Acta Mathematicae Applicatae Sinica, English Series
Vol. 20, No. 1 (2004) 167–178

Acta Mathematicae Applicatae
Sinica, English Series

Analyses of Bifurcations and Stability in a Predator-prey System with Holling Type-IV Functional Response

Ji-cai Huang[1], **Dong-mei Xiao**[2]

[1]Academy of Mathematics and Systems Science, Academia Sinica, Beijing 100080, China
(E-mail: hjc@mail.amss.ac.cn)
[2]Department of Mathematics, Shanghai Jiao Tong University, Shanghai 200030, China

Abstract In this paper the dynamical behaviors of a predator-prey system with Holling Type-IV functional response are investigated in detail by using the analyses of qualitative method, bifurcation theory, and numerical simulation. The qualitative analyses and numerical simulation for the model indicate that it has a unique stable limit cycle. The bifurcation analyses of the system exhibit static and dynamical bifurcations including saddle-node bifurcation, Hopf bifurcation, homoclinic bifurcation and bifurcation of cusp-type with codimension two (ie, the Bogdanov-Takens bifurcation), and we show the existence of codimension three degenerated equilibrium and the existence of homoclinic orbit by using numerical simulation.

Keywords Predator-prey system, Limit cycle, Bogdanov-Takens bifurcation
2000 MR Subject Classification 92B05, 34D05

1 Introduction

In population dynamics, a functional response of the predator to the prey density refers to the change in the density of prey attached per unit time per predator as the prey density changes. The simplest functional response is Lotka-Volterra function which is described as

$$P(x) = ax, \qquad 0 \le x \le \frac{k}{a}; \qquad P(x) = k, \qquad x \ge \frac{k}{a}, \tag{P_1}$$

which is also called Holling Type-I function in [8]. Michaelis and Menten proposed the response function

$$P(x) = \frac{mx}{a+x}. \tag{P_2}$$

in studying enzymatic reactions, where $m > 0$ denotes the maximal growth rate of the species and $a > 0$ is the half-saturation constant. It is now referred to as a Michaelis-Menten function or a Holling type-II function. Another class of response function is

$$P(x) = \frac{mx^2}{a+bx+x^2}, \tag{P_3}$$

which is called Sigmoidal response function, while the simplification

$$P(x) = \frac{mx^2}{a+x^2}, \tag{P_4}$$

Manuscript received May 23, 2003. Revised November 6, 2003.
[1] Supported by Chinese Academy of Sciences (KZCX2-SW-118);
[2] Supported by the NNSF of China (No. 10071027; No. 10231020).

is known as a Holling type-III function. However , $P(x)$ in $(P_1)-(P_4)$ is monotonic in the first quadrant. But some experiments and observations indicate that the nonmonotonic response occurs at this level: when the nutrient concentration reaches a high level an inhibitory effect on the specific growth rate may occur. To model such an inhibitory effect, Andrews[2] suggested a function

$$P(x)=\frac{mx}{a+bx+x^2}, \tag{P_5}$$

called the Monod-Haldane function , and also called a Holling type-IV function.Sokol and Howell[12] proposed a simplified Holling Type-IV function of the form

$$P(x)=\frac{mx}{a+x^2}. \tag{P_6}$$

Recently, Ruan and Xiao considered the predator-prey model with the simplified Holling type-IV function (P_6)

$$\begin{aligned}\dot{x}&=rx(1-\frac{x}{K})-\frac{xy}{a+x^2},\\ \dot{y}&=y(\frac{\mu x}{a+x^2}-D).\end{aligned} \tag{A}$$

The model describes the predator-prey interaction when the prey exhibits group defense, which was first proposed by Freedman and Wolkowicz[7], Mischaikow and Wolkowicz[9], and Wolkowicz[14] in a general form,

$$\begin{aligned}\dot{x}&=xg(x,K)-yp(x),\\ \dot{y}&=y(q(x)-D),\end{aligned} \tag{B}$$

where for the biological implications refer to [7,9,11,14] and to references therein. In [11] they analyzed the global dynamics of system (A) and showed that system (A) has a bifurcation of cusp-type with codimension two, but no bifurcations of codimension three.

In this paper, we consider the dynamics of a predator-prey system with Holling type-IV function as follows:

$$\begin{aligned}\dot{x}&=rx(1-\frac{x}{K})-\frac{xy}{a+bx+x^2},\\ \dot{y}&=y(\frac{\mu x}{a+bx+x^2}-D),\end{aligned} \tag{1}$$

where x and y are functions of time representing population densities of prey and predator, respectively. Thus, we only restrict our attention to system (1) in the closed first quadrant in the (x,y) plane. $K>0$ is the carrying capacity of the prey and $D>0$ is the death rate of the predator, and $r>0$ is the maximum growth rate of the prey, $\mu>0$ is the maximum predation rate , and $a>0$ is the so-called half-saturation constant.The parameter b is such that the denominator of above system does not vanish for non-negative x and $b>-2\sqrt{a}$. Therefore we study the dynamics of system (1) for $b>-2\sqrt{a}$ in the closed first quadrant of the (x,y) plane. We show that the system exhibits "paradox enrichment" and a unique stable limit cycle by qualitative analyses and numerical simulation. And on the basis of bifurcation analysis, we show that the system exhibits static and dynamical bifurcations including the saddle-node bifurcation, Hopf bifurcation,and homoclinic bifurcation. Moreover, system (1) has the cusp bifurcation of codimension 2 (i,e,Bogdanov-Takens bifurcation) and a degenarated equilibrium with codimension three.

This paper is organized as follows.The conditions for the existence of equilibria and limit cycles, the uniqueness of limit cycle for system (1) are given in Section 2. Saddle-node bifurcation, Hopf bifurcation , Homoclinic bifurcation and the Bogdanov-Takens bifurcation are obtained in Section 3. The biological explanation of the results is given in Section 4.

2 Qualitative Analysis of System (1)

In this section, we discuss the existence and stability of positive equilibria of system (1) in the closed first quadrant. And we show that system (1) has a unique limit cycle for some values of the parameters, and system (1) has not any closed orbits for some other values of the parameters. Some numerical simulations of system (1) are given.

It is clear that the solutions of system (1) with positive initial values are positive and bounded; and there is a hyperbolic saddle point at the origin and an equilibrium $(K, 0)$ on the x-axis for all permissible parameters. From (1), we can see that if there is a positive equilibrium, then we have the equation

$$\frac{\mu x}{a+bx+x^2} - D = 0.$$

For the sake of simplicity, we denote $d_1 = (\mu - bD)^2 - 4aD^2,\ d_2 = \mu - bD,\ d_3 = \frac{\mu - bD}{2D},\ d_4 = \frac{\mu - bD}{D}$. After some calculation, it's easy to check that the surface $SN = \{(\mu, b, D, a, K) :|\ 0 < d_3 < K, d_1 = 0\}$ is a *Saddle-Node bifurcation* surface, i.e. on one side of the surface SN system (1) has not any positive equilibria; on the surface SN system (1) has only one positive equilibrium; on the other side of the surface SN system (1) has two positive equilibria. Thus, system (1) has at most four equilibria: $(0, 0), (K, 0)$, and two positive equilibria $(x_1, y_1), (x_2, y_2)$, where

$$x_1 = \frac{\mu - bD - \sqrt{(\mu - bD)^2 - 4aD^2}}{2D}, \qquad y_1 = r\Big(1 - \frac{x_1}{K}\Big)(a + bx_1 + x_1^2),$$
$$x_2 = \frac{\mu - bD + \sqrt{(\mu - bD)^2 - 4aD^2}}{2D}, \qquad y_2 = r\Big(1 - \frac{x_2}{K}\Big)(a + bx_2 + x_2^2).$$

We also denote $d_0 = \frac{a+2bx_1+3x_1^2}{b+2x_1} = \frac{2\mu - \sqrt{(\mu-bD)^2-4aD^2}}{\mu - \sqrt{(\mu-bD)^2-4aD^2}} x_1$.

The characteristic equation of the Jacobian matrix at the equilibrium (x, y) of system (1) is

$$\lambda^2 - (a_1 + b_2)\lambda + a_1 b_2 - a_2 b_1 = 0,$$

where $a_1 = r - 2\frac{rx}{K} - y\frac{a-x^2}{(a+bx+x^2)^2},\ a_2 = \frac{x}{a+bx+x^2},\ b_1 = y\frac{\mu(a-x^2)}{(a+bx+x^2)^2},\ b_2 = \frac{\mu x}{a+bx+x^2} - D.$

From some calculation and qualitative analysis, we have the following theorem.

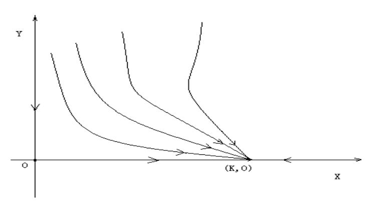
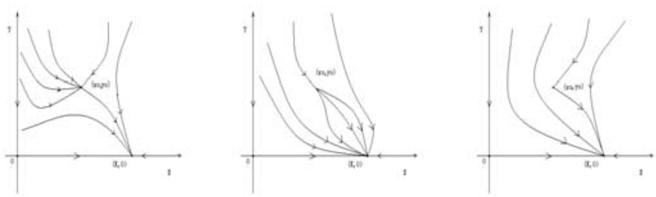


Fig.1. The phase portrait of system (1) when either $d_1 < 0$ or $d_2 \le 0$.

Theorem 2.1. *(i) If either $d_1 < 0$ or $d_2 \le 0$, system (1) has no interior equilibrium, and the equilibrium (0,0) is a saddle, (K,0) is a global stable node as shown in Fig.1.*

(ii) If both $d_1 = 0$ and $0 < d_3 < K$, system (1) has three equilibria: saddle (0,0), stable node (K,0), and an unique positive equilibrium (x_0, y_0), and system (1) has not any closed orbits. Moreover, (x_0, y_0) is a saddle-node when $K \ne d_4$ and a cusp when $K = d_4$. Detailed phase portraits can be seen from Fig.2, where $x_0 = d_3, y_0 = r(1 - \frac{x_0}{K})(a + bx_2 + x_0^2)$.

(iii) If both $d_1 > 0$ and $d_2 > 0$, system (1) has at most four equilibria: $(0, 0), (K, 0), (x_1, y_1)$ and (x_2, y_2). And, if $x_1 \le K$, then system (1) has only two equilibria: saddle (0,0), and stable



(a) (b) (c)

Fig.2. The phase portraits of system (1) when (a) $d_3 < K < d_4$; (b) $K = d_4$; (c) $K > d_4$.

node (K,0); if $x_1 < K \le x_2$, then system (1) has only three equilibria: saddles (0,0) and (K,0),focus or node (x_1, y_1); if $K > x_2$, then system (1) has four equilibria: saddles (0,0) and (x_2, y_2), stable node (K,0), stable (unstable) focus or node for $K < d_0$ $(K > d_0)$.

We note that system (1) has only a unique positive equilibrium (x_1, y_1) when both $d_1 > 0$, $d_2 > 0$ and $x_1 < K \le x_2$. The following theorems give the dynamics of system (1) in this case.

Theorem 2.2. *If both $b^2 < 3a$ and $x_1 < K < \min\{x_2, d_0, \frac{1}{2}(\sqrt{12a - 3b^2} - b)\}$ (or $x_2 = K < \min\{d_0, \frac{1}{2}(\sqrt{12a - 3b^2} - b)\}$), then system (1) has three equilibria, saddles $(0,0)$ and (saddle-node, respectively) $(K, 0)$, and a globally asymptotically stable equilibrium (x_1, y_1). The phase portrait is given in Fig.3.*

Proof. To show the globally asymptotically stability of (x_1, y_1), we need to prove that there are no periodic orbits in $\overline{R}_+ = \{(x, y) \mid x \ge 0, y \ge 0\}$.

We make the substitution $dt = (a + bx + x^2)d\tau$, and then system (1) becomes

$$\frac{dx}{d\tau} = rx\Big(1 - \frac{x}{K}\Big)(a + bx + x^2) - xy, \qquad \frac{dy}{d\tau} = \mu xy - D(a + bx + x^2)y. \tag{2}$$

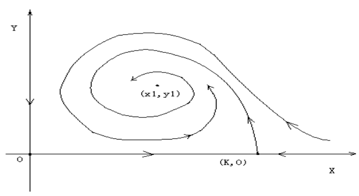


Fig.3. Phase Portrait of system (1) for $b^2 < 3a$, $x_1 < K < min\{x_2, d_0, \frac{1}{2}(\sqrt{12a - 3b^2} - b)\}$.

Taking Dulac function $D(x, y) = x^{-1}y^{-1}$ for system (2), then

$$div\mid_{(2)} = \frac{\partial}{\partial x}\big(P(x, y)D(x, y)\big) + \frac{\partial}{\partial y}\big(Q(x, y)D(x, y)\big) = \frac{r}{Ky}(-3x^2 - 2(b - K)x + Kb - a),$$

where

$$P(x, y) = rx\Big(1 - \frac{x}{K}\Big)(a + bx + x^2) - xy, Q(x, y) = \mu xy - D(a + bx + x^2)y.$$

It's easy to see that $4(b - K)^2 + 12(Kb - a) < 0$ for $0 < K < \frac{1}{2}(\sqrt{12a - 3b^2} - b), b^2 < 3a$. Then $\text{div}|_{(2)} < 0$, by Dulac's Theorem[17] and the local stability of (x_1, y_1), and so (x_1, y_1) is globally asymptotically stable.

Theorem 2.3. *If $d_1 > 0$, $d_2 > 0$, and $x_2 > K > d_0$, then system (1) has at least one stable limit cycle in $\overline{R}_+ = \{(x, y) \mid x \ge 0, y \ge 0\}$.*

Proof. Taking a line $L1 = \{(x, y) \mid x = K,\ y > 0\}$ at $(K, 0)$, we can see the direction of the vector field of system (1) on L1 is from right to left (see Fig.4.).

The periodic orbit of system (1) must be in the domain E_1 if it exists , where $E_1 = \{(x, y) \mid 0 < x < K,\ 0 < y < +\infty\}$.

Now we consider the solution $\big(x^*(t), y^*(t)\big)$ of system (1) passing the point $B(K, y_b)$, where $y_b > y_1$. Let $L2 = \{(x, y) \mid x = x_1, y > 0\}$. It is easy to see that the trajectory $\big(x^*(t), y^*(t)\big)$ must intersect L2 at $C(x_1, y_c)(y_c \geq y_b)$.

Let $L3 = \{(x, y) \mid 0 \leq x \leq x_c,\ y = y_c\}$ which begins at point $C(x_1,\ y_c)$ and ends at point $D(0, y_c)$. The direction of the vector field of system (1) on L3 is a downward one (see Fig.4.). Therefore the trajectory of system (1) in the interior of the region $\Omega = OABCDO$ can't cross the boundary of Ω.

On the other hand, we can see that equilibrium (x_1, y_1) is an unstable focus or node for $K > d_0$. By the Poincaré-Bendixson Theoem there is at least a stable limit cycle.

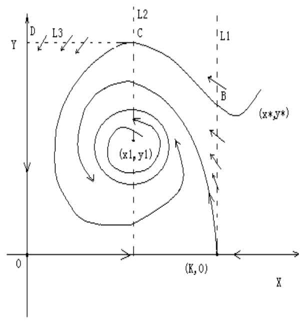


Fig.4. The phase portrait of system (1) when $d_1 > 0$, $d_2 > 0$, and $x_2 > K > d_0$.

According to Theorem 2.2 in [15], we have

Theorem 2.4. *If the following conditions are satisfied:*

(i) $d_1 > 0$, $d_2 > 0$, *and* $d_0 < K < \min\{x_2, x_1 + \frac{a}{x_1 + b}\}$,

(ii) if $G(x_Q) \leq G(x_P)$, $\sup\limits_{0 \leq x \leq x_Q} \big(G(x) + \Phi(\phi^{-1}F(x))\big) \geq G(x_P)$; *if* $G(x_P) < G(x_Q)$, $\sup\limits_{x_P \leq x \leq 0} (G(x) + \Phi(\phi^{-1}(F(x))) \geq G(x_Q)$; *where* $G(x) = \int_0^x g(s)ds$, $\Phi(y) = \int_0^y \phi(s)ds$, ϕ^{-1} *is the inverse function of* $\phi(y)$, *and points* x_P, x_Q *and functions* $F(x)$, $g(x)$ *and* $\phi(y)$ *are as indicated in the proof.*

Then system (1) has a limit cycle in R_+, and it is stable.

Proof. By Theorem 2.3, system (1) has limit cycles, which are located in E_1. Thus, we only need to consider system (1) in $E_1 = \big\{(x, y) \mid 0 < x < K,\ 0 < y < +\infty\big\}$.

Let $x - x_1 = -X, y - y_1 = y_1(e^Y - 1)$ and $xdt = (a + bx + x^2)d\tau$, and still denote X, Y, τ by x, y, t. Then system (1) becomes

$$\frac{dx}{dt} = \phi(y) - F(x), \qquad \frac{dy}{dt} = -g(x), \tag{3}$$

where $\phi(y) = y_1(e^y - 1), F(x) = r\big(1 - \frac{x_1 - x}{K}\big)(a + b(x_1 - x) + (x_1 - x)^2) - y_1$, and $g(x) = \frac{Dx(x - x_1 + x_2)}{x_1 - x}, x_1 - k < x < x_1,\ -\infty < y < +\infty$.

Note that the existence of limit cycles of system (1) in E_1 is equivalent to that of system (3) in $E_2 = \big\{(x, y) \mid x_1 - K < x < x_1,\ -\infty < y < +\infty\big\}$.

When $d_0 < K < min\{x_2, x_1 + \frac{a}{x_1+b}\}$, the isocline $\phi(y) = F(x)$ of system (3) in E_2 has two humps, namely, a local maximum and a local minimum, and intersects the x-axis at P, O and Q (see Fig.5).

Let

$$\begin{aligned}\phi(y) =& y_1(e^y - 1) = F(x) = \frac{rxf(x)}{K},\\ f(x) =& x^2 + (K - b - 3x_1)x + (3x_1^2 + 2(b - K)x_1 + a - Kb).\end{aligned} \tag{4}$$

Now considering function $f(x)$, when $d_0 < K < \min\left\{x_2, x_1 + \frac{a}{x_1+b}\right\}$, we have

$$f(x_1) > 0, \qquad f(0) < 0, \qquad f(x_1 - K) > 0;$$

thus the equation $f(x) = 0$ has two roots in E_2: one is positive x_Q, the other is negative x_P, such that

$$\phi(y) = F(x) = \frac{rx(x - x_P)(x - x_Q)}{K}, \qquad x_1 - K < x_P < 0 < x_Q < x_1. \tag{5}$$

Obviously, $\phi(y) = F(x)$ has a local maximum and a local minimum in E_2.

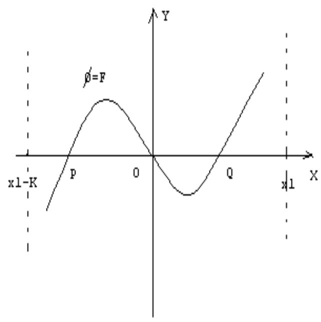


Fig.5. Illustrating the proof of Theorem 2.4.

According to Theorem 2.2 in [15], we know that system (1) has at most one limit cycle, and it is stable if it exists. Hence, we complete the proof.

It is easy to find some values of the parameters which satisfy the conditions in Theorem 2.4. In what follows, we show that one limit cycle is in R_+ by numerical simulation as in Fig.6, which is in consistence with Theorem 2.4. In this case, we take $r = 5,\ k = 0.7,\ D = 1,\ \mu = 1,\ b = 0.001,\ a = 0.1$.

Theorem 2.5. *If $d_1 > 0,\ d_2 > 0$, and $K \geq d_4$, then system (1) has no limit cycles in R_+.*

Proof. Note that the existence of limit cycles of system (1) in E_3 is equivalent to that of system (3) in E_4 for $K > x_2$.

When $K \geq d_4$,we have

$$f(x_1) < 0, \qquad f(0) < 0, \qquad f(x_1 - x_2) \leq 0$$

where $f(x)$ is the same as that of Theorem 2.4. So the isocline $\phi(y) = F(x)$ of system (3) has no humps in E_4, see Fig.7.

On the contrary,we suppose that system (3) has a limit cycle Γ in E_4, which intersects the y-axis at A and B.(see Fig.7.)

Now we define the function

$$W(x, y) = \int_0^x g(s)ds + \int_0^y \phi(s)ds;$$

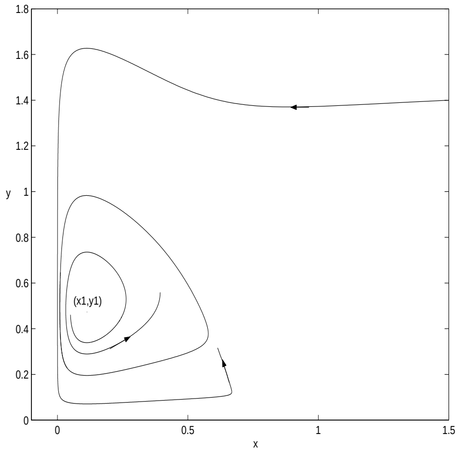


Fig.6. A unique limit cycle of system (1) by numerical simulation for $r = 5, K = 0.7, D = 1, \mu = 1, b = 0.001, a = 0.1$.

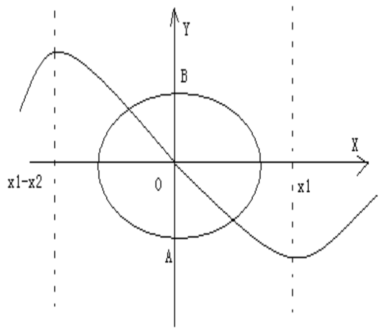


Fig.7. Portrait for showing no limit cycle for $K \geq d_4$.

then

$$\oint_{\Gamma} dW(x,y) = 0. \tag{6}$$

On the other hand ,

$$\oint_{\Gamma} dW(x,y) = \int_{\widehat{AB}} dW + \int_{\widehat{BA}} dW = \int_{\widehat{AB}} F(x)dy + \int_{\widehat{BA}} F(x)dy < 0. \tag{7}$$

Obviously (6) contradicts (7). Thus there is no limit cycle in R_+ for system (1).

Theorem 2.7. *If $d_1 > 0$, $d_2 > 0$, and $K > \frac{2\mu+\sqrt{(\mu-bD)^2-4aD^2}}{\mu+\sqrt{(\mu-bD)^2-4aD^2}}x_2$, then system (1) has four equilibria : two saddles $(0,0)$,(x_2,y_2), a stable node $(K,0)$ and an unstable equilibrium (x_1,y_1). And system (1) has not any closed orbits and homoclinic loops, that is , it exhibits the so-called "paradox of enrichment". The phase portrait is shown in Fig.8.*

Proof. Suppose that system (1) has a homoclinic loop. Then the homoclinic loop is unstable. In fact, the saddle quantity of system (1) at (x_2,y_2) is given by

$$\sigma_0 = \frac{\partial P(x_2,y_2)}{\partial x} + \frac{\partial Q(x_2,y_2)}{\partial y} = \frac{rx_2(2x_2+b)}{K(a+bx_2+x_2^2)}\Big[K - \frac{2\mu+\sqrt{(\mu-bD)^2-4aD^2}}{\mu+\sqrt{(\mu-bD)^2-4aD^2}}x_2\Big],$$

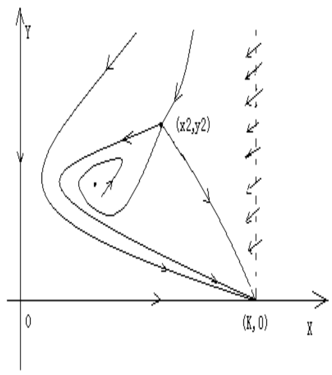


Fig.8. The phase portrait of system (1) for $d_1 > 0, K > \frac{2\mu+\sqrt{(\mu-bD)^2-4aD^2}}{\mu+\sqrt{(\mu-bD)^2-4aD^2}}x_2$.

where

$$P(x,y) = rx(1-\frac{x}{K}) - \frac{xy}{a+bx+x^2}, Q(x,y) = y\Big(\frac{\mu x}{a+bx+x^2} - D\Big).$$

Since $K > \frac{2\mu+\sqrt{(\mu-bD)^2-4aD^2}}{\mu+\sqrt{(\mu-bD)^2-4aD^2}}x_2$, $\sigma_0 > 0$. On the other hand, the equilibrium (x_1, y_1),which is unstable, is in the interior of the range surrounded by the homoclinic loop. By Poincaré-Bendixson Theorem, system (1) has at least one limit cycle inside the homoclinic loop. But when $K > \frac{2\mu+\sqrt{(\mu-bD)^2-4aD^2}}{\mu+\sqrt{(\mu-bD)^2-4aD^2}}x_2$, it is easily seen $K > d_4$. Thus, there is not any closed orbit for system (1) by Theorem 2.6. This leads to a contradiction. Hence, there is not any limit cycle or homoclinic orbit under the conditions of Theorem 2.7.

Remark. In the following section, we will show the existence of a homoclinic loop of system (1) for some suitable parameter values.

3 Bifurcation of a Degenarated Equilibrium

By (ii) in Theorem 2.1, system (1) has a cusp-type equilibrium (x_0, y_0) when $d_1 = 0$ and $0 < d_3 < K = d_4$, i.e. $K = d_4$ and $K^2 = 4a$. In this section, we discuss the bifurcation of the cusp (x_0, y_0) as the parameters vary in a small neighborhood of $(\mu_0, K_0, a_0, D_0, b_0)$, where μ_0, K_0, a_0, D_0 and b_0 satisfy the following conditions

$$K = d_4, \qquad K^2 = 4a.$$

Now we consider the following system:

$$\dot{x} = rx(1-\frac{x}{K_0}) - \frac{xy}{a_0+b_0x+x^2}, \dot{y} = y\Big(\frac{\mu_0 x}{a_0+b_0x+x^2} - D_0\Big). \tag{8}$$

First we expand system (8) into a power series around the point (x_0, y_0). Let $X = x - x_0,\ Y = y - y_0$. Then (8) can be rewritten as

$$\begin{aligned}\dot{X} &= -\frac{x_0}{a_0+b_0x_0+x_0^2}Y + \Big(\frac{x_0y_0}{(a_0+b_0x_0+x_0^2)^2} - \frac{r}{K_0}\Big)X^2 + P_1(X,Y),\\ \dot{Y} &= -\frac{\mu_0x_0y_0}{(a_0+b_0x_0+x_0^2)^2}X^2 + Q_1(X,Y),\end{aligned} \tag{9}$$

where $x_0 = \frac{\mu_0-b_0D_0}{2D_0},\ y_0 = r\big(1-\frac{x_0}{K_0}\big)(a_0+b_0x_0+x_0^2), P_1$ and Q_1 are C^∞ functions in (X,Y) at least of the third order. Making the transformation

$$x = X, \qquad y = -\frac{x_0}{a_0+b_0x_0+x_0^2}Y,$$

system (9) becomes

$$\dot{x} = y + \Big(\frac{x_0 y_0}{(a_0 + b_0 x_0 + x_0^2)^2} - \frac{r}{K_0}\Big)x^2 + \widetilde{P_1}(x,y),$$
$$\dot{y} = \frac{\mu_0 x_0^2 y_0}{(a_0 + b_0 x_0 + x_0^2)^3}x^2 + \widetilde{Q_1}(x,y). \qquad (10)$$

To find the normal form of the cusp, we take

$$X = x, \qquad Y = y + \Big(\frac{x_0 y_0}{(a_0 + b_0 x_0 + x_0^2)^2} - \frac{r}{K_0}\Big)x^2 + \widetilde{P_1}(x,y).$$

Then system (10) becomes

$$\dot{X} = Y, \qquad \dot{Y} = \frac{\mu_0 x_0^2 y_0}{(a_0 + b_0 x_0 + x_0^2)^3}X^2 + 2\Big(\frac{x_0 y_0}{(a_0 + b_0 x_0 + x_0^2)^2} - \frac{r}{K_0}\Big)XY + R(X,Y), \qquad (11)$$

where R is a C^∞ function in (X,Y) at least of the third order. Since

$$\frac{\mu_0 x_0^2 y_0}{(a_0 + b_0 x_0 + x_0^2)^3} = \frac{r\mu_0 a_0}{2(2a_0 + b_0 x_0)^2} > 0,$$
$$2\Big(\frac{x_0 y_0}{(a_0 + b_0 x_0 + x_0^2)^2} - \frac{r}{K_0}\Big) = -\frac{rD_0(a_0 + b_0 x_0)}{a_0 \mu_0},$$

$-\frac{rD_0(a_0+b_0x_0)}{a_0\mu_0} < 0$ for $b > 0 (b_0 > 0)$, and $-\frac{rD_0(a_0+b_0x_0)}{a_0\mu_0} = 0$ for $b = -\sqrt{a} < 0$,
we can get the following theorem:

Theorem 3.1. *The interior equilibrium (x_0, y_0) of system (8) is a cusp of codimension 2 for $b > -2\sqrt{a}$ and $b \neq -\sqrt{a}$, and the interior equilibrium (x_0, y_0) a cusp of codimension at least 3 for $b = -\sqrt{a}$.*

The parameters K and D are chosen as bifurcation parameters. Consider the following system

$$\dot{x} = rx\Big(1 - \frac{x}{K_0 + \lambda_1}|\Big) - \frac{xy}{a_0 + b_0 x + x^2},$$
$$\dot{y} = y\Big(\frac{\mu_0 x}{a_0 + b_0 x + x^2} - D_0 - \lambda_2\Big), \qquad (12)$$

where μ_0, K_0, a_0, b_0, and D_0 are positive constants while satisfy $K_0 = d_4$ and $K_0^2 = 4a_0$, and r is a positive constant, λ_1 and λ_2 are in the small neighborhood of (0,0), x and y are in the small neighborhood of $(x_0, y_0) = \big(\frac{\mu_0 - b_0 D_0}{2D_0}, \ \frac{1}{2}r(2a_0 + b_0 x_0)\big)$.

We expand system (12) into a power series around the point (x_0, y_0) and translate (x_0, y_0) to the origin, and then, using an affine translation, system (12) becomes

$$\dot{X} = \frac{r}{4}\lambda_1 + b_1(\lambda_1) + Y + \Big[\frac{x_0 y_0}{(2a_0 + b_0 x_0)^2} - \frac{r}{K_0} + \frac{r}{4a_0}\lambda_1 + b_3(\lambda_1)\Big]X^2 + \widehat{B}(X,Y,\lambda_1),$$
$$\dot{Y} = \frac{x_0 y_0}{2a_0 + b_0 x_0}\lambda_2 + c_1(\lambda_1) + \Big(\frac{rx_0}{2a_0}\lambda_1 - \lambda_2 + b_2(\lambda_1)\Big)Y + c_2(\lambda_1, \lambda_2)X$$
$$+ \Big[\frac{\mu_0 x_0^2 y_0}{(2a_0 + b_0 x_0)^3} + c_3(\lambda_1)\Big]X^2 + \widehat{C}(X,Y,\lambda_1,\lambda_2), \qquad (13)$$

where $\widehat{B}, \widehat{C}$ are C^∞ functions in variables (X,Y) at least of the third order and the coefficients depend smoothly on λ_1 and λ_2, c_1, c_2 and c_3 are smooth functions of their variables . Let

$$x = X, \quad y = \frac{r}{4}\lambda_1 + b_1(\lambda_1) + Y + \Big[\frac{x_0 y_0}{(2a_0 + b_0 x_0)^2} - \frac{r}{K_0} + \frac{r}{4a_0}\lambda_1 + b_3(\lambda_1)\Big]X^2 + \widehat{B}(X,Y,\lambda_1).$$

Then system (13) becomes

$$\begin{aligned}
\dot{x} =& y,\\
\dot{y} =& \frac{x_0 y_0}{2a_0+b_0x_0}\lambda_2 + \widehat{c}_1(\lambda_1,\lambda_2) + \Big(\frac{rx_0}{2a_0}\lambda_1 - \lambda_2 + b_2(\lambda_1)\Big)y + \widehat{c}_2(\lambda_1,\lambda_2)x\\
&+ \Big[\frac{r\mu_0 a_0}{2(2a_0+b_0x_0)^2} + \widehat{c}_3(\lambda_1,\lambda_2)\Big]x^2\\
&- \Big[\frac{r(a_0+b_0x_0)}{x_0(2a_0+b_0x_0)} - \frac{r}{2a_0}\lambda_1\\
&- 2b_3(\lambda_1)\Big]xy + \widehat{R}(x,y,\lambda_1,\lambda_2),
\end{aligned} \tag{14}$$

where $\widehat{c}_i, (i = 1, 2, 3)$ are smooth functions of (λ_1, λ_2), $\widehat{R}$ is a C^∞ function in variables (λ_1, λ_2) at least of the third order with respect to (x,y) and the coefficients depend smoothly on λ_1 and λ_2. Using the method in the proof of Lemma 3.2 in [11] , system (14) can be rewritten as

$$\begin{aligned}
\dot{x} =& y,\\
\dot{y} =& \frac{x_0(2a_0+b_0x_0)^2}{a_0\mu_0}\lambda_2 + \phi_1(\lambda_1,\lambda_2) + \phi_2(\lambda_1,\lambda_2)x\\
&+ \Big[\frac{\frac{rx_0}{2a_0}\lambda_1 - \lambda_2}{\sqrt{\frac{r\mu_0 a_0}{2(2a_0+b_0x_0)^2}}} + \phi_3(\lambda_1,\lambda_2)\Big]y + x^2\\
&- \Big[\frac{\frac{r(a_0+b_0x_0)}{x_0(2a_0+b_0x_0)}}{\sqrt{\frac{r\mu_0 a_0}{2(2a_0+b_0x_0)^2}}} + \phi_4(\lambda_1,\lambda_2)\Big]xy + R(x,y,\lambda_1,\lambda_2),
\end{aligned} \tag{15}$$

where ϕ_1, ϕ_2 and ϕ_3 are smooth functions in variables (λ_1, λ_2) at least of the second order, ϕ_4 is a smooth function of λ_1 and λ_2 at least of the first order, and R is a C^∞ function in variables (x, y) at least of the third order and the coefficients depend smoothly on λ_1 and λ_2. Let

$$X = x + \frac{1}{2}\phi_2(\lambda_1,\lambda_2), \qquad Y = y.$$

System (15) becomes

$$\dot{X} = Y, \qquad \dot{Y} = \gamma_1 + \gamma_2 Y + X^2 - \gamma_3 XY + Q(X,Y,\lambda_1,\lambda_2), \tag{16}$$

where

$$\gamma_1 = \frac{x_0(2a_0+b_0x_0)^2}{a_0\mu_0}\lambda_2 + \psi_1(\lambda_1,\lambda_2),$$

$$\gamma_2 = \frac{\frac{rx_0}{2a_0}\lambda_1 - \lambda_2}{\sqrt{\frac{r\mu_0 a_0}{2(2a_0+b_0x_0)^2}}} + \psi_3(\lambda_1,\lambda_2), \qquad \gamma_3 = \frac{\frac{r(a_0+b_0x_0)}{x_0(2a_0+b_0x_0)}}{\sqrt{\frac{r\mu_0 a_0}{2(2a_0+b_0x_0)^2}}} + \psi_4(\lambda_1,\lambda_2),$$

in which ψ_1, ψ_3, ψ_4 are C^∞ functions in (λ_1, λ_2) and Q is a C^∞ function in (X, Y) .

By the theorems in [3] and [4], we get the local representations of bifurcation curves in a small neighborhood of the origin as follows:

1. Saddle-node bifurcation curve $SN = \big\{(\gamma_1, \gamma_2) \mid \gamma_2 = 0,\ \gamma_1 \neq 0\big\}$,
2. Hopf bifurcation curve $H = \big\{(\gamma_1, \gamma_2) \mid \gamma_2 = -\frac{r(a_0+b_0x_0)}{x_0(2a_0+b_0x_0)}\sqrt{-\frac{2(2a_0+b_0x_0)^2\gamma_1}{r\mu_0 a_0}} = -\frac{r(a_0+b_0x_0)}{x_0}$ $\sqrt{\frac{-2}{r\mu_0 a_0}\gamma_1}, \gamma_1 < 0\big\}$,

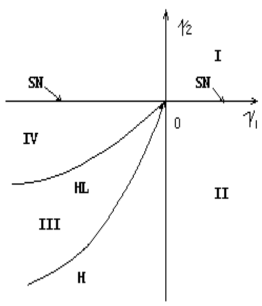
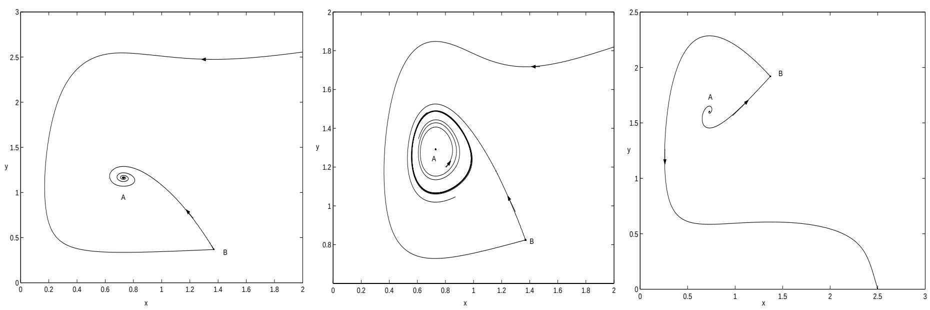


Fig.9. The bifurcation curves of system (12) for $b > -2\sqrt{a}$ and $b \neq -\sqrt{a}$.

3. Homoclinic bifurcation curve $HL = \{(\gamma_1, \gamma_2) \mid \gamma_2 = -\frac{5}{7}\frac{r(a_0+b_0x_0)}{x_0}\sqrt{\frac{-2}{r\mu_0 a_0}\gamma_1}, \gamma_1 < 0\}$.

The bifurcation curves in a small neighborhood of the origin in the (γ_1, γ_2) are shown in Fig.9, and the bifurcation curves divide the parameter plane into four parts:I,II, III and IV.

Remark 3.2. In Fig.10, by using numerical simulation we show the Hopf bifurcation and the existence of homoclinic orbit. We fix $\mu = 3.1, b = D = a = r = 1$ and change K: $K = 1.5, 1.7,$ and 2.5 in Fig.10(a), (b) and (c), respectively. A and B are two positive equilibria, A is a focus which is stable (unstable) in Fig.10(a) (Fig.10(b) and (c)), B is a saddle. From Fig.10(a) and (b) we can see the occurence of Hopf bifurcation, and the existence of homoclinic orbit can be seen from Fig.10(a) and (c), where the relative locations of the stable manifold and unstable manifold for the saddle B are opposite, then there must exist some $K(1.5 < K < 2.5)$ such that the stable manifold and unstable manifold coincide.



(a) (b) (c)

Fig.10. Hopf bifurcation and the existence of homoclinic orbit of system (1) by numerical simulation for $\mu = 3.1,\ b = D = a = r = 1$. (a) For $K = 1.5$. (b) For $K = 1.7$. (c) For $K = 2.5$.

Remark 3.3. When $b = -\sqrt{a} < 0$, then system (11) can be written as

$$\dot{X} = Y, \qquad \dot{Y} = \frac{r\mu_0}{2a_0}X^2 + R(X, Y), \tag{17}$$

where R is a C^∞ function in the x, y plane. In this case, system (1) has a degenerate cusp with codimension 3. In [16] Zhu, Campbell and Wolkowicz carried out bifurcation analysis of this degenerate cusp with codimension 3.

4 Biological Explanation.

The biological implications for these two different classes of equilibria (the boundary equilibrium (K,0) on the x-axis , and the interior equilibria (x_1, y_1) and (x_2, y_2) in R_+) and the limit cycle and the homoclinic orbit are quite different, and indicate different results of the interaction of a predator-prey system (1).

(1) If the trajectories tend to boundary (extinction) equilibrium (K,0) as $t \to +\infty$, then it means that the predator population will ultimately tend to extinction, and the prey population with a different initial condition will ultimately get to the balance density K.

(2) If the trajectories tend to the stable equilibrium (x_1, y_1) at $t \to +\infty$, then it means that the predator-prey interactions will ultimately tend to the balance behavior.

(3) If there are three or four equilibria, then it means that the trajectory with a different initial condition will ultimately tend to a different equilibrium.

(4) If the stable limit cycle around the equilibrium (x_1, y_1) arises, then this indicates that the predator coexists with the prey with oscillatory balance behavior.

(5) If the homoclinic orbit or cusp bifurcation arises as the bifurcation parameters are varied, then the biological phenomena are very complex and interesting.

Acknowledgments. The first author would like to thank Dr. Ruiqi Wang and Dr. Wei Feng for their valuable suggestions and help. We are also grateful to the referees for their careful reading and constructive comments.

References

[1] Andronov, A., Leontovich, E.A., Gordon, I.I., Maier, A.G. Theory of Bifurcations of Dynamical Systems on a Plane. Israel Program for Scientific Translations, Jerusalem, 1971

[2] Andrews, J.F. A mathematical model for the continuous culture of microorganisms utilizing inhibitory substrates. Biotechnol. Bioeng, 10: 707–723 (1968)

[3] Bogdanov, R. Bifurcation of a limit cycle for a family of vector fields on the plane. Selecta Math. Soviet., 1: 373–388 (1981)

[4] Bogdanov, R. Versal deformations of a singular point on the plane in the case of zero eigenvalues. Selecta Math. Soviet., 1: 389–421 (1981)

[5] Chow, S.N., Hale, J.K. Methods of Bifurcation Theory. Springer-Verlag, New York, Heidelbeg, Berlin, 1982

[6] Collings, J.B. The effects of the functional response on the bifurcation behavior of a mite predator-prey interaction model. J. Math. Biol., 36: 149–168 (1997)

[7] Freedman, H.I., Wolkowicz, G.S.K. Predator-prey systems with group defence: the paradox of enrichment revisited, Bull. Math. Biol., 48: 493–508 (1986)

[8] Holling, C.S. The functional response of predators to prey density and its role in mimicry and population regulation. Mem. Entomolog. Soc. Can, 45: 3–60 (1965)

[9] Mischaikow, K., Wolkowicz, G.S.K. A predator-prey system involving group defense: a connection matrix approach. Nonlinear Anal., 14: 955–969 (1990)

[10] Rosenzweig, M.L. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. Science, 171: 385–387 (1971)

[11] Ruan, S., Xiao, D. Global analysis in a predator-prey system with nonmonotonic functional response. SIAM J. Appl.Math., 61: 1445–1472 (2001)

[12] W. Sokol, W., Howell, J.A. Kinetics of phenol oxidation by washed cells. Biotechnol. Bioeng. , 23: 2039–2049 (1980)

[13] Tener, J.S. Muskoxen. Queen's Printer, Ottawa, 1965

[14] Wolkowicz, G.S.K. Bifurcation analysis of a predator-prey system involving group defence. SIAM J. Appl. Math., 48: 592–606 (1988)

[15] Xiao, D., Zhang, Z. On the uniqueness and nonexistence of limit cycles for predator-prey systems. Nonlinearity., 16: 1185–1201 (2003)

[16] Zhu, H., Campbell, S.A., Wolkowicz, G.S.K. Bifurcation analysis of a predator-prey system with nonmonotonic functional response. (Preprint).

[17] Zhang, Z., Ding, T., Huang, W., Dong, Z. The qualitative theory of differential equation, Science press, 1997 (in chinese)