Bogdanov-Takens Bifurcations in Predator-Prey Systems with Constant Rate Harvesting

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Abstract. In this paper, we consider a predator-prey system with constant rate predator harvesting. The system has a cusp of codimension 2 and exhibits the Bogdanov-Takens bifurcation. By choosing the death rate and the harvesting rate of the predator as the bifurcation parameters, we show that the system undergoes a sequence of bifurcations including the Hopf bifurcation, saddle-node bifurcations, and the homoclinic bifurcation. Global bifurcation diagrams and phase portraits in a small neighborhood of the cusp are sketched. Numerical simulations are given to illustrate the results.

1 Introduction

The study of population dynamics with harvesting is a very interesting subject in mathematical bioeconomics. It is related to the optimal management of renewable resources (see [9]). The exploitation of biological resources and the harvest of population species are commonly practiced in fishery, forestry, and wildlife management. The basic model, usually in the form of differential equations, is the generalized Gause-type model for two species,

$$\dot{x} = xg(x) - p(x)y - h_1,$$

 $\dot{y} = q(x)y - \delta y - h_2.$ (1.1)

¹⁹⁹¹ Mathematics Subject Classification. Primary 34C25, 92A15; Secondary 58F14. Research of the first author was supported by the National Science Foundations of China. Research of the second author was supported by NSERC of Canada and the Petro-Canada Young Innovator Award.

Here x and y, are functions of time, representing population densities of prey and predator respectively, and h_1, h_2 , and δ are positive constants. The biological setting requires that all functions be continuous. g(0) is positive and g(x) is decreasing in x. Both p(x) and q(x) are positive for x > 0 and vanish at 0.

System (1.1) is interesting for the biological implications as well as mathematically. In a sequence of papers by Brauer and Soudack [4, 5, 6], and the recent work by Dai and Tang in [10] and Dai and Xu in [11], the global behavior of system (1.1) for some special functions g(x), p(x) and q(x) was analyzed by using qualitative theory and numerical techniques.

Brauer and Soudack in [4] discussed the following model

$$\dot{x} = rx\left(1 - \frac{x}{k}\right) - \frac{yx}{a+x},$$

$$\dot{y} = y\left(-d + \frac{x}{a+x}\right) - h,$$
(1.2)

where k is the carrying capacity of the prey population, d is the death rate of the predator, r is the intrinsic growth rate of the prey population, and h is the harvesting rate. The function $\frac{x}{a+x}$ is often called the functional response of Holling type II. k, d, r, a and h are positive constants. Numerical studies in [4] indicated the existence of a homoclinic loop and a periodic orbit for some parameter values in (1.2).

In this paper, we do a bifurcation analysis of model (1.2). In particular we are interested in codimension 2 bifurcations that occur in a two-dimensional parameter region. Under some conditions we prove that system (1.2) undergoes the Bogdanov-Takens bifurcation, i.e., the bifurcation of a cusp of codimension 2 (see [8] and [12]). An example is given to show the existence of the Bogdanov-Takens bifurcation. In this framework, we demonstrate that system (1.2) can exhibit qualitatively different dynamical behavior, including Hopf bifurcations, saddle-node bifurcations as well as homoclinic bifurcations. In particular, for certain parameter values, the system can have a unique limit cycle or even a homoclinic loop. The corresponding bifurcation diagrams and phase portraits are sketched. Our analysis supports the numerical simulation in [4].

The paper is organized as follows. The general analysis and conditions appear in the next section. In Section 3 we reduce system (1.2) to the canonical family and obtain the main theorem. Finally, we choose two parameters, d and h, as the bifurcation parameters for system (1.2) and show that system (1.2) exhibits the Bogdanov-Takens bifurcation. The global bifurcation diagram and all possible phase portraits are sketched when the bifurcation parameters vary in a small neighborhood of the origin in the two dimensional parameter plane. Numerical simulations are given to illustrate the obtained results.

2 Preliminaries

From system (1.2), we can see that the y-axis is invariant under the flow. However, this is not the case on the x-axis. All solutions touching the x-axis cross out of the first quadrant. Thus, the first quadrant is no longer positively invariant under the flow generated by the harvested system. From the standpoint of biology, we are only interested in the dynamics of system (1.2) in the first quadrant.

First, we consider the existence of equilibria of system (1.2). The prey isocline of system (1.2) is

$$y = r(1 - \frac{x}{k})(a + x).$$

This curve is convex and passes through the points (0, ar) and (k, 0). The predator isocline is

$$y = \frac{h(a+x)}{x - d(a+x)},$$

which passes through the point $(k, \frac{h(a+k)}{k-d(a+k)})$ and if d < 1 then $y \to \infty$ as x approaches the straight line $x = \frac{ad}{1-d}$ from the right. We sketch the predator isocline curve and prey isocline curve in the first quadrant (see Figure 2.1).

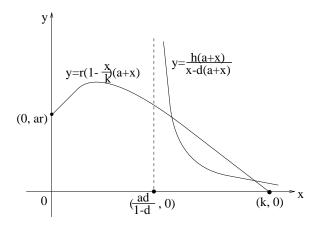


Figure 2.1 The predator and prey isoclines

We assume throughout that 0 < d < 1. Then it follows from the equations that the x component of any equilibrium is less than k. If we fixed the parameters r, k, a, and d, then we can easily see that the number of equilibria of system (1.2) depends on the harvesting rate h. When h is sufficiently large, system (1.2) has no equilibrium, and the species will be driven to extinction. From the point of view of the optimal management of renewable resources, we would like to determine the maximum sustainable yield (abbreviated as MSY) of the harvesting rates to ensure that the predator population can sustain itself. Straightforward calculations show that system (1.2) has a unique positive equilibrium if and only if the parameters (r, k, d, a, h) satisfy

$$\left(d - 1 + \frac{ad}{k}\right)^2 - 4\frac{(1 - d)(adr + h)}{kr} = 0 \quad \text{and} \quad k > \frac{ad}{1 - d}.$$
 (2.1)

The unique positive equilibrium is given by

$$(x_0, y_0) = \left(\frac{k(1-d) - ad}{2(1-d)}, r(1 - \frac{x_0}{k})(a+x_0)\right).$$

Mathematically, the surface, represented by the equation in (2.1), is called the saddle-node bifurcation surface. System (1.2) undergoes a saddle-node bifurcation

when the parameters (r, k, d, a, h) vary from one side to the other side of the surface. When the parameters (r, k, d, a, h) satisfy the following inequality

$$\left(d-1+\frac{ad}{k}\right)^2-4\frac{(1-d)(adr+h)}{kr}>0 \text{ (or } <0) \text{ and } k>\frac{ad}{1-d},$$

system (1.2) has two positive equilibria (or no equilibrium respectively).

In the following we will concentrate on the case when there exist parameter values $(r_0, k_0, d_0, a_0, h_0)$, denoted by λ_0 , such that the unique equilibrium (x_0, y_0) of system (1.2) is degenerate, and the variational matrix of system (1.2) at (x_0, y_0)

$$\left(\begin{array}{ccc}
r - \frac{2rx}{k} - \frac{ay}{(a+x)^2} & -\frac{x}{a+x} \\
\frac{ay}{(a+x)^2} & -d + \frac{x}{a+x}
\end{array}\right)_{(x_0,y_0)}$$

has two zero eigenvalues. This is equivalent to the following conditions:

$$r - \frac{2rx_0}{k} - \frac{ay_0}{(a+x_0)^2} - d + \frac{x_0}{a+x_0} = 0,$$
$$-rd + \frac{2rdx_0}{k} + \frac{ady_0}{(a+x_0)^2} + \frac{rx_0}{a+x_0} - \frac{2rx_0^2}{k(a+x_0)} = 0.$$

According to bifurcation theory ([8] and [12]), we know that under certain nondegeneracy conditions, the equilibrium (x_0, y_0) is a cusp of codimension 2. If we choose suitable bifurcation parameters, then the system undergoes the Bogdanov-Takens bifurcation. In the next section we will introduce the nondegeneracy conditions and show how to choose the bifurcation parameters so that the system exhibits the Bogdanov-Takens bifurcation.

3 Reduction to canonical Bogdanov-Takens family

We consider system (1.2) as the parameters take value λ_0 and rewrite the system in the generic form

$$\dot{x} = f(x, y, \lambda_0),
\dot{y} = q(x, y, \lambda_0).$$
(3.1)

According to the assumptions in Section 2, we know that system (3.1) has an isolated degenerate singular point (x_0, y_0) , $x_0 > 0$, $y_0 > 0$, the trace and the determinant of the variational matrix of system (3.1) at (x_0, y_0) are zero but the variational matrix is not a zero matrix. System (3.1) is C^{∞} smooth with respect to the variables x, y and λ in a small neighborhood of (x_0, y_0, λ_0) . Next, we reduce system (3.1) to canonical form by using normal form theory.

Let $x_1 = x - x_0$, $x_2 = y - y_0$. Then system (3.1) can be transformed into

$$\begin{pmatrix} \dot{x}_1 \\ \dot{x}_2 \end{pmatrix} = Lx + \begin{pmatrix} \langle Px, x \rangle \\ \langle Qx, x \rangle \end{pmatrix} + O(|x|^3), \tag{3.2}$$

where $\langle \cdot, \cdot \rangle$ is a Cartesian product in \mathbb{R}^2 , the term $O(|x|^3)$ is \mathbb{C}^{∞} in all variables, at least to the third order with respect to $x = col(x_1, x_2)$, and the matrices L, P and

Q are defined as follows

$$L = \begin{pmatrix} \frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} \\ \\ \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} \end{pmatrix}_{(x_0, y_0, \lambda_0)} \qquad \stackrel{\triangle}{=} \begin{pmatrix} a & b \\ c & d \end{pmatrix},$$

$$P = \begin{pmatrix} \frac{\partial^2 f}{\partial x^2} & \frac{\partial^2 f}{\partial x \partial y} \\ \frac{\partial^2 f}{\partial x \partial y} & \frac{\partial^2 f}{\partial y^2} \end{pmatrix}_{(x_0, y_0, \lambda_0)} \stackrel{\triangle}{=} \begin{pmatrix} p_{11} & p_{12} \\ p_{21} & p_{22} \end{pmatrix},$$

$$Q = \begin{pmatrix} \frac{\partial^2 g}{\partial x^2} & \frac{\partial^2 g}{\partial x \partial y} \\ & & & \\ \frac{\partial^2 g}{\partial x \partial y} & \frac{\partial^2 g}{\partial y^2} \end{pmatrix}_{(x_0, y_0, \lambda_0)} \stackrel{\triangle}{=} \begin{pmatrix} q_{11} & q_{12} \\ q_{21} & q_{22} \end{pmatrix}.$$

By the above assumptions, the matrix L is similar to the Jordan block form $\begin{pmatrix} 0 & 1 \\ 0 & 0 \end{pmatrix}$. Hence $b^2 + c^2 \neq 0$. Assume that $b \neq 0$. Making the linear change of variables y = Mx, where $M = \begin{pmatrix} 1 & 0 \\ a & b \end{pmatrix}$ (if b = 0 and $c \neq 0$, then set $M = \begin{pmatrix} 0 & 1 \\ c & -d \end{pmatrix}$), system (3.2) becomes

$$\begin{pmatrix} \dot{y}_1 \\ \dot{y}_2 \end{pmatrix} = MLM^{-1} \begin{pmatrix} y_1 \\ y_2 \end{pmatrix} + M \begin{pmatrix} \langle (M^{-1})^T P M^{-1} y, y \rangle \\ \langle (M^{-1})^T Q M^{-1} y, y \rangle \end{pmatrix} + O(|y|^3),$$

or in an abstract form

$$\dot{y} = Ay + h^2(y) + O(|y|^3), \tag{3.3}$$

where

$$A = \left(\begin{array}{cc} 0 & 1 \\ bc - ad & a + d \end{array}\right) = \left(\begin{array}{cc} 0 & 1 \\ 0 & 0 \end{array}\right),$$

the components of the vector function $h^2(y) \in C^{\infty}(\mathbb{R}^2, \mathbb{R}^2)$ are the homogeneous polynomials of degree 2 given by

$$h^{2}(y) = \begin{pmatrix} (p_{11} - \frac{2a}{b}p_{12} + \frac{a^{2}}{b^{2}}p_{22})y_{1}^{2} + (\frac{2}{b}p_{12} - \frac{2a}{b^{2}}p_{22})y_{1}y_{2} + \frac{1}{b^{2}}p_{22}y_{2}^{2} \\ d_{1}y_{1}^{2} + \bar{d}_{1}y_{1}y_{2} + (\frac{a}{b^{2}}p_{22} + \frac{1}{b}q_{22})y_{2}^{2} \end{pmatrix},$$

 $d_1 = ap_{11} - \frac{2a^2}{b}p_{12} + \frac{a^3}{b^2}p_{22} + bq_{11} - 2aq_{12} + \frac{a^2}{b}q_{22}$, and $\bar{d}_1 = \frac{2a}{b}p_{12} - \frac{2a^2}{b^2}p_{22} + 2q_{12} - \frac{2a}{b}q_{22}$. By the theory of normal forms, there exists a C^{∞} change of variables of system (2.3) in a small neighborhood of (0,0),

$$\left(\begin{array}{c} z_1 \\ z_2 \end{array} \right) = \left(\begin{array}{c} y_1 \\ y_2 \end{array} \right) + \left(\begin{array}{c} -\frac{1}{2} (\frac{2}{b} p_{12} - \frac{a}{b^2} p_{22} + \frac{1}{b} q_{22}) y_1^2 - \frac{1}{b^2} p_{22} y_1 y_2 \\ (p_{11} - \frac{2a}{b} p_{12} + \frac{a^2}{b^2}) y_1^2 - (\frac{a}{b^2} p_{22} + \frac{1}{b} q_{22}) y_1 y_2 \end{array} \right),$$

i.e.,

$$\begin{pmatrix} y_1 \\ y_2 \end{pmatrix} = \begin{pmatrix} z_1 \\ z_2 \end{pmatrix} + \begin{pmatrix} \frac{1}{2} (\frac{2}{b} p_{12} - \frac{a}{b^2} p_{22} + \frac{1}{b} q_{22}) z_1^2 + \frac{1}{b^2} p_{22} z_1 z_2 \\ -(p_{11} - \frac{2a}{b} p_{12} + \frac{a^2}{b^2}) z_1^2 + (\frac{a}{b^2} p_{22} + \frac{1}{b} q_{22}) z_1 z_2 \end{pmatrix}$$

such that system (3.3) can be written as

$$\begin{pmatrix} \dot{z}_1 \\ \dot{z}_2 \end{pmatrix} = A \begin{pmatrix} z_1 \\ z_2 \end{pmatrix} + \begin{pmatrix} 0 \\ d_1 z_1^2 + d_2 z_1 z_2 \end{pmatrix} + O(|z|^3), \tag{3.4}$$

where $d_2 = 2q_{12} + 2p_{11} - (p_{12} + p_{22})\frac{2a}{b}$. If $d_1d_2 \neq 0$, then the singular point (x_0, y_0) of system (3.1) is a cusp of codim 2 by the qualitative theory of ordinary differential equations and the theory of differential manifolds. The condition $d_1d_2 \neq 0$ is called the nondegeneracy condition of the cusp type of codimension 2 for the equilibrium (x_0, y_0) of system (3.1). Moreover, we might as well assume that $d_1 > 0$.

From the above analysis, we obtain the following lemma.

Lemma 3.1 If $d_1d_2 \neq 0$, then in a small neighborhood of (x_0, y_0, λ_0) , system (1.2) is C^{∞} equivalent to

$$\dot{x}_1 = x_2 + w_1(x, \lambda),
\dot{x}_2 = d_1 x_1^2 + d_2 x_1 x_2 + w_2(x, \lambda),$$
(3.5)

where $\lambda = (r, k, d, a, h)$, $w_1, w_2 \in C^{\infty}(R^2 \times R^5, R^2)$ and $w_1(x, \lambda_0), w_2(x, \lambda_0)$ are power series in (x_1, x_2) of powers $x_1^i x_2^j$ satisfying $i + j \geq 3$.

Lemma 3.2 In a small neighborhood of $(0,0,\lambda_0)$, system (3.5) is C^{∞} equivalent to

$$\dot{y}_1 = y_2,
\dot{y}_2 = \phi_1(\lambda) + \phi_2(\lambda)y_1 + y_1^2 + y_2(\psi(\lambda) + \Phi(y_1, \lambda)) + y_2^2 \Psi(y, \lambda),$$
(3.6)

where $\Phi, \Psi \in C^{\infty}$ and $\Phi(y_1, \lambda_0) = \frac{d_2}{\sqrt{d_1}} y_1 \neq 0$, $\Psi(y, \lambda_0) = 0$, $\phi_1(\lambda_0) = \phi_2(\lambda_0) = \psi(\lambda_0) = 0$.

Proof Consider the λ -dependent change of coordinates

$$z_1 = x_1, \quad z_2 = x_2 + w_1(x, \lambda).$$

Then system (3.5) is transformed into

$$\dot{z}_1 = z_2,
\dot{z}_2 = P_1(z_1, \lambda) + z_2 \Phi_1(z_1, \lambda) + z_2^2 \Psi_1(z, \lambda),$$
(3.7)

where $P_1, \Phi_1, \Psi_1 \in C^{\infty}$ and

$$P_1(0, \lambda_0) = \frac{\partial P_1(0, \lambda_0)}{\partial z_1} = 0, \ \frac{\partial^2 P_1(0, \lambda_0)}{\partial z_1^2} = 2d_1 \neq 0,$$

$$\Phi_1(0,\lambda_0) = 0, \ \frac{\partial \Phi_1(0,\lambda_0)}{\partial z_1} = d_2 \neq 0.$$

Applying the Malgrange Preparation Theorem (see [7], pp. 43) to the function $P_1(z_1, \lambda)$, we have

$$P_1(z_1, \lambda) = (\phi_1(\lambda) + \phi_2(\lambda)z_1 + z_1^2)B(z_1, \lambda),$$

where $\phi_1, \phi_2, B \in C^{\infty}$ and $B(0, \lambda_0) = d_1 \neq 0, \phi_i(\lambda_0) = 0, i = 1, 2.$

Hence, system (3.7) becomes

$$\dot{z}_1 = z_2,$$

$$\dot{z}_2 = \left(\phi_1(\lambda) + \phi_2(\lambda)z_1 + z_1^2 + z_2 \frac{\Phi_1(z_1, \lambda)}{B(z_1, \lambda)} + z_2^2 \frac{\Psi_1(z, \lambda)}{B(z_1, \lambda)}\right) B(z_1, \lambda).$$
(3.8)

Since $\Phi_1(0,\lambda_0) = 0$ and $\frac{\partial \Phi_1(0,\lambda_0)}{\partial z_1} = d_2 \neq 0$, there exists a function $\psi(\lambda)$ such that $\frac{\Phi_1(0,\lambda)}{\sqrt{B(0,\lambda)}} = \psi(\lambda)$. Set

$$y_1 = z_1, \ y_2 = \frac{z_2}{\sqrt{B(z_1, \lambda)}}, \ \tau = \int_0^t \sqrt{B(z_1(s), \lambda)} ds,$$

$$\Phi(z_1,\lambda) = \frac{\Phi_1(z_1,\lambda)}{\sqrt{B(z_1,\lambda)}} - \psi(\lambda), \ \Psi(z,\lambda) = \frac{\Psi_1(z,\lambda)}{B(z_1,\lambda)}.$$

We can transform system (3.8) into system (3.6). This completes the proof. \Box

In the following theorem we show how to choose the bifurcation parameters such that the system exhibits the Bogdanov-Takens bifurcation.

Theorem 3.3 If the rank of the matrix

$$\begin{pmatrix}
\frac{\partial(\phi_1(\lambda) - \frac{1}{4}\phi_2^2(\lambda))}{\partial \lambda_1} & \cdots & \frac{\partial(\phi_1(\lambda) - \frac{1}{4}\phi_2^2(\lambda))}{\partial \lambda_5} \\
\frac{\partial(\psi(\lambda) - \frac{d_2}{2\sqrt{d_1}}\phi_2(\lambda))}{\partial \lambda_1} & \cdots & \frac{\partial(\psi(\lambda) - \frac{d_2}{2\sqrt{d_1}}\phi_2(\lambda))}{\partial \lambda_5}
\end{pmatrix}_{\lambda_0}$$

is two, then we can choose two bifurcation parameters such that system (1.2) undergoes the Boqdanov-Takens bifurcation.

Proof By using the C^{∞} equivalences in Lemmas 3.1 and 3.2, we have transformed system (3.1) into the parameter dependent system (3.6). Let $x_1 = y_1 + \frac{1}{2}\phi_2(\lambda)$, $x_2 = y_2$. System (3.6) can be written as

$$\dot{r}_1 \equiv r_2$$

$$\dot{x}_2 = \phi_1(\lambda) - \frac{1}{4}\phi_2^2(\lambda) + \left(\psi(\lambda) - \frac{d_2}{2\sqrt{d_1}}\phi_2(\lambda)\right)x_2 + x_1^2 + \frac{d_2}{\sqrt{d_1}}x_1x_2 + Q(x,\lambda),\tag{3.9}$$

where $Q(x,\lambda)$ is a power series in (x_1,x_2) with powers $x_1^i x_2^j$ satisfying $i+j \geq 3$ and coefficients depending on $(\lambda_1,\ldots,\lambda_5)$.

Without loss of generality, we assume that the determinant of the matrix

$$\begin{pmatrix}
\frac{\partial(\phi_1(\lambda) - \frac{1}{4}\phi_2^2(\lambda))}{\partial \lambda_1} & \frac{\partial(\phi_1(\lambda) - \frac{1}{4}\phi_2^2(\lambda))}{\partial \lambda_2} \\
\frac{\partial(\psi(\lambda) - \frac{d_2}{2\sqrt{d_1}}\phi_2(\lambda))}{\partial \lambda_1} & \frac{\partial(\psi(\lambda) - \frac{d_2}{2\sqrt{d_1}}\phi_2(\lambda))}{\partial \lambda_2}
\end{pmatrix}_{\lambda_0}$$

is not zero. Denote

$$\mu_1 = \phi_1(\lambda) - \frac{1}{4}\phi_2^2(\lambda), \ \mu_2 = \psi(\lambda) - \frac{d_2}{2\sqrt{d_1}}\phi_2(\lambda), \ \mu_3 = \lambda_3, \ \mu_4 = \lambda_4, \ \mu_5 = \lambda_5.$$

Obviously, the parameter transformation is nonsingular. System (3.9) can be rewritten as

$$\dot{x}_1 = x_2,
\dot{x}_2 = \mu_1 + \mu_2 x_2 + x_1^2 + \frac{d_2}{\sqrt{d_1}} x_1 x_2 + Q(x, \mu).$$
(3.10)

By the theorems in [2, 3] and [13], we know that system (3.10) is strongly topologically equivalent to

$$\dot{x}_1 = x_2,
\dot{x}_2 = \mu_1 + \mu_2 x_2 + x_1^2 \pm x_1 x_2,$$
(3.11)

where $\pm = sign(\frac{d_2}{d_1})$. Therefore, we can choose μ_1 and μ_2 as the bifurcation parameters such that system (1.1) undergoes the Bogdanov-Takens bifurcation (i.e., bifurcation of cusp singularity of codim 2).

4 An example

In this section, as an example we consider system (1.2) with fixed r, k and a, that is, we consider the following model

$$\dot{x} = x \left(1 - \frac{x}{2} \right) - \frac{xy}{1+x},$$

$$\dot{y} = y \left(-d + \frac{x}{1+x} \right) - h,$$
(4.1)

where d and h are parameters. We will show that d and h in fact are the bifurcation parameters and system (4.1) exhibits the Bogdanov-Takens bifurcation.

From the analysis in Section 2 and Section 3, we know that the positive equilibrium $(x_0, y_0) = (1.12415, 0.930219)$ is a cusp of codimension 2 when $(d_0, h_0) = (0.19891, 0.30726)$.

Now we study the dynamics of system (4.1) when the parameters d and h vary in a small neighborhood of (d_0, h_0) . We use a series of changes of coordinates to transform system (4.1) into the canonical family in Section 3. Consider

$$\dot{x} = x \left(1 - \frac{x}{2} \right) - \frac{xy}{1+x},
\dot{y} = y \left(-d_0 + \lambda_1 + \frac{x}{1+x} \right) - h_0 + \lambda_2,$$
(4.2)

where λ_1 and λ_2 are small parameters.

Let $x_1 = x - x_0$, $x_2 = y - y_0$, then system (4.2) becomes

$$\dot{x}_{1} = \left(1 - x_{0} - \frac{y_{0}}{(1+x_{0})^{2}}\right) x_{1} - \frac{x_{0}}{1+x_{0}} x_{2} + \left(-\frac{1}{2} + \frac{2-x_{0}}{2(1+x_{0})^{2}}\right) x_{1}^{2}
- \frac{1}{(1+x_{0})^{2}} x_{1} x_{2} + P_{1}(x_{1}, x_{2}),
\dot{x}_{2} = y_{0} \lambda_{1} + \lambda_{2} + \frac{y_{0}}{(1+x_{0})^{2}} x_{1} + \left(-d_{0} + \lambda_{1} + \frac{x_{0}}{1+x_{0}}\right) x_{2}
- \frac{y_{0}}{(1+x_{0})^{3}} x_{1}^{2} + \frac{1}{(1+x_{0})^{2}} x_{1} x_{2} + P_{2}(x_{1}, x_{2}),$$
(4.3)

where P_1 and P_2 are power series in (x_1, x_2) with powers $x_1^i x_2^j$ satisfying $i + j \ge 3$. Denote

$$a = 1 - x_0 - \frac{y_0}{(1 + x_0)^2}, \ b = -\frac{x_0}{1 + x_0}, \ c = \frac{y_0}{(1 + x_0)^2}, \ d = -d_0 + \lambda_1 + \frac{x_0}{1 + x_0};$$

$$p_{11} = -\frac{1}{2} + \frac{2 - x_0}{2(1 + x_0)^2}, \ p_{12} = -\frac{1}{2(1 + x_0)^2}, \ q_{11} = -\frac{y_0}{(1 + x_0)^3}, \ q_{12} = \frac{1}{2(1 + x_0)^2}.$$

Making the affine transformation

$$y_1 = x_1, \ y_2 = ax_1 + bx_2,$$

we see that system (4.3) becomes

$$\dot{y}_{1} = y_{2} + \left(p_{11} - \frac{2ap_{12}}{b}\right)y_{1}^{2} + \frac{2p_{12}}{b}y_{1}y_{2} + Q_{1}(y_{1}, y_{2}),$$

$$\dot{y}_{2} = b(y_{0}\lambda_{1} + \lambda_{2}) + a\lambda_{1}y_{1} + \lambda_{1}y_{2} + \left(ap_{11} - \frac{2a^{2}p_{12}}{b} + bq_{11} - 2aq_{12}\right)y_{1}^{2}$$

$$+ \left(\frac{2ap_{12}}{b} + 2q_{12}\right)y_{1}y_{2} + Q_{2}(y_{1}, y_{2}).$$

$$(4.4)$$

Here Q_1 and Q_2 are power series in (y_1, y_2) with powers $y_1^i y_2^j$ satisfying $i + j \ge 3$. Consider the C^{∞} change of coordinates in a small neighborhood of (0,0)

$$z_1 = y_1 - \frac{p_{12}}{b}y_1^2$$
, $z_2 = y_2 + \left(p_{11} - \frac{2ap_{12}}{b}\right)y_1^2$.

Then system (4.4) is transformed into

$$\dot{z}_1 = z_2 + R_1(z_1, z_2),$$

$$\dot{z}_{2} = b(y_{0}\lambda_{1} + \lambda_{2}) + a\lambda_{1}z_{1} + \lambda_{1}z_{2} + \left(2p_{11} - \frac{2ap_{12}}{b} + 2q_{12}\right)z_{1}z_{2}
+ \left(ap_{11} - \frac{2a^{2}p_{12}}{b} + bq_{11} - 2aq_{12} + \frac{p_{12}a}{b}\lambda_{1} - \lambda_{1}(p_{11} - \frac{2ap_{12}}{b})\right)z_{1}^{2}
+ R_{2}(z_{1}, z_{2}).$$
(4.5)

Here R_1 and R_2 are power series in (z_1, z_2) with powers $z_1^i z_2^j$ satisfying $i + j \ge 3$. We choose the C^{∞} change of coordinates in a small neighborhood of (0,0)

$$x_1 = z_1, \ x_2 = z_2 + R_1(z_1, z_2),$$

so that system (4.5) becomes

$$\dot{x}_1 = x_2,$$

$$\dot{x}_{2} = b(y_{0}\lambda_{1} + \lambda_{2}) + a\lambda_{1}x_{1} + \lambda_{1}x_{2} + \left(2p_{11} - \frac{2ap_{12}}{b} + 2q_{12}\right)x_{1}x_{2} + F_{1}(x_{1}) + \left(ap_{11} - \frac{2a^{2}p_{12}}{b} + bq_{11} - 2aq_{12} + \frac{p_{12}a}{b}\lambda_{1} - \lambda_{1}(p_{11} - \frac{2ap_{12}}{b})\right)x_{1}^{2} + x_{2}F_{2}(x_{1}) + x_{2}^{2}F_{3}(x_{1}, x_{2}).$$

$$(4.6)$$

Here F_1 , F_2 and F_3 are power series in x_1 and (x_1, x_2) with powers $x_1^{k_1}$, $x_1^{k_2}$ and $x_1^i x_2^j$ satisfy $k_1 \geq 3$, $k_2 \geq 2$ and $i + j \geq 1$, respectively.

We substitute values of $a, b, c, d, p_{11}, p_{12}, q_{11}$ and q_{12} for the above system and obtain the following equations

$$\dot{x}_1 = x_2,
\dot{x}_2 = 0.52922(0.93022\lambda_1 + \lambda_2) - 0.33032\lambda_1x_1 + \lambda_1x_2 - 0.44592x_1x_2
+ F_1(x_1) + (0.211978 - 0.19545\lambda_1)x_1^2 + x_2F_2(x_1) + x_2^2F_3(x_1, x_2),$$
(4.7)

Applying the Malgrange Preparation Theorem, we have

$$0.52922(0.93022\lambda_1 + \lambda_2) - 0.33032\lambda_1x_1 + (0.211978 - 0.19545\lambda_1)x_1^2 + F_1(x_1)$$

$$= \left(x_1^2 - \frac{0.33032\lambda_1}{0.211978 - 0.19545\lambda_1}x_1 + \frac{0.52922(0.93022\lambda_1 + \lambda_2)}{0.211978 - 0.19545\lambda_1}\right)B_1(x_1, \lambda),$$

where $B_1(0,\lambda) = 0.211978 - 0.19545\lambda_1$ and B_1 is a power series in x_1 whose coefficients depend on parameters $\lambda = (\lambda_1, \lambda_2)$.

Let
$$y_1 = x_1, \ y_2 = \frac{x_2}{\sqrt{B_1(x_1,\lambda)}}, \ \tau = \int_0^t \sqrt{B_1(x_1(s),\lambda)} ds$$
. Then system (4.7)

becomes

$$\dot{y}_{2} = \frac{0.52922(0.93022\lambda_{1} + \lambda_{2})}{0.211978 - 0.19545\lambda_{1}} - \frac{0.33032\lambda_{1}}{0.211978 - 0.19545\lambda_{1}} y_{1}
+ y_{1}^{2} + \frac{\lambda_{1}}{\sqrt{B_{1}(y_{1}, \lambda)}} y_{2} - \frac{0.44592}{\sqrt{B_{1}(y_{1}, \lambda)}} y_{1} y_{2} + G(y_{1}, y_{2}, \lambda),$$
(4.8)

where $\dot{y}_1 = \frac{dy_1}{d\tau}$, $\dot{y}_2 = \frac{dy_2}{d\tau}$, $G(y_1, y_2, 0)$ is a power series in (y_1, y_2) with power $y_1^i y_2^j$ satisfying $i + j \geq 3$ and $j \geq 2$.

Making the parameter dependent affine transformation in (4.8)

$$x_1 = y_1 - \frac{0.33032\lambda_1}{2(0.211978 - 0.19545\lambda_1)}, \quad x_2 = y_2,$$

we have

$$\dot{x}_1 = x_2$$

$$\dot{x}_{2} = \frac{0.52922(0.93022\lambda_{1} + \lambda_{2})}{0.211978 - 0.19545\lambda_{1}} - \left(\frac{0.33032\lambda_{1}}{2(0.211978 - 0.19545\lambda_{1})}\right)^{2} + x_{1}^{2} + \frac{0.65257\lambda_{1} + \alpha_{1}(\lambda)}{\sqrt{B_{1}(\frac{0.33032\lambda_{1}}{2(0.211978 - 0.19545\lambda_{1})}, \lambda)}} x_{2} - (0.96853 + \alpha_{2}(\lambda))x_{1}x_{2} + R(x_{1}, x_{2}, \lambda), \tag{4.9}$$

where $\alpha_1(0,\lambda_2) = 0$, $\frac{\partial \alpha_1(0,\lambda_2)}{\partial \lambda_1} = 0$, $\alpha_2(0) = 0$, and $R(x_1,x_2,0)$ is a power series in (x_1,x_2) with powers $x_1^i x_2^j$ satisfying $i+j \geq 3$ and $j \geq 2$.

For the sake of convenience, we assume that

$$\mu_1(\lambda_1, \lambda_2) = \frac{0.52922(0.93022\lambda_1 + \lambda_2)}{0.211978 - 0.19545\lambda_1} - \left(\frac{0.33032\lambda_1}{2(0.211978 - 0.19545\lambda_1)}\right)^2,$$

$$\mu_2(\lambda_1, \lambda_2) = \frac{0.65257\lambda_1 + \alpha_1(\lambda)}{\sqrt{B_1(\frac{0.33032\lambda_1}{2(0.211978 - 0.19545\lambda_1)}, \lambda)}},$$

which is a nonsingular parameter transformation. System (4.9) can be rewritten as

$$\dot{x}_1 = x_2,
\dot{x}_2 = \mu_1(\lambda_1, \lambda_2) + \mu_2(\lambda_1, \lambda_2)x_2 + x_1^2 - 0.96853x_1x_2 + S(x_1, x_2, \mu),$$
(4.10)

where $S(x_1, x_2, \mu)$ is a power series in (x_1, x_2, μ_1, μ_2) with powers $x_1^i x_2^j \mu_1^k \mu_2^l$ satisfying $i + j + k + l \ge 4$ and $i + j \ge 3$.

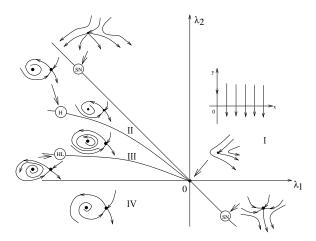


Figure 4.1 The bifurcation set and the corresponding phase portraits for system (4.2)

By Theorem 3.3, we know that system (4.10) undergoes the Bogdanov-Takens bifurcation when the parameters vary in a small neighborhood of the origin. The local representations of the bifurcation curves in the small neighborhood of the origin are as follows:

(a) The saddle-node bifurcation curve

$$SN = \{(\lambda_1, \lambda_2) : \mu_1(\lambda_1, \lambda_2) = 0\}.$$

From the expression for $\mu_1(\lambda_1,\lambda_2)$, we can see that SN is approximately a straight line when λ_1 is small. On the curve SN, system (4.10) has only a unique equilibrium which is a saddle-node. Some solutions of system (4.10) tend to the saddle-node and others either leave the first quadrant or increase without bound depending on the initial conditions (see Figure 4.1). If the parameter λ_1 and λ_2 satisfy $\mu_1(\lambda_1,\lambda_2)>0$, then system (4.10) has no equilibrium. Hence all predator will tend to extinction. From this we can see that the harvesting rate must be limited, since otherwise the population cannot sustain itself. If the parameter λ_1 and λ_2 satisfy $\mu_1(\lambda_1,\lambda_2)<0$, then system (4.10) has two positive equilibria. One is a hyperbolic saddle and the other is a focus. The trajectories of system (4.10) can either tend to an equilibrium or oscillate depending on the parameters.

(b) The Hopf bifurcation curve

$$H = \{(\lambda_1, \lambda_2) : \mu_2(\lambda_1, \lambda_2) = -0.96853\sqrt{-\mu_1(\lambda_1, \lambda_2)}, \mu_1(\lambda_1, \lambda_2) < 0\}.$$

When the parameters lie between the curve SN and the curve H, system (4.10) has a hyperbolic saddle and a stable hyperbolic focus and no periodic orbit. On the curve H system (4.10) has a hyperbolic saddle and a weak focus of degree one. The focus is stable and there are no periodic orbits.

(c) The homoclinic bifurcation curve

$$HL = \{(\lambda_1, \lambda_2) : \mu_2(\lambda_1, \lambda_2) = -0.6918\sqrt{-\mu_1(\lambda_1, \lambda_2)}, \mu_1(\lambda_1, \lambda_2) < 0\}.$$

When the parameters lie between the curve H and the curve HL, system (4.10) has a unique stable limit cycle. However, system (4.10) has a hyperbolic saddle, an unstable focus, and no periodic orbits when the parameters lie between the curve HL and the curve SN (see Figure 4.1). On the HL curve, system (4.10) has an unstable focus and a stable homoclinic loop.

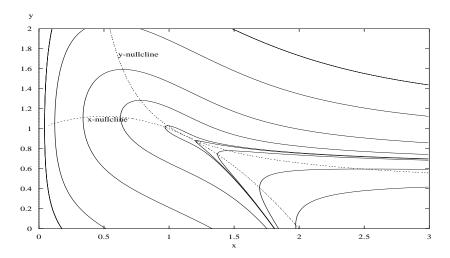


Figure 4.2 When $(\lambda_1, \lambda_2) = (0, 0)$, the unique positive equilibrium is a cusp of codimension 2.

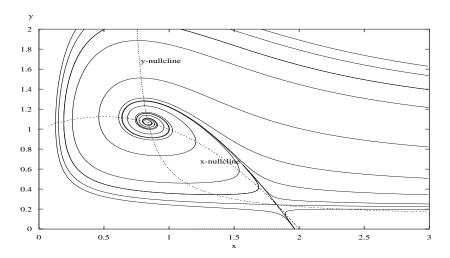


Figure 4.3 When $(\lambda_1, \lambda_2) = (-0.20109, 0.24726)$ lies in the region II, there are two positive equilibria, a saddle and a stable focus.

Numerical simulations (using XPP) of system (4.2) are depicted in Figures 4.2 - 4.6. When $(\lambda_1, \lambda_2) = (0, 0)$, that is, when $(d_0, h_0) = (0.19891, 0.30726)$, there is a unique positive equilibrium $(x_0, y_0) = (1.12415, 0.930219)$, which is a cusp of

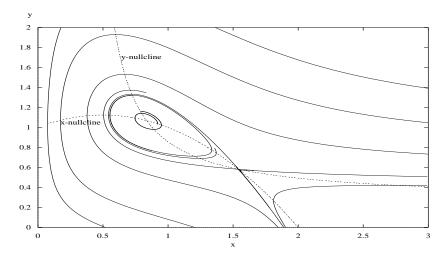


Figure 4.4 When $(\lambda_1, \lambda_2) = (-0.07442, 0.11323)$ lies in the region III, the stable focus becomes unstable and there is a stable periodic orbit.

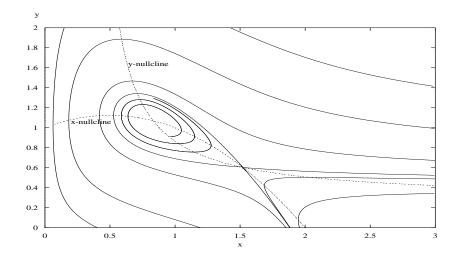


Figure 4.5 When $(\lambda_1, \lambda_2) = (-0.06224, 0.10088)$ lies on the HL curve, there is a homoclinic loop.

codimension 2 (Figure 4.2). When (λ_1, λ_2) varies, there is a saddle-node bifurcation. When $(\lambda_1, \lambda_2) = (-0.20109, 0.24726)$ lies in the region II, two positive equilibria bifurcate from the saddle-node, one is a saddle and the other is a stable focus (Figure 4.3). As (λ_1, λ_2) keeps varying, there is a Hopf bifurcation. When $(\lambda_1, \lambda_2) = (-0.07442, 0.11323)$ lies in the region III, the stable focus becomes unstable and a stable periodic orbit bifurcates from the focus (Figure 4.4). When (λ_1, λ_2) changes to (-0.06224, 0.10088), the periodic orbit expands and reaches the stable and unstable manifolds of the saddle to create a homoclinic loop (Figure 4.5). When $(\lambda_1, \lambda_2) = (-0.04224, 0.07668)$ lies in the region IV, the homoclinic loop is broken, there are an unstable focus and a saddle (Figure 4.6).

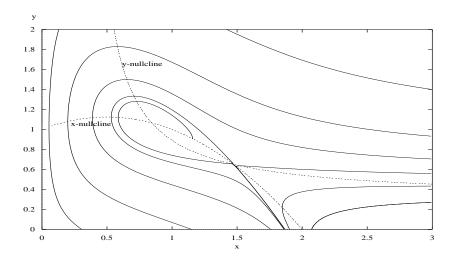


Figure 4.6 When $(\lambda_1, \lambda_2) = (-0.04224, 0.07668)$ lies in the region IV, there is an unstable focus and a saddle.

Acknowledgements

We would like to thank the referee for helpful comments and suggestions and Gail Wolkowicz for careful reading and corrections.

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