2ax_0+b)(4ax_0+b)}{(ax_0^2+bx_0+c)^3}+\frac{y_0(2ax_0+b)^2(ax_0^2-c)}{(ax_0^2+bx_0+c)^4}+\frac{p^2E_0(ax_0^2-c)}{(ax_0^2+bx_0+c)(px_0-n)^2},$$

then the bifurcating periodic solutions are stable.

Proof. For simplicity, we let $\tau = \omega(v_0)t$ and use $\dot{y}$ to denote the derivative of y at τ. Then the normal form (2.10) can be rewritten as

$$\begin{cases}\dot{y}_1 = -y_2+\left(\dfrac{a\sqrt{x_0}y_0}{\omega(v_0)(ax_0^2+bx_0+c)^2}-\dfrac{\sqrt{x_0}y_0(2ax_0+b)^2}{\omega(v_0)(ax_0^2+bx_0+c)^3}\right.\\ \qquad\left.-\dfrac{p^2\sqrt{x_0}E_0}{\omega(v_0)(px_0-n)^2}\right)y_1^2+\dfrac{(ax_0^2-c)\sqrt{dy_0}}{\omega(v_0)(ax_0^2+bx_0+c)^{\frac{3}{2}}}y_1y_2\\ \qquad+\left(\dfrac{ax_0y_0}{\omega(v_0)(ax_0^2+bx_0+c)^2}-\dfrac{x_0y_0(2ax_0+b)(4ax_0+b)}{\omega(v_0)(ax_0^2+bx_0+c)^3}\right.\\ \qquad\left.+\dfrac{x_0^2y_0(2ax_0+b)^3}{\omega(v_0)(ax_0^2+bx_0+c)^4}+\dfrac{p^2nx_0E_0}{\omega(v_0)(px_0-n)^3}\right)y_1^3\\ \qquad+\left(\dfrac{(3ax_0+b)\sqrt{dx_0y_0}}{\omega(v_0)(ax_0^2+bx_0+c)^{\frac{3}{2}}}-\dfrac{x_0^{\frac{3}{2}}(2ax_0+b)^2\sqrt{dy_0}}{\omega(v_0)(ax_0^2+bx_0+c)^{\frac{5}{2}}}\right)y_1^2y_2+o(|Y|^4),\\ \dot{y}_2 = y_1+\dfrac{d\sqrt{x_0}}{\omega(v_0)}y_1y_2.\end{cases}\tag{3.1}$$

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For the system (3.1), we construct the Lyapunov function

$$V(y_1, y_2) = y_1^2 + y_2^2 + V_3(y_1, y_2) + V_4(y_1, y_2)\,,$$

where $V_3(y_1, y_2)$ and $V_4(y_1, y_2)$ represent the three degree homogeneous polynomial and the four degree homogeneous polynomial in y_1 and y_2, so

$$\begin{aligned}\left.\frac{\mathrm{d}V(y_1, y_2)}{\mathrm{d}\tau}\right|_{(3.1)} &= (2y_1 + D_{y_1}V_3(y_1, y_2) + D_{y_1}V_4(y_1, y_2)) \cdot \dot{y}_1 \\ &\quad + (2y_2 + D_{y_2}V_3(y_1, y_2) + D_{y_2}V_4(y_1, y_2)) \cdot \dot{y}_2\,. \end{aligned} \tag{3.2}$$

Setting the third degree homogeneous polynomial in Eq. (3.2) to 0, we have

$$\begin{aligned} &y_1 D_{y_2}V_3(y_1, y_2) - y_2 D_{y_1}V_3(y_1, y_2) \\ &= \left(\frac{2\sqrt{x_0}y_0(2ax_0 + b)^2}{\omega(v_0)(ax_0^2 + bx_0 + c)^3} + \frac{2p^2\sqrt{x_0}E_0}{\omega(v_0)(px_0 - n)^2} - \frac{2a\sqrt{x_0}y_0}{\omega(v_0)(ax_0^2 + bx_0 + c)^2}\right) y_1^3 \\ &\quad - \frac{2(ax_0^2 - c)\sqrt{dy_0}}{\omega(v_0)(ax_0^2 + bx_0 + c)^{\frac{3}{2}}} y_1^2 y_2 - \frac{2d\sqrt{x_0}}{\omega(v_0)} y_1 y_2^2\,. \end{aligned} \tag{3.3}$$

Furthermore, on writing $y_1 = r\cos\theta$, $y_2 = r\sin\theta$ we obtain

$$\begin{aligned} &\frac{\mathrm{d}V_3(\cos\theta, \sin\theta)}{\mathrm{d}\theta} \\ &= \left(\frac{2\sqrt{x_0}y_0(2ax_0 + b)^2}{\omega(v_0)(ax_0^2 + bx_0 + c)^3} + \frac{2p^2\sqrt{x_0}E_0}{\omega(v_0)(px_0 - n)^2} - \frac{2a\sqrt{x_0}y_0}{\omega(v_0)(ax_0^2 + bx_0 + c)^2}\right)\cos^3\theta \\ &\quad - \frac{2(ax_0^2 - c)\sqrt{dy_0}}{\omega(v_0)(ax_0^2 + bx_0 + c)^{\frac{3}{2}}}\sin\theta\cos^2\theta - \frac{2d\sqrt{x_0}}{\omega(v_0)}\sin^2\theta\cos\theta \\ &:= -H_3(\cos\theta, \sin\theta) = \frac{a_0}{2} + \sum_{i=1}^{\infty}(a_i\cos i\theta + b_i\sin i\theta)\,, \end{aligned}$$

where $a_0/2 + \sum_{i=1}^{\infty}(a_i\cos i\theta + b_i\sin i\theta)$ is the Fourier series of $H_3(\cos\theta, \sin\theta)$, and such a $V_3(\cos\theta, \sin\theta)$ exists if and only if $a_0 = 0$ — i.e. $\int_0^{2\pi} H_3(\cos\theta, \sin\theta)\mathrm{d}\theta = 0$. Indeed, since

$$\begin{aligned} \int_0^{2\pi} \Bigg\{ &\left(\frac{2\sqrt{x_0}y_0(2ax_0 + b)^2}{\omega(v_0)(ax_0^2 + bx_0 + c)^3} + \frac{2p^2\sqrt{x_0}E_0}{\omega(v_0)(px_0 - n)^2} - \frac{2a\sqrt{x_0}y_0}{\omega(v_0)(ax_0^2 + bx_0 + c)^2}\right)\cos^3\theta \\ &- \frac{2(ax_0^2 - c)\sqrt{dy_0}}{\omega(v_0)(ax_0^2 + bx_0 + c)^{\frac{3}{2}}}\sin\theta\cos^2\theta - \frac{2d\sqrt{x_0}}{\omega(v_0)}\sin^2\theta\cos\theta\Bigg\}\mathrm{d}\theta = 0\,, \end{aligned}$$

we obtain

$$V_3(y_1, y_2) = \left(\frac{2(ax_0^2 - c)\sqrt{dy_0}}{3\omega(v_0)(ax_0^2 + bx_0 + c)^{\frac{3}{2}}}\right) y_1^3 + \left(\frac{2\sqrt{x_0}y_0(2ax_0 + b)^2}{\omega(v_0)(ax_0^2 + bx_0 + c)^3}\right.$$

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$$+\frac{2p^2\sqrt{x_0}E_0}{\omega(v_0)(px_0-n)^2}-\frac{2a\sqrt{x_0}y_0}{\omega(v_0)(ax_0^2+bx_0+c)^2}\Bigg)y_1^2y_2$$
$$-\Bigg(\frac{4a\sqrt{x_0}y_0}{3\omega(v_0)(ax_0^2+bx_0+c)^2}-\frac{4\sqrt{x_0}y_0(2ax_0+b)^2}{3\omega(v_0)(ax_0^2+bx_0+c)^3}$$
$$-\frac{4p^2\sqrt{x_0}E_0}{3\omega(v_0)(px_0-n)^2}+\frac{2d\sqrt{x_0}}{3\omega(v_0)}\Bigg)y_2^3. \tag{3.4}$$

Again, setting the fourth degree homogeneous polynomial y_1 and y_2 in Eq. (3.2) to 0 gives

$$y_1D_{y_2}V_4(y_1,y_2)-y_2D_{y_1}V_4(y_1,y_2)$$
$$=\Bigg(\frac{\sqrt{x_0}y_0(2ax_0+b)^2}{\omega(v_0)(ax_0^2+bx_0+c)^3}+\frac{p^2\sqrt{x_0}E_0}{\omega(v_0)(px_0-n)^2}-\frac{a\sqrt{x_0}y_0}{\omega(v_0)(ax_0^2+bx_0+c)^2}\Bigg)y_1^2$$
$$\times D_{y_1}V_3(y_1,y_2)-\frac{(ax_0^2-c)\sqrt{dy_0}}{\omega(v_0)(ax_0^2+bx_0+c)^{\frac{3}{2}}}y_1y_2\times D_{y_1}V_3(y_1,y_2)$$
$$-\Bigg(\frac{2ax_0y_0}{\omega(v_0)(ax_0^2+bx_0+c)^2}-\frac{2x_0y_0(2ax_0+b)(4ax_0+b)}{\omega(v_0)(ax_0^2+bx_0+c)^3}+\frac{2x_0^2y_0(2ax_0+b)^3}{\omega(v_0)(ax_0^2+bx_0+c)^4}$$
$$+\frac{2p^2nx_0E_0}{\omega(v_0)(px_0-n)^3}\Bigg)y_1^4+\Bigg(\frac{2x_0^{\frac{3}{2}}(2ax_0+b)^2\sqrt{dy_0}}{\omega(v_0)(ax_0^2+bx_0+c)^{\frac{5}{2}}}-\frac{2(3ax_0+b)\sqrt{dx_0y_0}}{\omega(v_0)(ax_0^2+bx_0+c)^{\frac{3}{2}}}\Bigg)y_1^3y_2$$
$$-\frac{d\sqrt{x_0}}{\omega(v_0)}y_1y_2\times D_{y_2}V_3(y_1,y_2)\,. \tag{3.5}$$

Given Eq. (3.4), it follows that

$$D_{y_1}V_3(y_1,y_2)$$
$$=\Bigg(\frac{2(ax_0^2-c)\sqrt{dy_0}}{\omega(v_0)(ax_0^2+bx_0+c)^{\frac{3}{2}}}\Bigg)y_1^2$$
$$+\Bigg(\frac{4\sqrt{x_0}y_0(2ax_0+b)^2}{\omega(v_0)(ax_0^2+bx_0+c)^3}+\frac{4p^2\sqrt{x_0}E_0}{\omega(v_0)(px_0-n)^2}-\frac{4a\sqrt{x_0}y_0}{\omega(v_0)(ax_0^2+bx_0+c)^2}\Bigg)y_1y_2\,,$$

$$D_{y_2}V_3(y_1,y_2)$$
$$=\Bigg(\frac{2\sqrt{x_0}y_0(2ax_0+b)^2}{\omega(v_0)(ax_0^2+bx_0+c)^3}+\frac{2p^2\sqrt{x_0}E_0}{\omega(v_0)(px_0-n)^2}-\frac{2a\sqrt{x_0}y_0}{\omega(v_0)(ax_0^2+bx_0+c)^2}\Bigg)y_1^2$$
$$-\Bigg(\frac{4a\sqrt{x_0}y_0}{\omega(v_0)(ax_0^2+bx_0+c)^2}-\frac{4\sqrt{x_0}y_0(2ax_0+b)^2}{\omega(v_0)(ax_0^2+bx_0+c)^3}-\frac{4p^2\sqrt{x_0}E_0}{\omega(v_0)(px_0-n)^2}+\frac{2d\sqrt{x_0}}{\omega(v_0)}\Bigg)y_2^2\,.$$

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Substituting the above $D_{y_1}V_3(y_1,y_2)$ and $D_{y_2}V_3(y_1,y_2)$ into Eq. (3.5), we have

$$
\begin{aligned}
&y_1D_{y_2}V_4(y_1,y_2)-y_2D_{y_1}V_4(y_1,y_2)\\
&=-\left\{\frac{2(ax_0^2-c)\sqrt{dy_0}}{\omega^2(v_0)(ax_0^2+bx_0+c)^{\frac{3}{2}}}\left(\frac{a\sqrt{x_0}y_0}{(ax_0^2+bx_0+c)^2}-\frac{\sqrt{x_0}y_0(2ax_0+b)^2}{(ax_0^2+bx_0+c)^3}-\frac{p^2\sqrt{x_0}E_0}{(px_0-n)^2}\right)\right.\\
&\quad+\frac{2ax_0y_0}{\omega(v_0)(ax_0^2+bx_0+c)^2}-\frac{2x_0y_0(2ax_0+b)(4ax_0+b)}{\omega(v_0)(ax_0^2+bx_0+c)^3}+\frac{2x_0^2y_0(2ax_0+b)^3}{\omega(v_0)(ax_0^2+bx_0+c)^4}\\
&\quad\left.+\frac{2p^2nx_0E_0}{\omega(v_0)(px_0-n)^3}\right\}y_1^4-\left\{\frac{(6ax_0+2b)\sqrt{dx_0y_0}}{\omega(v_0)(ax_0^2+bx_0+c)^{\frac{3}{2}}}-\frac{2x_0^{\frac{3}{2}}(2ax_0+b)^2\sqrt{dy_0}}{\omega(v_0)(ax_0^2+bx_0+c)^{\frac{5}{2}}}\right.\\
&\quad+\frac{2dy_0(ax_0^2-c)^2}{\omega^2(v_0)(ax_0^2+bx_0+c)^3}-\left(\frac{2a\sqrt{x_0}y_0}{\omega(v_0)(ax_0^2+bx_0+c)^2}-\frac{2\sqrt{x_0}y_0(2ax_0+b)^2}{\omega(v_0)(ax_0^2+bx_0+c)^3}\right.\\
&\quad\left.-\frac{2p^2\sqrt{x_0}E_0}{\omega(v_0)(px_0-n)^2}\right)^2-\frac{2adx_0y_0}{\omega^2(v_0)(ax_0^2+bx_0+c)^2}+\frac{2dx_0y_0(2ax_0+b)^2}{\omega^2(v_0)(ax_0^2+bx_0+c)^3}\\
&\quad\left.+\frac{2dp^2x_0E_0}{\omega^2(v_0)(px_0-n)^2}\right\}y_1^3y_2+\left\{\frac{4(ax_0^2-c)\sqrt{dy_0}}{\omega^2(v_0)(ax_0^2+bx_0+c)^{\frac{3}{2}}}\left(\frac{a\sqrt{x_0}y_0}{(ax_0^2+bx_0+c)^2}\right.\right.\\
&\quad\left.\left.-\frac{\sqrt{x_0}y_0(2ax_0+b)^2}{(ax_0^2+bx_0+c)^3}-\frac{p^2\sqrt{x_0}E_0}{(px_0-n)^2}\right)\right\}y_1^2y_2^2+\left\{\frac{4adx_0y_0}{\omega^2(v_0)(ax_0^2+bx_0+c)^2}\right.\\
&\quad\left.-\frac{4dx_0y_0(2ax_0+b)^2}{\omega^2(v_0)(ax_0^2+bx_0+c)^3}-\frac{4dp^2x_0E_0}{\omega^2(v_0)(px_0-n)^2}+\frac{2d^2x_0}{\omega^2(v_0)}\right\}y_1y_2^3. \qquad (3.6)
\end{aligned}
$$

On setting $y_1=r\cos\theta$, $y_2=r\sin\theta$ in Eq. (3.6), we now have

$$
\begin{aligned}
&\frac{\mathrm{d}V_4(\cos\theta,\sin\theta)}{\mathrm{d}\theta}\\
&=-\left\{\frac{2(ax_0^2-c)\sqrt{dy_0}}{\omega^2(v_0)(ax_0^2+bx_0+c)^{\frac{3}{2}}}\left(\frac{a\sqrt{x_0}y_0}{(ax_0^2+bx_0+c)^2}-\frac{\sqrt{x_0}y_0(2ax_0+b)^2}{(ax_0^2+bx_0+c)^3}-\frac{p^2\sqrt{x_0}E_0}{(px_0-n)^2}\right)\right.\\
&\quad+\frac{2ax_0y_0}{\omega(v_0)(ax_0^2+bx_0+c)^2}-\frac{2x_0y_0(2ax_0+b)(4ax_0+b)}{\omega(v_0)(ax_0^2+bx_0+c)^3}+\frac{2x_0^2y_0(2ax_0+b)^3}{\omega(v_0)(ax_0^2+bx_0+c)^4}\\
&\quad\left.+\frac{2p^2nx_0E_0}{\omega(v_0)(px_0-n)^3}\right\}\cos^4\theta-\left\{\frac{(6ax_0+2b)\sqrt{dx_0y_0}}{\omega(v_0)(ax_0^2+bx_0+c)^{\frac{3}{2}}}-\frac{2x_0^{\frac{3}{2}}(2ax_0+b)^2\sqrt{dy_0}}{\omega(v_0)(ax_0^2+bx_0+c)^{\frac{5}{2}}}\right.\\
&\quad+\frac{2dy_0(ax_0^2-c)^2}{\omega^2(v_0)(ax_0^2+bx_0+c)^3}-\left(\frac{2a\sqrt{x_0}y_0}{\omega(v_0)(ax_0^2+bx_0+c)^2}-\frac{2\sqrt{x_0}y_0(2ax_0+b)^2}{\omega(v_0)(ax_0^2+bx_0+c)^3}\right.\\
&\quad\left.-\frac{2p^2\sqrt{x_0}E_0}{\omega(v_0)(px_0-n)^2}\right)^2-\frac{2adx_0y_0}{\omega^2(v_0)(ax_0^2+bx_0+c)^2}+\frac{2dx_0y_0(2ax_0+b)^2}{\omega^2(v_0)(ax_0^2+bx_0+c)^3}
\end{aligned}
$$

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$$+\frac{2dp^2x_0E_0}{\omega^2(v_0)(px_0-n)^2}\Bigg\}\sin\theta\cos^3\theta+\Bigg\{\frac{4(ax_0^2-c)\sqrt{dy_0}}{\omega^2(v_0)(ax_0^2+bx_0+c)^{\frac{3}{2}}}\Bigg(\frac{a\sqrt{x_0}y_0}{(ax_0^2+bx_0+c)^2}$$
$$-\frac{\sqrt{x_0}y_0(2ax_0+b)^2}{(ax_0^2+bx_0+c)^3}-\frac{p^2\sqrt{x_0}E_0}{(px_0-n)^2}\Bigg)\Bigg\}\sin^2\theta\cos^2\theta+\Bigg\{\frac{4adx_0y_0}{\omega^2(v_0)(ax_0^2+bx_0+c)^2}$$
$$-\frac{4dx_0y_0(2ax_0+b)^2}{\omega^2(v_0)(ax_0^2+bx_0+c)^3}-\frac{4dp^2x_0E_0}{\omega^2(v_0)(px_0-n)^2}+\frac{2d^2x_0}{\omega^2(v_0)}\Bigg\}\sin^3\theta\cos\theta$$

$$:=-H_4(\cos\theta,\sin\theta).$$

Similar to the construction of $V_3(\cos\theta,\sin\theta)$, there exists a $V_4(\cos\theta,\sin\theta)$ if and only if $\int_0^{2\pi}H_4(\cos\theta,\sin\theta)\mathrm{d}\theta=0$. However, we have

$$\int_0^{2\pi}H_4(\cos\theta,\sin\theta)\mathrm{d}\theta$$
$$=\frac{\pi(ax_0^2-c)\sqrt{dy_0}}{2\omega^2(v_0)(ax_0^2+bx_0+c)^{\frac{3}{2}}}\left(\frac{a\sqrt{x_0}y_0}{(ax_0^2+bx_0+c)^2}-\frac{\sqrt{x_0}y_0(2ax_0+b)^2}{(ax_0^2+bx_0+c)^3}-\frac{p^2\sqrt{x_0}E_0}{(px_0-n)^2}\right)$$
$$+\frac{3\pi ax_0y_0}{2\omega(v_0)(ax_0^2+bx_0+c)^2}-\frac{3\pi x_0y_0(2ax_0+b)(4ax_0+b)}{2\omega(v_0)(ax_0^2+bx_0+c)^3}+\frac{3\pi x_0^2y_0(2ax_0+b)^3}{2\omega(v_0)(ax_0^2+bx_0+c)^4}$$
$$+\frac{3\pi p^2nx_0E_0}{2\omega(v_0)(px_0-n)^3}\neq 0,$$

hence we need to modify $V_4(\cos\theta,\sin\theta)$ such that $V_4(\cos\theta,\sin\theta)$ satisfies

$$\frac{\mathrm{d}V_4(\cos\theta,\sin\theta)}{\mathrm{d}\theta}=-H_4(\cos\theta,\sin\theta)+C_4:=-H_4'(\cos\theta,\sin\theta),$$

where

$$C_4=\frac{1}{2\pi}\int_0^{2\pi}H_4(\cos\theta,\sin\theta)\mathrm{d}\theta$$
$$=\frac{a\sqrt{dx_0}y_0^{\frac{3}{2}}(ax_0^2-c)}{4\omega^2(v_0)(ax_0^2+bx_0+c)^{\frac{7}{2}}}-\frac{\sqrt{dx_0}y_0^{\frac{3}{2}}(ax_0^2-c)(2ax_0+b)^2}{4\omega^2(v_0)(ax_0^2+bx_0+c)^{\frac{9}{2}}}$$
$$-\frac{p^2\sqrt{dx_0y_0}(ax_0^2-c)E_0}{4\omega^2(v_0)(ax_0^2+bx_0+c)^{\frac{3}{2}}(px_0-n)^2}+\frac{3ax_0y_0}{4\omega(v_0)(ax_0^2+bx_0+c)^2}$$
$$-\frac{3x_0y_0(2ax_0+b)(4ax_0+b)}{4\omega(v_0)(ax_0^2+bx_0+c)^3}+\frac{3x_0^2y_0(2ax_0+b)^3}{4\omega(v_0)(ax_0^2+bx_0+c)^4}$$
$$+\frac{3p^2nx_0E_0}{4\omega(v_0)(px_0-n)^3}\neq 0\,.$$

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We can verify that $\int_0^{2\pi} H_4'(\cos\theta, \sin\theta)\mathrm{d}\theta = 0$, so the modified $V_4(\cos\theta, \sin\theta)$ exists, and from the above construction process of $V(y_1, y_2)$ one has

$$\left.\frac{\mathrm{d}V(y_1, y_2)}{\mathrm{d}\tau}\right|_{(3.1)} = C_4 r^4 + o(r^4).$$

According to Lyapunov stability theory [18], we can therefore derive the stated stability results for the bifurcating periodic solutions — viz. the bifurcating periodic solutions are unstable if $C_4 > 0$ and the bifurcating periodic solutions are stable if $C_4 < 0$. □

4. Numerical Simulations

A simple example demonstrates our theoretical results. In order to satisfy the assumptions (2.1) and (2.6) in addition to the conditions (I) of Theorem 2.1 and Theorem 3.1, we consider the predator-prey model (1.6) with the coefficients

$$\begin{cases} \dot{x} = x\left(1 - x - \dfrac{y}{x^2 + 8x + 0.75} - E\right), \\ \dot{y} = y\,(-0.5 + x), \\ 0 = E(12x - 1) - v\,, \end{cases} \tag{4.1}$$

which has a positive equilibrium point $X_0 = (1/2, 5/3, 1/6)$. From the discussion in Section 2, the bifurcation value is $v_0 = 5/6$. According to Theorem 2.1 (on choosing $\varepsilon = 0.06$) and Theorem 3.1, the positive equilibrium point X_0 is locally asymptotically stable when $v = 0.78 < v_0$ as illustrated in Fig. 1, there are periodic solutions bifurcating from the equilibrium point X_0 when $v = 0.8333 < v_0$ as illustrated in Fig. 2, the bifurcating periodic solutions are unstable when $v = v_0 = 5/6$ as illustrated in Fig. 3, and the equilibrium point X_0 is unstable when $v = 0.868 > v_0$ as illustrated in Fig. 4.

5. Discussion

We have investigated the dynamical behaviour of a modified predator-prey model (1.6) with a generalised Holling type IV functional response, established by a differential-algebraic system. Stability and bifurcation analysis defined a range of economic profit v for which the predator-prey ecosystem sustains all of the species.

It is notable that the Hopf bifurcation theorem [17] and the formal series method [18] cannot be applied to our differential-algebraic system (1.6) directly, since the application objects of the Hopf bifurcation theorem and the formal series method are differential equations. Using the local parameterisation described in Ref. [16], we found that the differential-algebraic model (1.6) can be locally equivalent to a two-dimensional differential system (2.9) near the equilibrium point X_0. Consequently, by applying to the Hopf bifurcation theorem [17] and formal series method [18] to the locally equivalent differential system (2.9), we obtained Theorem 2.1 and Theorem 3.1.

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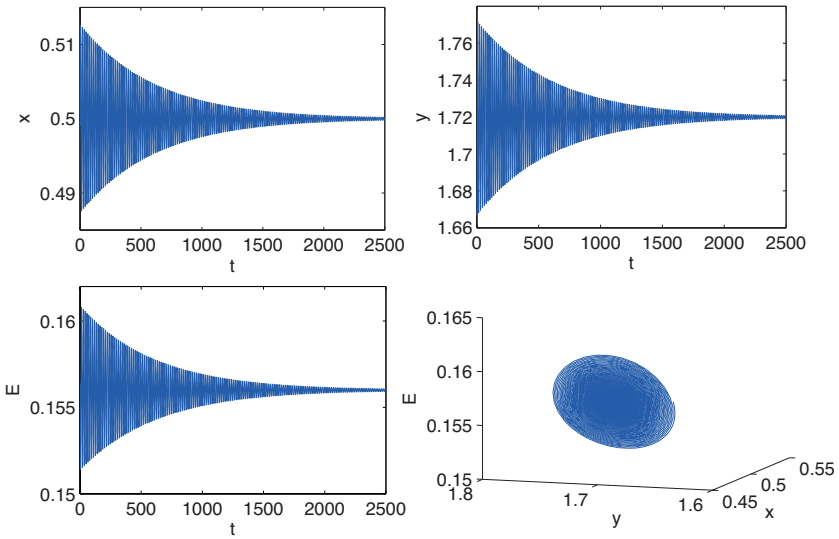


Figure 1: The equilibrium point X_0 is locally asymptotically stable when $v = 0.78 < v_0$. Here the initial condition for computer simulations is chosen as $(x_0, y_0, E_0) = (0.499, 1.667, 0.167)$.

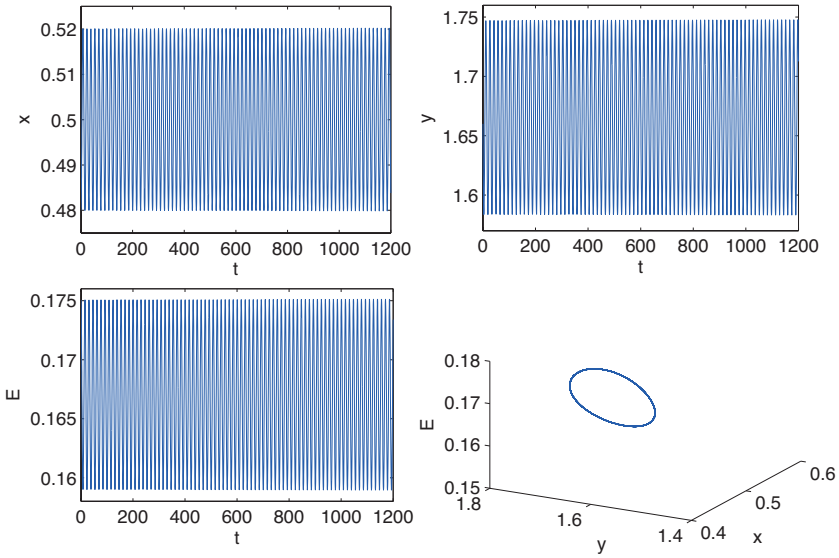


Figure 2: Periodic solutions bifurcate from the equilibrium point X_0 when $v = 0.8333 < v_0$. Here the initial condition for computer simulations is chosen as $(x_0, y_0, E_0) = (0.48, 1.66, 0.16)$.

Theorem 2.1 gives theoretical results on the stability of equilibrium point X_0 and the existence of a Hopf bifurcation, which occurs in a small neighbourhood of the critical bifurcation value v_0. From Theorem 2.1, we find that there are periodic solutions arising from the equilibrium point as the bifurcation parameter v increases through the value v_0 in our predator-prey model, which implies that the predator and prey populations undergo peri-

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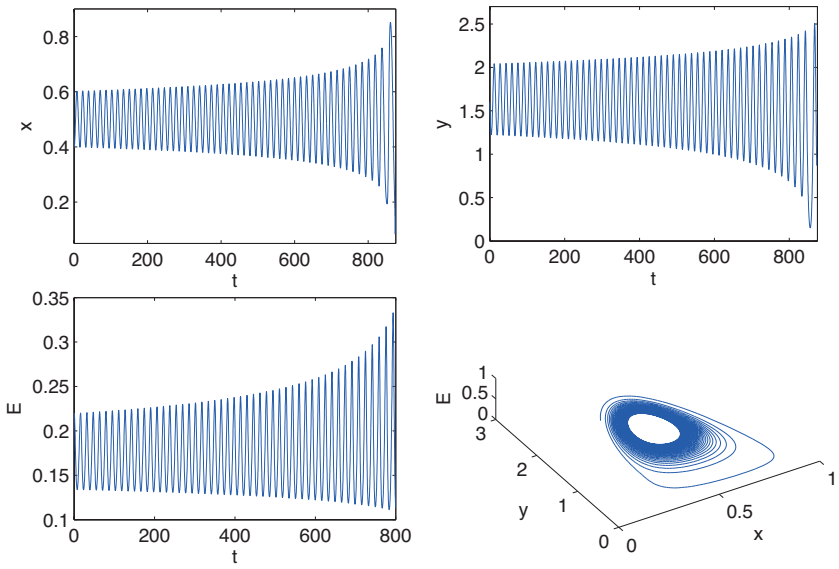


Figure 3: The bifurcating periodic solutions are unstable when $\nu = \nu_0 = 5/6$. Here the initial condition for computer simulations is chosen as $(x_0, y_0, E_0) = (0.4, 1.6, 0.06)$.

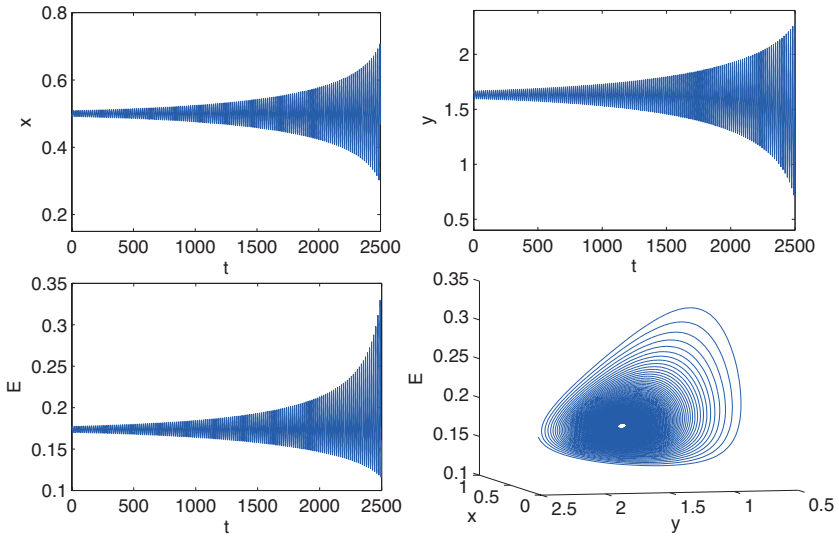


Figure 4: The equilibrium point X_0 is unstable when $\nu = 0.868 > \nu_0$. Here the initial condition for computer simulations is chosen as $(x_0, y_0, E_0) = (0.499, 1.667, 0.167)$.

odic oscillations that may harm the sustainable development of the biological populations. When bifurcating periodic solutions are stable, predator and the prey species with harvesting may coexist in an oscillatory mode. Accordingly, we are naturally keen to determine whether oscillatory prey, predator and harvesting can coexist. Thus in Section 3 we studied the stability of the bifurcating periodic solutions, by constructing a suitable Lyapunov

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function and using the formal series method [18].

Theorem 2.1 and Theorem 3.1 show that the dynamics of the predator-prey model (1.6) is very sensitive to varying the economic profit v. From these two theorems, we can conclude that fishermen in the long run would better maintain their economic profit from harvesting corresponding to a bifurcation value less than v_0. The local parameterisation and the formal series method we employed are valuable research tools for investigating the dynamics of modified predator-prey models, and could be applied to study the dynamical behaviours of more complicated differential-algebraic systems in engineering.

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A. Appendix

The local parameterisation in Ref. [16] is briefly summarised here. We consider the differential-algebraic system

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

where $f : R^n \to R^n$, $g : R^n \to R^m$, f and g are continuously differentiable functions, with $f = (f_1, f_2, \cdots, f_n)^T$, $g = (g_1, g_2, \cdots, g_m)^T$.

Let $\overline{X}_0$ be an equilibrium point of (A.1). Assuming the differential-algebraic system (A.1) satisfies

(H_1) $n - m = 2$,

(H_2) $\operatorname{rank} D_{\overline{X}} g(\overline{X}_0) = m$,

(H_3) $D_{\overline{X}} g(\overline{X}_0) = (0, P)_{m\times n}$,

where $P_{m\times m}$ is a nonsingular matrix, we can employ the following local parameterisation for (A.1):

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

where $U_0 = \begin{pmatrix} I_2 \\ 0 \end{pmatrix}_{n\times 2}$, $V_0 = \begin{pmatrix} 0 \\ I_m \end{pmatrix}_{n\times m}$, $Y(t) = (y_1(t), y_2(t))^T \in R^2$, $h(Y)$ is a smooth mapping from R^2 into R^m. The differential-algebraic system (A.1) is then locally equivalent to the parameterised system (2.4) near the equilibrium point $\overline{X}_0$.

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B. Appendix

The coefficients of the parameterised system (2.9) are calculated as follows. From Eqs. (2.3), we have that

$$D_{\overline{X}} f_1(\overline{X}) = \left(1 - 2x - \frac{y}{ax^2+bx+c} + \frac{xy(2ax+b)}{(ax^2+bx+c)^2} + \frac{2pE_0 x}{px_0 - n} - \overline{E}, -\frac{x}{ax^2+bx+c}, -x\right),$$

$$D_{\overline{X}} f_2(\overline{X}) = (dy, -k + dx, 0),$$

$$D_{\overline{X}} g(\overline{X}) = \left(p\overline{E} + \frac{pnE_0}{px_0 - n} - \frac{2p^2 E_0}{px_0 - n}x\,, 0, px - n\right). \tag{B.1}$$

and it can also be shown that

$$D_Y \psi(Y) = \begin{pmatrix} D_{\overline{X}} g(\overline{X}) \\ U_0^T \end{pmatrix}^{-1} \begin{pmatrix} 0 \\ I_2 \end{pmatrix}. \tag{B.2}$$

Substituting the expression of $D_{\overline{X}} g(\overline{X})$ from Eqs. (B.1) into Eq. (B.2) yields

$$\begin{aligned} D_Y \psi(Y) &= \left(D_{y_1}\psi(Y),\ D_{y_2}\psi(Y)\right) \\ &= \begin{pmatrix} p\overline{E} + \dfrac{pnE_0}{px_0 - n} - \dfrac{2p^2E_0}{px_0 - n}x & 0 & px - n \\ 1 & 0 & 0 \\ 0 & 1 & 0 \end{pmatrix}^{-1} \begin{pmatrix} 0 & 0 \\ 1 & 0 \\ 0 & 1 \end{pmatrix} \\ &= \begin{pmatrix} 1 & & 0 \\ 0 & & 1 \\ \dfrac{1}{px - n}\left(\dfrac{2p^2E_0}{px_0 - n}x - \dfrac{pnE_0}{px_0 - n} - p\overline{E}\right) & & 0 \end{pmatrix}, \end{aligned} \tag{B.3}$$

and Eqs. (B.1) and (B.3) lead to

$$\begin{aligned} f_{1y_1}(\overline{X}) &= D_{\overline{X}} f_1(\overline{X}) D_{y_1}\psi(Y) \\ &= 1 - 2x - \frac{y}{ax^2+bx+c} + \frac{xy(2ax+b)}{(ax^2+bx+c)^2} + \frac{2pE_0x}{px_0 - n} - \overline{E} \\ &\quad - \frac{x}{px - n}\left(\frac{2p^2E_0}{px_0 - n}x - \frac{pnE_0}{px_0 - n} - p\overline{E}\right), \\ f_{1y_2}(\overline{X}) &= D_{\overline{X}} f_1(\overline{X}) D_{y_2}\psi(Y) = -\frac{x}{ax^2+bx+c}, \\ f_{2y_1}(\overline{X}) &= D_{\overline{X}} f_2(\overline{X}) D_{y_1}\psi(Y) = dy, \\ f_{2y_2}(\overline{X}) &= D_{\overline{X}} f_2(\overline{X}) D_{y_2}\psi(Y) = -k + dx. \end{aligned} \tag{B.4}$$

Substituting $\overline{X}_0$ into Eq. (B.4) yields

$$f_{1y_1}(\overline{X}_0) = 0, \quad f_{1y_2}(\overline{X}_0) = -\frac{x_0}{ax_0^2 + bx_0 + c}, \quad f_{2y_1}(\overline{X}_0) = dy_0, \quad f_{2y_2}(\overline{X}_0) = 0, \tag{B.5}$$

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and from Eq. (B.4) we have

$$D_{\overline{X}} f_{1y_1}(\overline{X}) = \Bigg(-2 + \frac{2axy}{(ax^2+bx+c)^2} + \frac{2y(2ax+b)}{(ax^2+bx+c)^2} - \frac{2xy(2ax+b)^2}{(ax^2+bx+c)^3} + \frac{2pE_0}{px_0-n} - \frac{2p^2E_0x}{(px_0-n)(px-n)} - \frac{pn\overline{E}}{(px-n)^2} + \frac{2p^2nE_0x}{(px_0-n)(px-n)^2} - \frac{pn^2E_0}{(px_0-n)(px-n)^2}, -\frac{1}{ax^2+bx+c} + \frac{x(2ax+b)}{(ax^2+bx+c)^2}, \frac{n}{px-n} \Bigg),$$

$$D_{\overline{X}} f_{1y_2}(\overline{X}) = \left(-\frac{1}{ax^2+bx+c} + \frac{x(2ax+b)}{(ax^2+bx+c)^2}, 0, 0 \right),$$

$$D_{\overline{X}} f_{2y_1}(\overline{X}) = (0, d, 0)\,, \qquad D_{\overline{X}} f_{2y_2}(\overline{X}) = (d, 0, 0)\,. \tag{B.6}$$

Eqs. (B.3) and (B.6) lead to

$$\begin{aligned}
f_{1y_1y_1}(\overline{X}) =& D_{\overline{X}} f_{1y_1}(\overline{X}) D_{y_1}\psi(Y) \\
=& -2 + \frac{2axy}{(ax^2+bx+c)^2} + \frac{2y(2ax+b)}{(ax^2+bx+c)^2} - \frac{2xy(2ax+b)^2}{(ax^2+bx+c)^3} + \frac{2pE_0}{px_0-n} \\
& - \frac{2pn\overline{E}}{(px-n)^2} - \frac{2p^2E_0x}{(px_0-n)(px-n)} + \frac{4p^2nE_0x}{(px_0-n)(px-n)^2} - \frac{2pn^2E_0}{(px_0-n)(px-n)^2}, \\
f_{1y_1y_2}(\overline{X}) =& D_{\overline{X}} f_{1y_1}(\overline{X}) D_{y_2}\psi(Y) = -\frac{1}{ax^2+bx+c} + \frac{x(2ax+b)}{(ax^2+bx+c)^2}, \\
f_{1y_2y_2}(\overline{X}) =& D_{\overline{X}} f_{1y_2}(\overline{X}) D_{y_2}\psi(Y) = 0\,, \qquad f_{2y_1y_1}(\overline{X}) = D_{\overline{X}} f_{2y_1}(\overline{X}) D_{y_1}\psi(Y) = 0\,, \\
f_{2y_1y_2}(\overline{X}) =& D_{\overline{X}} f_{2y_1}(\overline{X}) D_{y_2}\psi(Y) = d\,, \qquad f_{2y_2y_2}(\overline{X}) = D_{\overline{X}} f_{2y_2}(\overline{X}) D_{y_2}\psi(Y) = 0\,,
\end{aligned} \tag{B.7}$$

and substituting $\overline{X}_0$ into Eqs. (B.7) yields

$$\begin{aligned}
& f_{1y_1y_1}(\overline{X}_0) = \frac{2ax_0y_0}{(ax_0^2+bx_0+c)^2} - \frac{2x_0y_0(2ax_0+b)^2}{(ax_0^2+bx_0+c)^3} - \frac{2p^2x_0E_0}{(px_0-n)^2}, \\
& f_{1y_1y_2}(\overline{X}_0) = \frac{ax_0^2-c}{(ax_0^2+bx_0+c)^2}, \\
& f_{1y_2y_2}(\overline{X}_0) = 0\,, \qquad f_{2y_1y_1}(\overline{X}_0) = 0\,, \qquad f_{2y_1y_2}(\overline{X}_0) = d\,, \qquad f_{2y_2y_2}(\overline{X}_0) = 0\,.
\end{aligned} \tag{B.8}$$

From Eqs. (B.7) it follows that

$$D_{\overline{X}} f_{1y_1y_1}(\overline{X}) = \Bigg(\frac{6ay}{(ax^2+bx+c)^2} - \frac{6y(2ax+b)(4ax+b)}{(ax^2+bx+c)^3} + \frac{6xy(2ax+b)^3}{(ax^2+bx+c)^4} + \frac{6p^2nE_0}{(px_0-n)(px-n)^2} - \frac{8p^3nE_0x}{(px_0-n)(px-n)^3} + \frac{4p^2n^2E_0}{(px_0-n)(px-n)^3} + \frac{4p^2n\overline{E}}{(px-n)^3}, \frac{2ax}{(ax^2+bx+c)^2} + \frac{2(2ax+b)}{(ax^2+bx+c)^2} - \frac{2x(2ax+b)^2}{(ax^2+bx+c)^3}, -\frac{2pn}{(px-n)^2} \Bigg),$$

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$$
\begin{aligned}
&D_{\overline{X}} f_{1y_1y_2}(\overline{X}) = \left(\frac{6ax+2b}{(ax^2+bx+c)^2} - \frac{2x(2ax+b)^2}{(ax^2+bx+c)^3}, 0, 0 \right), \\
&D_{\overline{X}} f_{1y_2y_2}(\overline{X}) = (0,0,0)\,, \qquad D_{\overline{X}} f_{2y_1y_1}(\overline{X}) = (0,0,0)\,, \\
&D_{\overline{X}} f_{2y_1y_2}(\overline{X}) = (0,0,0)\,, \qquad D_{\overline{X}} f_{2y_2y_2}(\overline{X}) = (0,0,0)\,.
\end{aligned} \tag{B.9}
$$

Substituting $\overline{X}_0$ into Eqs. (B.3) and (B.9), yields

$$
\begin{aligned}
D_{\overline{X}} f_{1y_1y_1}(\overline{X_0}) &= \left(\frac{6ay_0}{(ax_0^2+bx_0+c)^2} - \frac{6y_0(2ax_0+b)(4ax_0+b)}{(ax_0^2+bx_0+c)^3} + \frac{6x_0y_0(2ax_0+b)^3}{(ax_0^2+bx_0+c)^4} \right. \\
&\quad \left. + \frac{6p^2nE_0}{(px_0-n)^3}, \frac{2ax_0}{(ax_0^2+bx_0+c)^2} + \frac{2(2ax_0+b)}{(ax_0^2+bx_0+c)^2} - \frac{2x_0(2ax_0+b)^2}{(ax_0^2+bx_0+c)^3}, -\frac{2pn}{(px_0-n)^2} \right), \\
D_{\overline{X}} f_{1y_1y_2}(\overline{X_0}) &= \left(\frac{6ax_0+2b}{(ax_0^2+bx_0+c)^2} - \frac{2x_0(2ax_0+b)^2}{(ax_0^2+bx_0+c)^3}, 0, 0 \right), \\
D_{\overline{X_0}} f_{1y_2y_2}(\overline{X}) &= (0,0,0)\,, \qquad D_{\overline{X}} f_{2y_1y_1}(\overline{X_0}) = (0,0,0)\,, \\
D_{\overline{X}} f_{2y_1y_2}(\overline{X_0}) &= (0,0,0)\,, \qquad D_{\overline{X}} f_{2y_2y_2}(\overline{X_0}) = (0,0,0)\,, \\
D_Y \psi(0) &= \left(D_{y_1}\psi(0),\ D_{y_2}\psi(0) \right) \\
&= \begin{pmatrix} 1 & 0 \\ 0 & 1 \\ \dfrac{1}{px_0-n}\left(\dfrac{2p^2x_0E_0}{px_0-n} - \dfrac{pnE_0}{px_0-n} - p\overline{E}_0 \right) & 0 \end{pmatrix} \\
&= \begin{pmatrix} 1 & 0 \\ 0 & 1 \\ \dfrac{1}{px_0-n}\left[\dfrac{2p^2x_0E_0}{px_0-n} - \dfrac{pnE_0}{px_0-n} - p\left(E_0 + \dfrac{px_0E_0}{px_0-n} \right) \right] & 0 \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ 0 & 1 \\ 0 & 0 \end{pmatrix}.
\end{aligned} \tag{B.10}
$$

Eqs. (B.10) lead to

$$
\begin{aligned}
f_{1y_1y_1y_1}(\overline{X}_0) &= D_{\overline{X}} f_{1y_1y_1}(\overline{X}_0) D_{y_1}\psi(0) \\
&= \frac{6ay_0}{(ax_0^2+bx_0+c)^2} - \frac{6y_0(2ax_0+b)(4ax_0+b)}{(ax_0^2+bx_0+c)^3} + \frac{6x_0y_0(2ax_0+b)^3}{(ax_0^2+bx_0+c)^4} + \frac{6p^2nE_0}{(px_0-n)^3}\,, \\
f_{1y_1y_1y_2}(\overline{X}_0) &= D_{\overline{X}} f_{1y_1y_1}(\overline{X}_0) D_{y_2}\psi(0) = \frac{6ax_0+2b}{(ax^2+bx+c)^2} - \frac{2x_0(2ax_0+b)^2}{(ax^2+bx+c)^3}\,, \\
f_{1y_1y_2y_2}(\overline{X}_0) &= D_{\overline{X}} f_{1y_1y_2}(\overline{X}_0) D_{y_2}\psi(0) = 0\,, \qquad f_{1y_2y_2y_2}(\overline{X}_0) = D_{\overline{X}} f_{1y_2y_2}(\overline{X}_0) D_{y_2}\psi(0) = 0\,, \\
f_{2y_1y_1y_1}(\overline{X}_0) &= D_{\overline{X}} f_{2y_1y_1}(\overline{X}_0) D_{y_1}\psi(0) = 0\,, \qquad f_{2y_1y_1y_2}(\overline{X}_0) = D_{\overline{X}} f_{2y_1y_1}(\overline{X}_0) D_{y_2}\psi(0) = 0\,, \\
f_{2y_1y_2y_2}(\overline{X}_0) &= D_{\overline{X}} f_{2y_1y_2}(\overline{X}_0) D_{y_2}\psi(0) = 0\,, \qquad f_{2y_2y_2y_2}(\overline{X}_0) = D_{\overline{X}} f_{2y_2y_2}(\overline{X}_0) D_{y_2}\psi(0) = 0\,.
\end{aligned} \tag{B.11}
$$

On substituting the coefficients (B.5), (B.8) and (B.11) into Eqs. (2.8), we obtain the parameterised system (2.9).

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