Available online at www.sciencedirect.com
ScienceDirect
J. Math. Anal. Appl. 324 (2006) 14–29
Journal of MATHEMATICAL ANALYSIS AND APPLICATIONS
www.elsevier.com/locate/jmaa

Dynamics in a ratio-dependent predator–prey model with predator harvesting

Dongmei Xiao [a,1,*], Wenxia Li [b,2], Maoan Han [a,3]

[a] *Department of Mathematics, Shanghai Jiao Tong University, Shanghai 200030, China*
[b] *Department of Mathematics, East China Normal University, Shanghai 200062, China*

Received 22 April 2005
Available online 4 January 2006
Submitted by H.R. Thieme

Abstract

The objective of this paper is to study systematically the dynamical properties of a ratio-dependent predator–prey model with nonzero constant rate predator harvesting. It is shown that the model has at most two equilibria in the first quadrant and can exhibit numerous kinds of bifurcation phenomena, including the bifurcation of cusp type of codimension 2 (i.e., Bogdanov–Takens bifurcation), the subcritical and supercritical Hopf bifurcations. These results reveal far richer dynamics compared to the model with no harvesting and different dynamics compared to the model with nonzero constant rate prey harvesting in [D. Xiao, L. Jennings, Bifurcations of a ratio-dependent predator–prey system with constant rate harvesting, SIAM Appl. Math. 65 (2005) 737–753]. Biologically, it is shown that nonzero constant rate predator harvesting can prevent mutual extinction as a possible outcome of the predator prey interaction, and remove the singularity of the origin, which was regarded as "pathological behavior" for a ratio-dependent predator prey model in [P. Yodzis, Predator–prey theory and management of multispecies fisheries, Ecological Applications 4 (2004) 51–58].

Keywords: Predator–prey system; Predator harvesting; Coexistence; Bifurcations; Limit cycle

* Corresponding author.
E-mail addresses: xiaodm@sjtu.edu.cn (D. Xiao), wxli@math.ecnu.edu.cn (W. Li), mahan@sjtu.edu.cn (M. Han).
[1] Research supported by the NNSF of China (No. 10231020) and Program for New Century Excellent Talents in University.
[2] Research supported by the NNSF of China (No. 10371043).
[3] Research supported by the NNSF of China (No. 10371072).

0022-247X/$ – see front matter
doi:10.1016/j.jmaa.2005.11.048

1. Introduction

In population dynamics, the following Michaelis–Menten type predator–prey model, or called ratio-dependent predator–prey model,

$$\dot{x} = rx\left(1 - \frac{x}{K}\right) - \frac{cxy}{my + x},$$
$$\dot{y} = y\left(-D + \frac{fx}{my + x}\right) \tag{1.1}$$

is interesting because of laboratory experiments and observations (Abrams et al. [1], Arditi et al. [3–5], Akcakaya et al. [2], Cosner et al. [14] and Gutierrez [15]) and its rich dynamics (Berezovskaya et al. [7], Hsu et al. [16], Jost et al. [17], Kuang [18], Kuang and Beretta [19], Xiao and Ruan [22], and references their cited). In model (1.1), $x(t)$ and $y(t)$ represent population densities of prey and predator at time t, respectively. r, K, c, m, D and f are positive constants. The prey grows with intrinsic growth rate r and carrying capacity K in the absence of predation. D, c, m and f stand for the predator death rate, capturing rate, half saturation constant and conversion rate, respectively. Research on this ratio dependent predator–prey model revealed rich interesting dynamics such as deterministic extinction, existence of multiple attractors, etc. This dynamics provides a simple and plausible support to observation in addition to providing a plausible explanation of the success of biological controls. For very small patch or field, even when the numbers of individuals of prey and predators are low, their densities may remain high.

From the point of view of human needs, the exploitation of biological resources and the harvest of population are commonly practiced in fishery, forestry and wildlife management. Concerning the conservation for the long-term benefits of humanity, there is a wide-range of interest in the use of bioeconomic modeling to gain insight in the scientific management of renewable resources like fisheries and forestries (cf. [8–10,13,21,23]). In [23] authors studied model (1.1) with nonzero constant rate prey harvesting by considering two folds from biology and mathematics. They obtained that this model had at most four equilibria in the first quadrant and exhibited complex bifurcation phenomena. In this paper, we assume that the prey in the model (1.1) is not of commercial importance. The predator which is continuously being harvested with constant rate in time by a harvesting agency. The harvesting activity does not affect the prey population directly. Before going into details, let us simplify model (1.1) as in Kuang and Beretta [19] with the following scaling:

$$t \to rt, \qquad x \to x/K, \qquad y \to my/k.$$

Then model (1.1) takes the form

$$\dot{x} = x(1 - x) - \frac{axy}{y + x},$$
$$\dot{y} = y\left(-d + \frac{bx}{y + x}\right), \tag{1.2}$$

here $a = \frac{c}{mr}$, $b = \frac{f}{r}$ and $d = \frac{D}{r}$ are positive constants. For simplicity, we consider the biological meanings of a, b and d are same as c, f and D, respectively.

We formulate the above problem as follows:

$$\dot{x} = x(1-x) - \frac{axy}{y+x},$$
$$\dot{y} = y\left(-d + \frac{bx}{y+x}\right) - h, \tag{1.3}$$

where h represents the rate of harvesting or removal, $h > 0$.

The objective of this paper is to study systematically the dynamical properties of model (1.3), and determine how the constant harvesting affects the dynamics of (1.3). From the standpoint of biology, we are only interested in the dynamics of model (1.3) in the closed first quadrant R_+^2. We will show that model (1.3) has at most two equilibria in R_+^2, and can exhibit numerous kinds of bifurcation phenomena, including the bifurcation of cusp type of codimension 2 (i.e., Bogdanov–Takens bifurcation), the subcritical and supercritical Hopf bifurcations. In particular, prey and predator species in model (1.3) cannot become extinct simultaneously (mutual extinction) for all values of parameters and initial values, i.e., positive harvesting rate h can prevent mutual extinction. Prey and predator species can coexist in a positive equilibrium (or a stable limit cycle, or a unstable limit cycle, or a unstable homoclinic loop) for some values of parameters and initial values, respectively. These results reveal far richer dynamics compared to the model with no harvesting and different dynamics compared to the model with nonzero constant rate prey harvesting in [23].

The organization of this paper is as follows. In Section 2, we present a qualitative analysis of the model. We show the existence of equilibria and dynamical property in the neighborhoods of the equilibria for the model. In Section 3, we show that the model admits a saddle-node bifurcation, supercritical and subcritical Hopf bifurcations and Bogdanov–Takens bifurcation for $a = 1$. A brief discussion is given in Section 4.

2. Equilibria and their stability

The objective of this section is to perform a qualitative analysis of model (1.3). We rewrite the ratio-dependent predator–prey model (1.3) with nonzero constant predator harvesting as

$$\dot{x} = x(1-x) - \frac{axy}{y+x} \triangleq f_1(x,y),$$
$$\dot{y} = y\left(-d + \frac{bx}{y+x}\right) - h \triangleq f_2(x,y), \tag{2.1}$$

where all parameters a, b, d and h are positive. Considering the biological background, we only care about the dynamics of system (2.1) in the closed first quadrant R_+^2 in the (x, y) plane. Let both $f_1(0,0) = 0$ and $f_2(0,0) = -h$. Straightforward computation shows that $f_1(x,y)$ and $f_2(x,y)$ are continuous and Lipschizian in the closed first quadrant R_+^2. Hence, solution of (2.1) with nonnegative initial condition exists and is unique. It is also easy to see that $(0,0)$ is not an equilibrium of (2.1) since $h > 0$, and the positive y-axis is invariant under the flow. However, this is not the case on the positive x-axis. All solutions touching the x-axis leave the first quadrant. Thus, the first quadrant is no longer positively invariant under the flow generated by system (2.1) with the nonzero constant harvesting rate h. In this section, we will discuss the existence and stability of equilibria of system (2.1) in R_+^2.

Since $h > 0$, it is clear that there does not exist any equilibrium at the positive y-axis or the positive x-axis. Hence, system (2.1) has equilibria in R_+^2, equivalently the equations in x and y,

$$1 - x - \frac{ay}{x+y} = 0,$$
$$y\left(-d + \frac{bx}{x+y}\right) - h = 0 \tag{2.2}$$

have positive solutions.

For the positive solutions of Eqs. (2.2), we only need to consider the positive solutions of the following equations in x and y:

$$x^3 + \left(a - 2 - \frac{ad}{b}\right)x^2 + \left(1 - a + \frac{ad}{b} + \frac{ah}{b}\right)x + \frac{ah(a-1)}{b} = 0,$$
$$y - \frac{x(1-x)}{x+a-1} = 0. \tag{2.3}$$

It is clear that system (2.3) has at most three real solutions. We claim that system (2.3) has at most two real positive solutions.

Let (x^*, y^*) be a positive solution of (2.3). Then it has to be either

$$1 \leqslant a, \qquad 0 < x^* < 1; \tag{2.4}$$

or

$$0 < a < 1, \qquad 1 - a < x^* < 1. \tag{2.5}$$

Let

$$F(x) = x^3 + \left(a - 2 - \frac{ad}{b}\right)x^2 + \left(1 - a + \frac{ad}{b} + \frac{ah}{b}\right)x + \frac{ah(a-1)}{b}.$$

Lemma 2.1. *System* (2.1) *has no three equilibria in the first quadrant.*

Proof. The proof is simply based on analysis of zero points of $F(x)$. Note that

$$F(0) = \frac{ah(a-1)}{b} \quad \text{and} \quad F(1-a) = \frac{a^2 d(1-a)}{b}.$$

If $a = 1$ then $F(0) = 0$, obviously implying the conclusion.

For the case $a > 1$, $F(x)$ has a zero point in the interval $(1-a, 0)$ just by noting that $F(1-a) < 0$ and $F(0) > 0$. Thus the conclusion holds by (2.4).

Finally when $0 < a < 1$, $F(x)$ has a zero point in the interval $(0, 1-a)$ since $F(0) < 0$ and $F(1-a) > 0$. It implies the conclusion by (2.5). □

Lemma 2.1 indicates that system (2.1) has no an equilibrium whose x-coordinate is of multiplicity three. However, it is still possible that system (2.1) has either two equilibria or one equilibrium in R^2_+. Next we give the conditions to guarantee the existence of equilibria for system (2.1) in R^2_+.

Lemma 2.2. *Let* $S = 2 - a + \frac{ad}{b}$, $T = 3\left(1 - a + \frac{ad}{b} + \frac{ah}{b}\right)$ *and* $u = \frac{1}{3}\left(S + \sqrt{S^2 - T}\right)$.

(I) *System* (2.1) *has a unique equilibrium in the first quadrant if and only if either*

$$\text{(I.a)}\quad \begin{cases} \leqslant a; \\ 0 < S^2 - T; \\ 0 < u < 1; \\ F(u) = 0 \end{cases} \qquad \textit{or} \qquad \text{(I.b)}\quad \begin{cases} 0 < a < 1; \\ 0 < S^2 - T; \\ 1 - a < u < 1; \\ F(u) = 0. \end{cases}$$

For both cases, the equilibrium is at $(u, \frac{u(1-u)}{u+a-1})$ *and* u *is the positive zero point of multiplicity two of* $F(x)$*.*

(II) *System* (2.1) *has two distinct equilibria in the first quadrant if and only if*

$$\text{(II.a)}\quad \begin{cases} 1 \leqslant a; \\ 0 < S^2 - T; \\ 0 < u < 1; \\ F(u) < 0 \end{cases} \qquad \textit{or} \qquad \text{(II.b)}\quad \begin{cases} 0 < a < 1; \\ 0 < S^2 - T; \\ 1 - a < u < 1; \\ F(u) < 0. \end{cases}$$

In case (II.a)*, the* x*-coordinates of equilibria lie in the intervals* $(0, u)$ *and* $(u, 1)$*, respectively. While, In case* (II.b)*, the* x*-coordinates of equilibria lie in the intervals* $(1 - a, u)$ *and* $(u, 1)$*, respectively.*

Proof. When $a = 1$, $F(x)$ is reduced to

$$F(x) = x\left(x^2 - \left(1 + \frac{d}{b}\right)x + \frac{(d+h)}{b}\right).$$

Straightforward computation shows that conditions (I.a) and (II.a) are equivalent to

$$\begin{cases} a = 1; \\ h = \frac{(b-d)^2}{4b}; \\ b > d; \\ u = \frac{b+d}{2b} \end{cases} \quad \text{and} \quad \begin{cases} a = 1; \\ 0 < h < \frac{(b-d)^2}{4b}; \\ b > d, \end{cases}$$

respectively. So it implies the conclusion for $a = 1$.

When $a \neq 1$, note that

$$F'(x) = 3x^2 + 2\left(a - 2 - \frac{ad}{b}\right)x + \left(1 - a + \frac{ad}{b} + \frac{ah}{b}\right) = 3x^2 - 2Sx + \frac{1}{3}T,$$

and

$$F(0) = \frac{ah(a-1)}{b}, \quad F(1-a) = \frac{a^2 d(1-a)}{b} \quad \text{and} \quad F(1) = \frac{a^2 h}{b} > 0. \tag{2.6}$$

Therefore, if system (2.1) has equilibria in the first quadrant then $F'(x)$ surely has two distinct real zero points $\frac{1}{3}(S - \sqrt{S^2 - T})$ and $\frac{1}{3}(S + \sqrt{S^2 - T}) = u$ with u being the minimal value point of $F(x)$. This is clear by (2.6).

(I) Suppose that system (2.1) has unique an equilibrium in the first quadrant. It is equivalent to (I.a) or (I.b) and u is the x-coordinate of the equilibrium. In fact, it is not difficult to obtain from (2.4), (2.5) and (2.6) when $a \neq 1$.

(II) Suppose that system (2.1) has two distinct equilibria in the first quadrant. Correspondingly it surely has $F(u) < 0$. From the analysis above the conclusion follows. □

It is very important that each of above four inequality groups for positive parameters a, b, d and h has solutions so as to make above Lemma 2.2 sense. By means of property analysis for $F(x)$ and with the aid of mathematical software, we have verified the existence of solutions for all of them, e.g., for the last inequality group we can take $0.95 < a < 1$, $S = 1.05$ and $T = 0.3$ which, correspondingly, give the values of b, d and h. On the other hand, from Lemma 2.2 we can obtain

Corollary 2.3. *System* (2.1) *has no equilibria in the first quadrant if one of the following conditions holds*:

(i) $h \geqslant \frac{1}{3ab}\{(1-a+a^2)b^2 + a(1-2a)bd + a^2d^2\} > 0$;
(ii) $d \geqslant \frac{b(1+a)}{a}$.

Proof. When $S^2 - T \leqslant 0$, $F'(x) \geqslant 0$ and so system (2.1) has not any equilibria in the first quadrant. This gives (i). On the other hand, if $S \geqslant 3$ then $u < 1$ does not happen, leading to (ii). □

Corollary 2.3 shows that if either predator harvest rate h or predator death rate d is large enough, then system (2.1) has no equilibria, and $\dot{y}(t) < 0$ in R_+^2. The dynamics of system (2.1) in R_+^2 is trivial and all orbits in R_+^2 will cross the x-axis and $y(t)$ becomes negative in finite time. This implies that the predator species goes extinct as either predator harvest rate h or predator death rate d is large enough.

Next we consider the dynamics of system (2.1) in the neighborhood of each equilibrium if the system has equilibria. The linear part of system (2.1) at the equilibrium (x, y) is determined by the matrix

$$D(x,y) = \begin{pmatrix} 1 - 2x - \frac{ay^2}{(x+y)^2} & -\frac{ax^2}{(x+y)^2} \\ \frac{by^2}{(x+y)^2} & -d + \frac{bx^2}{(x+y)^2} \end{pmatrix}.$$

The dynamics of system (2.1) in the neighborhood of an equilibrium (x, y) directly depends on the property of eigenvalues of the matrix $D(x, y)$.

Theorem 2.4.

(1) *Suppose that system* (2.1) *has a unique equilibrium* $\left(u, \frac{u(1-u)}{u+a-1}\right)$ *in* R_+^2. *Then the equilibrium is degenerate and system* (2.1) *has not any limit cycles in* R_0^+. *More precisely,*
  (1a) *the equilibrium is a saddle-node if* $-a + b + a^2 - 2ab + a^2b - a^2d + (2a - 2a^2 - 2b + 2ab)u + (-a + b)u^2 \neq 0$;
  (1b) *the equilibrium is a cusp if* $-a + b + a^2 - 2ab + a^2b - a^2d + (2a - 2a^2 - 2b + 2ab)u + (-a + b)u^2 = 0$.

(2) *Suppose that system* (2.1) *has two equilibria* (x_1, y_1) *and* (x_2, y_2) *in* R_+^2, *where* $0 < x_1 < x_2 < 1$. *Then equilibrium* (x_1, y_1) *is a focus* (*or a center or a node*) *and equilibrium* (x_2, y_2) *is a hyperbolic saddle.*

Proof. We first prove the conclusion (1).

It is clear that if the determinant of the matrix $D\left(u, \frac{u(1-u)}{u+a-1}\right)$ is zero, then the equilibrium $\left(u, \frac{u(1-u)}{u+a-1}\right)$ is degenerate. Now we calculate the determinant of the Jacobian $D\left(u, \frac{u(1-u)}{u+a-1}\right)$ of system (2.1) at $\left(u, \frac{u(1-u)}{u+a-1}\right)$ and obtain

$$\det D\left(u, \frac{u(1-u)}{u+a-1}\right) = \frac{1}{a^2}\bigl\{-2bu^3 + (5b-4ab+ad)u^2 + \bigl(-4b+6ab-2ad-2a^2b+2a^2d\bigr)u + b - 2ab + ad + a^2b - a^2d\bigr\}.$$

Note that system (2.1) has a unique equilibrium $\bigl(u, \frac{u(1-u)}{u+a-1}\bigr)$ in R_+^2. Then the root u is a double root of (2.3) from Lemma 2.2. Hence,

$$F(u) = 0,\quad F'(u) = 0. \tag{2.7}$$

From (2.7), we reduce

$$h = -\frac{1}{a}\bigl\{3bu^2 + (2ab-4b-ad)u + b - ab + ad\bigr\}$$
$$-2bu^3 + (5b-4ab+ad)u^2 + \bigl(-4b+6ab-2ad-2a^2b+2a^2d\bigr)u + b - 2ab + ad + a^2b - a^2d = 0. \tag{2.8}$$

Therefore, $\det D\bigl(u, \frac{u(1-u)}{u+a-1}\bigr) = 0$ by (2.8). This implies the equilibrium $\bigl(u, \frac{u(1-u)}{u+a-1}\bigr)$ is degenerate.

To determine the dynamics of system (2.1) in the neighborhood of the equilibrium $\bigl(u, \frac{u(1-u)}{u+a-1}\bigr)$, we first transform the equilibrium $\bigl(u, \frac{u(1-u)}{u+a-1}\bigr)$ of system (2.1) to the origin and expand the right-hand side of system as a Taylor series. Then system (2.1) becomes

$$\dot{x} = \left(1 - 2u - \frac{(1-u)^2}{a}\right)x - \frac{(u+a-1)^2}{a}y + g_1(x, y),$$
$$\dot{y} = \frac{b(1-u)^2}{a^2}x + \left(-d + \frac{b(u+a-1)^2}{a^2}\right)y + g_2(x, y), \tag{2.9}$$

where $g_1(x, y)$ and $g_2(x, y)$ are smooth functions with at least the second order with respect to (x, y).

Let us analyze the property of eigenvalues of the matrix

$$D\left(u, \frac{u(1-u)}{u+a-1}\right) = \begin{pmatrix} 1 - 2u - \frac{(1-u)^2}{a} & -\frac{(u+a-1)^2}{a} \\ \frac{b(1-u)^2}{a^2} & -d + \frac{b(u+a-1)^2}{a^2} \end{pmatrix}.$$

Since $\det D\bigl(u, \frac{u(1-u)}{u+a-1}\bigr) = 0$, at least one of the eigenvalues of the matrix $D\bigl(u, \frac{u(1-u)}{u+a-1}\bigr)$ is zero. If the trace of the matrix $D\bigl(u, \frac{u(1-u)}{u+a-1}\bigr)$ is also zero, then both eigenvalues of the matrix $D\bigl(u, \frac{u(1-u)}{u+a-1}\bigr)$ are zero. Otherwise, one of the eigenvalues of the matrix $D\bigl(u, \frac{u(1-u)}{u+a-1}\bigr)$ is zero and another is nonzero. However, if the condition in part (1a) holds, i.e., $\operatorname{tr} D\bigl(u, \frac{u(1-u)}{u+a-1}\bigr) \neq 0$. Hence, there exists a smooth nonsingular transformation $\bar{x} = p_1(x, y)$, $\bar{y} = q_1(x, y)$ such that system (2.9) becomes (for simplicity, we still denote $\bar{x}$ and $\bar{y}$ by x and y, respectively.)

$$\dot{x} = P_1(x, y),\quad \dot{y} = y + Q_1(x, y), \tag{2.10}$$

where $P_1(x, y)$ and $Q_1(x, y)$ are smooth functions with at least the second order with respect to (x, y).

Because u is a double root of Eq. (2.3), $P_1(x,0) = k_1x^2 + \bar{P}(x)$, here k_1 is a nonzero constant depending on parameter (a,b,d,h) and $\bar{P}(x)$ is a smooth function with at least the third order with respect to x. Therefore, the equilibrium $(0,0)$ of (2.10) is a saddle-node by [25, Theorem 7.1, Chapter 2]. We finish the proof of the part (1a).

If

$$-a+b+a^2-2ab+a^2b-a^2d+\bigl(2a-2a^2-2b+2ab\bigr)u+(-a+b)u^2=0,$$

i.e., $\operatorname{tr} D\bigl(u, \frac{u(1-u)}{u+a-1}\bigr)=0$, then both eigenvalues of the matrix $D\bigl(u, \frac{u(1-u)}{u+a-1}\bigr)$ are zero. Note that the matrix $D\bigl(u, \frac{u(1-u)}{u+a-1}\bigr)$ is not zero matrix. Thus, system (2.9) can be transformed to

$$\begin{aligned} \dot{x} &= y + P_2(x,y), \\ \dot{y} &= Q_2(x,y), \end{aligned} \tag{2.11}$$

where $P_2(x,y)$ and $Q_2(x,y)$ are smooth functions with at least the second order with respect to (x,y). Because u is a double root of Eq. (2.3), $Q_2(x,0) = k_2x^2 + \bar{Q}(x)$, where k_2 is a nonzero constant depending on parameter (a,b,d,h) and $\bar{Q}(x)$ is a smooth function with at least the third order with respect to x. By a series of nonsingular transformations in [25], system (2.11) becomes

$$\begin{aligned} \dot{x} &= y, \\ \dot{y} &= k_2x^2\bigl(1+h(x)\bigr) + k_3x^m y\bigl(1+g(x)\bigr) + y^2p(x,y), \end{aligned} \tag{2.12}$$

where $h(x)$, $g(x)$ and $p(x,y)$ are smooth functions in all variables. $h(0)=g(0)=p(0,0)=0$, k_2 and k_3 are constants depending on parameter (a,b,d,h) and $k_2 \neq 0$, m is an integer and $m \geqslant 1$. From [25, Theorem 7.3, Chapter 2], the equilibrium $(0,0)$ of system (2.12) is a cusp. This implies equilibrium $\bigl(u, \frac{u(1-u)}{u+a-1}\bigr)$ of system (2.1) is a cusp.

Nonexistence of limit cycles in R_+^2 comes from the following arguments. If there exists a limit cycle in R_0^+, then the limit cycle must contain some equilibria in its interior and the sum of index of these equilibria is one. However, $\bigl(u, \frac{u(1-u)}{u+a-1}\bigr)$ is a unique equilibrium of system (2.1) in R_+^2, and the equilibrium $\bigl(u, \frac{u(1-u)}{u+a-1}\bigr)$ is a saddle-node or a cusp, whose index is not one. Hence, it is impossible to have any limit cycles in R_0^+ if system (2.1) has a unique equilibrium in R_0^+. This completes the proof of conclusion (1).

Next we prove the conclusion (2). It is sufficient to consider the sign of the determinant of the matrix $D(x_i,y_i)$. Note that $y_i = \frac{x_i(1-x_i)}{x_i+a-1}$, $i=1,2$. Straightforward computation shows that

$$\begin{aligned} \det D(x_i,y_i) = \frac{1}{a^2}\bigl\{&-2bx_i^3 + (5b-4ab+ad)x_i^2 \\ &+ \bigl(-4b+6ab-2ad-2a^2b+2a^2d\bigr)x_i + b-2ab+ad+a^2b-a^2d\bigr\}, \end{aligned}$$

where $i=1,2$.

On the other hand, from Lemma 2.2, we have

$$\begin{aligned} &F(x_i) = 0, \\ &(-1)^i F'(x_i) > 0. \end{aligned} \tag{2.13}$$

After some computation, (2.13) reduces

$$(-1)^{i+1}\frac{1}{b}\big\{-2bx_i^3+(5b-4ab+ad)x_i^2+\big(-4b+6ab-2ad-2a^2b+2a^2d\big)x_i$$
$$+b-2ab+ad+a^2b-a^2d\big\}>0,$$

which implies that $\det D(x_1,y_1)>0$ and $\det D(x_2,y_2)<0$. Hence, the conclusion (2) holds. The proof is complete. □

3. Bifurcations of system (2.1)

From Theorem 2.4 we can see that system (2.1) has a unique degenerate positive equilibrium when one of conditions (I.a) and (I.b) of Lemma 2.2 holds. The degenerate positive equilibrium is a saddle-node or a cusp. By a standard argument of bifurcation theory, we conclude that some bifurcations may occur for system (2.1). It is interesting that what kinds of bifurcation system (2.1) can undergo when the original parameters of system vary. However, the expressions, which depend on all four parameters, of the unique positive equilibrium of system (2.1) in Lemma 2.1 are too complicated to analysis the number of codimension of the degenerate equilibrium. To discuss the bifurcation of system (2.1), we have to fix some values of parameters for system (2.1) such that the number of codimension of the unique degenerate equilibrium can be determined. From the analysis of bifurcations for system (2.1), we will see how rich dynamics system (2.1) has. In this section we fix $a=1$ to discuss bifurcations of (2.1) in the hyperplane of parameter space (a,b,d,h). In this case, b, d and h are free parameters, and the number of free parameters is three, which is maximum. Though $a=1$ is a special case biologically for system (2.1), the procedure of discussion for bifurcations of (2.1) in the case is generic, which can be applied to studying bifurcations of (2.1) in other cases of parameters which satisfies one of conditions (I.a) and (I.b) of Lemma 2.2, for example, taking $a=\frac{56}{585}$, $d=b$, $h=\frac{507}{160}b$ and $b>0$.

We now restrict our attentions to the bifurcations of system (2.1) when $a=1$

$$\begin{aligned}\dot{x}&=x(1-x)-\frac{xy}{y+x}\triangleq f_3(x,y),\\ \dot{y}&=y\left(-d+\frac{bx}{y+x}\right)-h\triangleq f_4(x,y).\end{aligned}\tag{3.1}$$

In order to find all conditions under which the equilibrium of system (3.1) is not hyperbolic, we analyze the property of the trace of matrix $D(x_1,y_1)$, and summarize Lemma 2.2 and Theorem 2.4 in the case $a=1$ as follows.

Lemma 3.1.

(1) *System* (3.1) *has no equilibria in the first quadrant* R_+^2 *if either* $h>h_0$ *or* $b\leqslant d$, *here* $h_0=\frac{(b-d)^2}{4b}$.
(2) *System* (3.1) *has a unique equilibrium in* R_+^2, *which is* $(x_0,y_0)=\big(\frac{b+d}{2b},\frac{b-d}{2b}\big)$ *if both* $h=h_0$ *and* $b>d$. *And* (x_0,y_0) *is a cusp if* $h=h_0$, $b>1$ *and* $d=d_0$, *here* $d_0=\frac{b(b+1)-2b\sqrt{b}}{b-1}$; *otherwise,* (x_0,y_0) *is a saddle-node.*
(3) *System* (3.1) *has two equilibria,* (x_1,y_1) *and* (x_2,y_2) *in* R_+^2 *if both* $0<h<h_0$ *and* $d<b$, *where*

$$x_i = \frac{b + d + (-1)^i\sqrt{(b-d)^2 - 4bh}}{2b},$$
$$y_i = \frac{b - d + (-1)^{i+1}\sqrt{(b-d)^2 - 4bh}}{2b}, \quad i = 1, 2.$$

Furthermore, (x_2, y_2) *is a hyperbolic saddle and* (x_1, y_1) *is a focus* (*or a center or a node*). *More precisely,*

(3a) (x_1, y_1) *is a hyperbolic stable focus* (*or node*) *if either*

$$\begin{cases} 0 < h < h_0; \\ 0 < d < b \leqslant 1; \end{cases} \quad \text{or} \quad \begin{cases} 0 < h < h^*; \\ 1 < b; \\ 0 < d < d_0; \end{cases}$$

here

$$h^* = \frac{(b-d)^2 - (b + d - 2b\sqrt{d/(b-1)})^2}{4b}.$$

(3b) (x_1, y_1) *is a weak focus* (*or a center*) *if*

$$\begin{cases} h = h^*; \\ 1 < b; \\ 0 < d < d_0. \end{cases}$$

(3c) (x_1, y_1) *is a hyperbolic unstable focus* (*or node*) *if*

$$\begin{cases} h^* < h < h_0; \\ 1 < b; \\ 0 < d < d_0. \end{cases}$$

3.1. Saddle-node bifurcations

From Lemma 3.1, we know there exists a surface in parameter space (b, d, h),

$$SN = \{(b, d, h):\ h = h_0,\ 0 < d < b,\ d \neq d_0 \text{ if } b > 1\},$$

such that for all parameters on the surface SN, system (3.1) has a unique equilibrium (x_0, y_0), which is a saddle-node. When the parameters (b, d, h) pass from one side of the surface to the other side, the number of equilibria of system (3.1) changes from zero to two. This implies that system (3.1) undergoes a saddle-node bifurcation of codimension 1. The surface SN is called a *saddle-node bifurcation surface*.

3.2. The cusp bifurcation of codimension 2 (i.e., the Bogdanov–Takens bifurcation)

In parameter space (b, d, h) there exists a curve

$$C = \{(b, d, h):\ h = h_0,\ d = d_0,\ b > 1\}$$

such that a unique equilibrium (x_0, y_0) of system (3.1) is a cusp for all parameters on the curve C by Lemma 3.1, here

$$x_0 = \frac{\sqrt{b}}{1 + \sqrt{b}}, \qquad y_0 = \frac{1}{1 + \sqrt{b}}.$$

In the following we present the cusp is codimension two.

Theorem 3.2. *Let $b > 1$. If $d = d_0$ and $h = h_0 = \frac{b}{(1+\sqrt{b})^2}$, then system* (3.1) *has a unique positive equilibrium $(\frac{\sqrt{b}}{1+\sqrt{b}}, \frac{1}{1+\sqrt{b}})$, which is a cusp of codimension two.*

Proof. Under assumptions of Theorem 3.2, we can see that equilibrium $(\frac{\sqrt{b}}{1+\sqrt{b}}, \frac{1}{1+\sqrt{b}})$ is a cusp by Lemma 3.1. Next we only transform system (3.1) to the canonical normal form of cusp of codimension two as in [20]. We translate the equilibrium $(\frac{\sqrt{b}}{1+\sqrt{b}}, \frac{1}{1+\sqrt{b}})$ of system (3.1) to the origin and expand the right-hand side of system as a Taylor series. Then system (3.1) becomes

$$\begin{aligned}
\dot{x} &= -\frac{b}{(1+\sqrt{b})^2}x - \frac{b}{(1+\sqrt{b})^2}y - \frac{b+2\sqrt{b}}{(1+\sqrt{b})^2}x^2 - \frac{2\sqrt{b}}{(1+\sqrt{b})^2}xy \\
&\quad + \frac{b}{(1+\sqrt{b})^2}y^2 + O_1(x,y), \\
\dot{y} &= \frac{b}{(1+\sqrt{b})^2}x + \frac{b}{(1+\sqrt{b})^2}y - \frac{b}{(1+\sqrt{b})^2}x^2 + \frac{2b\sqrt{b}}{(1+\sqrt{b})^2}xy \\
&\quad - \frac{b^2}{(1+\sqrt{b})^2}y^2 + O_2(x,y),
\end{aligned} \tag{3.2}$$

where $O_1(x,y)$ and $O_2(x,y)$ are smooth functions of x and y at least of order three in x and y.

For simplicity of computation, introducing the new time by $\tau = (1+\sqrt{b})^{-2}t$, we have

$$\begin{aligned}
\frac{dx}{d\tau} &= -bx - by - (b+2\sqrt{b})x^2 - 2\sqrt{b}xy + by^2 + O_3(x,y), \\
\frac{dy}{d\tau} &= bx + by - bx^2 + 2b\sqrt{b}xy - b^2y^2 + O_4(x,y).
\end{aligned} \tag{3.3}$$

In order to obtain the canonical normal forms, we perform the following C^∞ transformation of variables for system (3.3) in a small neighborhood of $(0,0)$ step-by-step:

$$\begin{aligned}
&X_1 = x, \qquad Y_1 = -bx - by; \\
&X_2 = X_1 - \frac{1}{2}\left(1 + \frac{2}{\sqrt{b}} + b\right)X_1^2 - \frac{1}{b}X_1Y_1, \qquad Y_2 = Y_1 - (b-1)X_1Y_1, \\
&X_3 = X_2, \qquad Y_3 = Y_2 + O_5(X_2, Y_2).
\end{aligned}$$

We finally obtain

$$\begin{aligned}
\frac{dX_3}{d\tau} &= Y_3, \\
\frac{dY_3}{d\tau} &= b^2(1+\sqrt{b})^2X_3^2 + 2\sqrt{b}(1+\sqrt{b})(b-1)X_3Y_3 + O(X_3,Y_3),
\end{aligned} \tag{3.4}$$

where $O(X_3,Y_3)$ is a smooth function of X_3 and Y_3 at least of order three in X_3 and Y_3. Since $b > 1$, this leads that the origin of (3.4) is a cusp of codimension 2. Hence, we prove the conclusion. □

In the following, we will find the versal unfolding of $(\frac{\sqrt{b}}{1+\sqrt{b}}, \frac{1}{1+\sqrt{b}})$ depending on the original parameters in system (3.1). We will show that d and h can be chosen as bifurcation parameters and system (3.1) can exhibit Bogdanov–Takens bifurcation. Let

$$d = d_0 - \lambda_1, \qquad h = h_0 - \lambda_2.$$

Consider the following system:

$$\begin{aligned}\dot{x} &= x(1-x) - \frac{bxy}{x+y},\\ \dot{y} &= y\left(-d_0 + \lambda_1 + \frac{bx}{x+y}\right) - h_0 + \lambda_2,\end{aligned} \tag{3.5}$$

where

$$b > 1, \quad d_0 = \frac{b(b+1) - 2b\sqrt{b}}{b-1}, \quad h_0 = \frac{b}{(1+\sqrt{b})^2},$$

λ_1 and λ_2 are very small parameters. When $\lambda_1 = \lambda_2 = 0$, system (3.5) has a unique positive equilibrium $\left(\frac{\sqrt{b}}{1+\sqrt{b}}, \frac{1}{1+\sqrt{b}}\right)$, which is a cusp of codimension 2.

Substituting

$$X = x - \frac{\sqrt{b}}{1+\sqrt{b}}, \qquad Y = y - \frac{1}{1+\sqrt{b}}$$

into (3.5) and using the Taylor expansion, we obtain that

$$\begin{aligned}\dot{X} &= -\frac{b}{(1+\sqrt{b})^2}X - \frac{b}{(1+\sqrt{b})^2}Y - \frac{b+2\sqrt{b}}{(1+\sqrt{b})^2}X^2 - \frac{2\sqrt{b}}{(1+\sqrt{b})^2}XY\\ &\quad + \frac{b}{(1+\sqrt{b})^2}Y^2 + O_1(X,Y),\\ \dot{Y} &= \frac{1}{1+\sqrt{b}}\lambda_1 + \lambda_2 + \frac{b}{(1+\sqrt{b})^2}X + \left(\frac{b}{(1+\sqrt{b})^2} + \lambda_1\right)Y - \frac{b}{(1+\sqrt{b})^2}X^2\\ &\quad + \frac{2b\sqrt{b}}{(1+\sqrt{b})^2}XY - \frac{b^2}{(1+\sqrt{b})^2}Y^2 + O_2(X,Y),\end{aligned} \tag{3.6}$$

where $O_i(X,Y)$ $(i = 1,2)$ represent the higher order terms. To be concise in notations, rescale (3.6) by $\tau = (1+\sqrt{b})^{-2}t$. For simplicity, we still use variables x, y, t instead of X, Y, τ. We obtain that

$$\begin{aligned}\dot{x} &= -bx - by - (b+2\sqrt{b})x^2 - 2\sqrt{b}xy + by^2 + O_3(x,y),\\ \dot{y} &= (1+\sqrt{b})\lambda_1 + (1+\sqrt{b})^2\lambda_2 + bx + \left(b + \lambda_1(1+\sqrt{b})^2\right)y - bx^2\\ &\quad + 2b\sqrt{b}xy - b^2y^2 + O_4(x,y),\end{aligned} \tag{3.7}$$

here $\dot{x} = \frac{dX}{d\tau}$, $\dot{y} = \frac{dY}{d\tau}$. Next we reduce system (3.7) to the normal form in successive steps. These steps are reminiscent of those performed in the proof of Theorem 3.2. For simplicity, we omit the laborious steps and write down the normal form directly:

$$\begin{aligned}\dot{x} &= y,\\ \dot{y} &= \mu_1(\lambda_1,\lambda_2) + \mu_2(\lambda_1,\lambda_2)y + x^2 + \frac{2(b-1)}{b(b+\sqrt{b})}xy + O(\lambda,x,y),\end{aligned} \tag{3.8}$$

where $\lambda = (\lambda_1, \lambda_2)$, $O(\lambda,x,y)$ is a smooth function of x, y and λ at least of order three in x and y, and

$$\mu_1(\lambda_1,\lambda_2)=-\frac{\lambda_1}{b(1+\sqrt{b})}-\frac{\lambda_2}{b}+O_5(\lambda_1,\lambda_2),$$
$$\mu_2(\lambda_1,\lambda_2)=-\frac{\sqrt{b}\lambda_1}{b^2(1+\sqrt{b})}+\frac{\lambda_2}{b^2}+O_6(\lambda_1,\lambda_2), \tag{3.9}$$

here $O_i(\lambda_1,\lambda_2)$ $(i=5,6)$ are higher order terms. Computing the Jacobian of (3.9) shows that the above parameter transformation from (λ_1,λ_2) to (μ_1,μ_2) is not singular in a small neighborhood of $(\lambda_1,\lambda_2)=(0,0)$. Thus, system (3.8) is strongly topologically equivalent to

$$\dot{x}=y,$$
$$\dot{y}=\mu_1+\mu_2 y+x^2+\frac{2(b-1)}{b(b+\sqrt{b})}xy. \tag{3.10}$$

By the theorems of Bogdanov and Takens in [20], we obtain

Theorem 3.3. *When $b>1$, $0<|h-h_0|\ll 1$ and $0<|d-d_0|\ll 1$, system* (3.5) *undergoes the cusp bifurcation of codimension* 2 (*i.e., the B–T bifurcation*). *Hence, there exist values of the parameters* (h,b,d) *such that system* (3.5) *has a unique unstable limit cycle for some parameter values, and system* (3.5) *has an unstable homoclinic loop for other parameter values.*

3.3. Hopf bifurcations

From the term (3b) of Lemma 3.1, we know that in parameter space (b,d,h), there exists a surface

$$H=\{(b,d,h):\ b>1,\ d_0>d>0,\ h=h^*\}$$

such that system (3.1) has two equilibria (x_1,y_1) and (x_2,y_2) in R^2_+, (x_2,y_2) is a hyperbolic saddle and (x_1,y_1) is a weak focus or a center, here $x_1=\sqrt{d/(b-1)}$, $y_1=1-x_1$. Hence, system (3.1) may undergo Hopf bifurcation. In this subsection, we discuss conditions under which the stability of (x_1,y_1) will change such that system (3.1) exhibits Hopf bifurcation.

We first determine the stability of the equilibrium (x_1,y_1) when parameter (b,d,h) belongs to H. In order to see the stability, we have to compute the Lyapunov coefficients of (x_1,y_1). Making a transformation of $X=x-x_1$, $Y=y-y_1$ to translate (x_1,y_1) to the origin and rewriting X,Y as x and y, respectively, we have

$$\dot{x}=a_{10}x+a_{01}y+a_{20}x^2+a_{11}xy+a_{02}y^2+a_{30}x^3+a_{21}x^2y+a_{12}xy^2$$
$$+a_{03}y^3+O_1(|(x,y)|^4),$$
$$\dot{y}=b_{10}x+b_{01}y+b_{20}x^2+b_{11}xy+b_{02}y^2+b_{30}x^3+b_{21}x^2y+b_{12}xy^2$$
$$+b_{03}y^3+O_2(|(x,y)|^4), \tag{3.11}$$

where a_{ij} and b_{ij} are the coefficients of the power series expansions of $f_3(x,y)$ and $f_4(x,y)$ at (x_1,y_1), respectively, $i,j=0,1,2,3$. $O_k(|(x,y)|^4)$ is the same order infinity, $k=1,2$.

It is clear that

$$a_{10}b_{01}-a_{01}b_{10}\neq 0,\quad a_{10}+b_{01}=0$$

because parameter (b,d,h) belongs to H. Hence, using the formula of the first Lyapunov number σ at the origin of (3.11) in [20, p. 344], we have after a tedious computation using Mathematica

$$\sigma=\frac{3\pi Q}{4x_1\sqrt{(b+d-2bx_1)^3}},$$

where

$$x_1 = \sqrt{\frac{d}{b-1}}, \quad b > 1, \quad 0 < d < d_0 = \frac{b(\sqrt{b}-1)}{\sqrt{b}+1}$$

and

$$\begin{aligned} Q = {} & \big(b^3 - 3b^2 + 3b - 1\big)x_1^4 - \big(2b^3 - 2b^2 + 2b + 2\big)x_1^3 \\ & + \big(2b^3 + b^2 + 2b + 1\big)x_1^2 - 2b^3 x + b^3 - b. \end{aligned}$$

Therefore, the sign of σ is determined by Q. If $Q \neq 0$, then the origin of (3.11) is a weak focus of multiplicity one, it is stable if $Q < 0$ and unstable if $Q > 0$.

Using the fact that $x_1 = \sqrt{d/(b-1)}$, with the aid of numerical calculation, we can see that the sign of σ is not determined. For example, when parameter $(b, d) = (2, 0.34)$ is on the surface H, $\sigma = 30507.2$. On the other hand, when parameter $(b, d) = (1.1, 0.0143)$ is also on the surface H, $\sigma = -0.3765$. Therefore, in the surface H there exists a curve

$$l = \big\{(b, d, h)\colon\ Q = 0,\ h = h^*,\ b > 1,\ d_0 > d > 0\big\}$$

such that $\sigma = 0$ since σ is a continuous function of (b, d). When parameter (b, d, h) is at the curve l, the origin of (3.11) is a weak focus of multiplicity at least two or a center. Hence, the surface H is divided into two parts H_b and H_p by the curve l, $\sigma > 0$ if (b, d, h) is in H_b and $\sigma < 0$ if (b, d, h) is in H_p. That is

$$\begin{aligned} H_b &= \big\{(b, d, h)\colon\ b > 1,\ d_0 > d > 0,\ h = h^*,\ Q > 0\big\}, \\ H_p &= \big\{(b, d, h)\colon\ b > 1,\ d_0 > d > 0,\ h = h^*,\ Q < 0\big\}. \end{aligned}$$

Summarizing the above discussion, we can obtain

Theorem 3.4.

(a) *If the parameter (b, d, h) is in H_b, then the equilibrium (x_1, y_1) of system* (3.1) *is a weak focus of multiplicity one and it is unstable.*
(b) *If the parameter (b, d, h) is at the curve l, then the equilibrium (x_1, y_1) of system* (3.1) *is a weak focus of multiplicity at least two or a center.*
(c) *If the parameter (b, d, h) is in H_p, then the equilibrium (x_1, y_1) of system* (3.1) *is a weak focus of multiplicity one and it is stable.*

From the conclusion (3a) of Lemma 3.1 and the third case (c) in Theorem 3.4, we know that the weak focus (x_1, y_1) generates a stable limit cycle as h passes through the bifurcation value $h = h^*$ from one side of the surface H_p to the other side, system (3.1) can undergo a supercritical Hopf bifurcation (see [20]). A stable limit cycle appears in the small neighborhood of (x_1, y_1) when $(b, d) \in H_p$, $h^* < h < h_0$ and $|h - h^*| \ll 1$. The surface H_p is called a *supercritical Hopf bifurcation*.

On the other hand, from the conclusion (3c) of Lemma 3.1 and the first case (a) in Theorem 3.4, we know that the weak focus (x_1, y_1) generates an unstable limit cycle as h passes through the bifurcation value $h = h^*$ from one side of the surface H_b to the other side, system (3.1) can undergo a subcritical Hopf bifurcation (see [20]). An unstable limit cycle appears in the small neighborhood of (x_1, y_1) when $(b, d) \in H_b$, $0 < h < h^*$ and $|h - h^*| \ll 1$. The surface H_b is called a *subcritical Hopf bifurcation*.

Summarizing the above, we have

Theorem 3.5.

(i) *System* (3.1) *has at least one unstable limit cycle if* $(b,d) \in H_b$, $0 < h < h^*$ *and* $|h - h^*| \ll 1$;
(ii) *system* (3.1) *has at least one stable limit cycle if* $(b,d) \in H_p$, $h^* < h < h_0$ *and* $|h - h^*| \ll 1$.

Remark 3.6. Since there exist some parameter values such that $\sigma = 0$, system (3.1) maybe undergo *degenerate Hopf bifurcation* for some parameter values (cf. [6,11,12,20]). It is possible that there exist two limit cycles of (3.1) in R_+^2.

4. Discussion

In [8–10] Brauer and Soudack have noticed some different types of dynamics whether the harvesting was in the prey or in the predator equation for a class of predator–prey system. In this paper, by combining qualitative and bifurcation analyzes we have studied the dynamics of the ratio-dependent model with a constant rate predator harvesting. We could show some differences for the model (2.1) with predator harvesting and the following model with prey harvesting (cf. [23]):

$$\begin{aligned} \dot{x} &= x(1-x) - \frac{axy}{y+x} - h, \\ \dot{y} &= y\left(-d + \frac{bx}{y+x}\right). \end{aligned} \tag{4.1}$$

For example, when the nonzero constant harvesting was in the prey, it has shown that the model (4.1) has four equilibria in R_+^2 and undergoes two saddle-node bifurcations, the separatrix connecting a saddle and a saddle-node bifurcation and heteroclinic bifurcation (cf. [23]). On the other hand, when the nonzero constant harvesting was in the predator, in this paper we shown that the model (2.1) has only two equilibria in R_+^2 and undergoes one saddle-node bifurcation. There does not exist the separatrix connecting a saddle and a saddle-node bifurcation and heteroclinic bifurcation for the model (2.1). However, it is common for the model (2.1) and the model (4.1) that both harvesting could lead some dangers in real-life harvesting such as no equilibrium exists and either prey or predator goes to extinction for some values of harvesting rate. It would be interesting that the nonzero constant harvesting in both models can prevent mutual extinction of prey and predator, and remove the singularity of the origin, which was regarded as "pathological behavior" by some researchers (cf. [24]). And in both models coexistence of predator and prey species is possible for some but not all initial conditions.

Acknowledgments

The authors are grateful to the anonymous referees for their valuable comments and suggestions.

References

[1] P.A. Abrams, L.R. Ginzburg, The nature of predation: Prey dependent, ratio-dependent or neither? Trends in Ecology and Evolution 15 (2000) 337–341.
[2] H.R. Akcakaya, R. Arditi, L.R. Ginzburg, Ratio-dependent prediction: An abstraction that works, Ecology 79 (1995) 995–1004.
[3] R. Arditi, A.A. Berryman, The biological paradox, Trends in Ecology and Evolution 6 (1991) 32.

[4] R. Arditi, L.R. Ginzburg, Coupling in predator–prey dynamics: Ratio-dependence, J. Theoret. Biol. 139 (1989) 311–326.
[5] R. Arditi, L.R. Ginzburg, H.R. Akcakaya, Variation in plankton densities among lakes: A case for ratio-dependent models, Amer. Naturalist 138 (1991) 1287–1296.
[6] A. Andronov, E.A. Leontovich, I.I. Gordon, A.G. Maier, Theory of Bifurcations of Dynamical Systems on a Plane, Israel Program for Scientific Translations, Jerusalem, 1971.
[7] F. Berezovskaya, G. Karev, R. Arditi, Parametric analysis of the ratio-dependent predator–prey model, J. Math. Biol. 43 (2001) 221–246.
[8] F. Brauer, A.C. Soudack, Stability regions and transition phenomena for harvested predator–prey systems, J. Math. Biol. 7 (1979) 319–337.
[9] F. Brauer, A.C. Soudack, Stability regions in predator–prey systems with constant rate prey harvesting, J. Math. Biol. 8 (1979) 55–71.
[10] F. Brauer, A.C. Soudack, Coexistence properties of some predator–prey systems under constant rate harvesting and stocking, J. Math. Biol. 12 (1981) 101–114.
[11] S.-N. Chow, J.K. Hale, Methods of Bifurcation Theory, Springer, New York, 1982.
[12] S.-N. Chow, C.Z. Li, D. Wang, Normal Forms and Bifurcation of Planar Vector Fields, Cambridge Univ. Press, Cambridge, 1994.
[13] C.W. Clark, Mathematical Bioeconomics, The Optimal Management of Renewable Resources, second ed., Wiley, New York, 1990.
[14] C. Cosner, D.L. DeAngelis, J.S. Ault, D.B. Olson, Effects of spatial grouping on the functional response of predators, Theor. Pop. Biol. 56 (1999) 65–75.
[15] A.P. Gutierrez, The physiological basis of ratio-dependent predator–prey theory: A metabolic pool model of Nicholson's blowflies as an example, Ecology 73 (1992) 1552–1563.
[16] S.B. Hsu, T.W. Hwang, Y. Kuang, Global analysis of the Michaelis–Menten type ratio-dependent predator–prey system, J. Math. Biol. 42 (2001) 489–506.
[17] C. Jost, O. Arino, R. Arditi, About deterministic extinction in ratio-dependent predator–prey models, Bull. Math. Biol. 61 (1999) 19–32.
[18] Y. Kuang, Rich dynamics of Gause-type ratio-dependent predator–prey system, Fields Inst. Commun. 21 (1999) 325–339.
[19] Y. Kuang, E. Beretta, Global qualitative analysis of a ratio-dependent predator–prey system, J. Math. Biol. 36 (1998) 389–406.
[20] L. Perko, Differential Equations and Dynamical Systems, Springer, New York, 1996.
[21] D. Xiao, S. Ruan, Bogdanov–Takens bifurcations in predator–prey systems with constant rate harvesting, Fields Inst. Commun. 21 (1999) 493–506.
[22] D. Xiao, S. Ruan, Global dynamics of a ratio-dependent predator–prey system, J. Math. Biol. 43 (2001) 268–290.
[23] D. Xiao, L. Jennings, Bifurcations of a ratio-dependent predator–prey system with constant rate harvesting, SIAM Appl. Math. 65 (2005) 737–753.
[24] P. Yodzis, Predator–prey theory and management of multispecies fisheries, Ecological Applications 4 (2004) 51–58.
[25] Z. Zhang, T. Ding, W. Huang, Z. Dong, Qualitative Theory of Differential Equations, Science Press, Beijing, 1992 (in Chinese). English edition: Transl. Math. Monogr., vol. 101, Amer. Math. Soc., Providence, RI, 1992.