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Global dynamics of a ratio-dependent predator-prey system

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Abstract. Recently, ratio-dependent predator-prey systems have been regarded by some researchers to be more appropriate for predator-prey interactions where predation involves serious searching processes. However, such models have set up a challenging issue regarding their dynamics near the origin since these models are not well-defined there. In this paper, the qualitative behavior of a class of ratio-dependent predator-prey system at the origin in the interior of the first quadrant is studied. It is shown that the origin is indeed a critical point of higher order. There can exist numerous kinds of topological structures in a neighborhood of the origin including the parabolic orbits, the elliptic orbits, the hyperbolic orbits, and any combination of them. These structures have important implications for the global behavior of the model. Global qualitative analysis of the model depending on all parameters is carried out, and conditions of existence and non-existence of limit cycles for the model are given. Computer simulations are presented to illustrate the conclusions.

1. Introduction

In population dynamics, a functional response of the predator to the prey density refers to the change in the density of prey per unit time per predator as a function of the prey density. The most important and useful functional response is the Michaelis-Menten or Holling type II function of the form

$$p(x) = \frac{cx}{m+x},$$

where $c > 0$ is the maximal growth rate of the predator, and $m > 0$ is the half-saturation constant. Because the function $p(x)$ depends solely on prey density, it is usually called a *prey-dependent* response function. Predator-prey systems with prey-dependent response have been studied extensively and the dynamics of such

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systems are now very well understood (for example, see Freedman [7] and the references cited therein).

Recently, the traditional prey-dependent predator-prey models have been challenged by several biologists (Arditi and Ginzburg [3], Arditi, Ginzburg and Akcakaya [4], Akcakaya [1], Gutierrez [9], etc.) based on the fact that functional and numerical responses over typical ecological timescales ought to depend on the densities of both prey and predators, especially when predators have to search for food (and therefore have to share or compete for food). Such a functional response is called a *ratio-dependent* response function. Based on the Michaelis-Menten or Holling type II function, Arditi and Ginzburg [3] proposed a ratio-dependent function of the form

$$p(\frac{x}{y}) = \frac{c\frac{x}{y}}{m + \frac{x}{y}} = \frac{cx}{my + x}$$

and the following ratio-dependent predator-prey model

$$\begin{aligned} \dot{x} &= x(a - bx) - \frac{cxy}{my + x}, \\ \dot{y} &= y(-d + \frac{fx}{my + x}). \end{aligned} \tag{1.1}$$

Here, $x(t)$ and $y(t)$ represent population densities of prey and predator at time t, respectively; $\frac{a}{b} > 0$ is the carrying capacity of the prey, $d > 0$ is the death rate of the predator, and a, c, m, and f are positive constants that stand for prey intrinsic growth rate, capturing rate, half saturation constant and conversion rate, respectively.

The merits of ratio-dependent versus prey-dependent models have been contested, see, for example, Berryman [5], Lundberg and Fryxell [14], and the references cited therein. Differing from the prey-dependent predator-prey models, the ratio-dependent predator-prey systems have two principal predictions: (a) equilibrium abundances are positively correlated along a gradient of enrichment (see Arditi and Ginzburg [3]) and (b) the "paradox of enrichment" (see Rosenzweig [16]) either completely disappears or enrichment is linked to stability in a more complex way. We will study some particular mathematical features rather than discuss the general ecological significance of this class of models.

The ratio-dependent predator-prey model (1.1) has been studied by several researchers recently and very rich dynamics have been observed. Freedman and Mathsen [8] restricted their analysis to parameter values that ensure the equilibrium $(0, 0)$ behaves like a saddle point and established conditions for persistence of the model. Jost, Arino and Arditi [11] studied the analytical behavior at $(0, 0)$ for a general ratio-dependent predator-prey model and showed that this equilibrium can be either a saddle point or an attractor for certain trajectories. Thus, the equilibrium $(0, 0)$ has its own basin of attraction in the phase space even if there exists an interior stable or unstable equilibrium. Kuang and Beretta [13] investigated the global behavior of solutions of system (1.1). They observed very rich boundary dynamics and showed that if the positive equilibrium of system (1.1) is locally asymptotically stable, then the system does not have any nontrivial positive periodic solutions. They also studied the global stability of the three equilibria $(0, 0)$, $(\frac{a}{b}, 0)$, and (x^*, y^*). Kuang and Beretta mentioned that there are still many interesting and challenging questions regarding the dynamics of system (1.1), such as the existence and uniqueness of a positive limit cycle when (x^*, y^*) exists and is unstable, etc. We also refer to Kuang [12] for a Gause-type predator-prey model with ratio-dependent response.

As observed by Freedman and Mathsen [8], Jost, Arino and Arditi [11], and Kuang and Beretta [13], system (1.1) is not well-defined at the origin $(0, 0)$ and thus cannot be linearized at $(0, 0)$. This is the main reason for system (1.1) to have very rich and complicated dynamics. In this paper, by redefining the system at $(0, 0)$ and making a transformation in the time variable, we transform system (1.1) into a polynomial system. The new system is well defined at $(0, 0)$ and can be linearized at $(0, 0)$. However, the Jacobian matrix at $(0, 0)$ is a zero matrix. Using the terminology of Andronov et al. [2] and Zhang et al. [18], we know that $(0, 0)$ is a *critical point of higher order* of system (1.1) (it is called a *nonhyperbolic critical point* in Perko [15]). By using the results in Zhang et al. [18], we will study the topological structures of system (1.1) around the critical point of high order $(0, 0)$ in the interior of the first quadrant and their implications on the global behavior of the solutions. We will also perform a global qualitative study on system (1.1) in the first quadrant and show that very interesting dynamic behaviors such as deterministic extinction, existence of multiple attractors and limit cycles can occur.

We would like to mention that some of our results coincide with that of Kuang and Beretta's in [13], and some of our results include theirs. Also, compared with Kuang and Beretta's paper, our analysis and results are more detailed and global in the sense that we classify and determine all possible topological structures near $(0, 0)$ and the global behaviors near $(\frac{a}{b}, 0)$ and (x^*, y^*) depending on all parameters. Moreover, inspired by the numerical simulations of Jost, Arino and Arditi [11], we carry out some computer simulations (using XPP) which not only support and illustrate our results very well but also provide more interesting cases and scenarios than that in [11]. Thus, our paper can be regarded as a complement of the papers of Kuang and Beretta [13] and Jost, Arino and Arditi [11].

This paper is organized as follows: in section 2, we study the singularity $(0, 0)$ of system (1.1) and give all possibilities for the orbits of system (1.1) to approach $(0, 0)$ as $t \to +\infty$ or $t \to -\infty$ depending on all parameters in the interior of the first quadrant. In section 3, existence and stability of equilibria of system (1.1) except $(0, 0)$ are discussed. Global qualitative analysis of system (1.1) is carried out in section 4, which contains some results on the global stability of the positive steady state and existence of multiple attractors and a limit cycle of system (1.1). In section 5, we summarize and classify the global dynamics of the system into three tables by considering all possible cases of the parameters.

2. Asymptotic behavior of the System (1.1) at $(0, 0)$

As it is typical for the predator-prey systems, the x-axis, y-axis and the interior of the first quadrant are all invariant under system (1.1), and solutions with positive initial values are positive and bounded. Since system (1.1) is not well-defined at

$(0, 0)$, we redefine system (1.1) as

$$\begin{aligned} \dot{x} &= x(a - bx) - \frac{cxy}{my + x}, \\ \dot{y} &= y(-d + \frac{fx}{my + x}), \\ \dot{x} &= \dot{y} = 0 \text{ when } (x, y) = (0, 0). \end{aligned} \tag{2.1}$$

It is easy to prove that system (2.1) is continuous and satisfies the Lipschitz condition in the closed first quadrant in the (x, y)-plane, denoted by I. Hence, system (2.1) has two equilibria, one is the origin and the other is $(K, 0)$ in the x-axis for all permissible parameters. However, system (2.1) cannot be linearized at $(0, 0)$. So local stability of $(0, 0)$ cannot be studied. Note that we are only interested in the dynamics of system (2.1) in the interior of the first quadrant, denoted by I^+. Thus, we can make a time scale change $dt = (my + x)d\tau$ such that system (2.1) is equivalent to the following system in the interior of the first quadrant

$$\begin{aligned} \dot{x} &= ax^2 + (am - c)xy - bx^3 - bmx^2y \equiv X_2(x, y) + \Phi(x, y), \\ \dot{y} &= (f - d)xy - dmy^2 \equiv Y_2(x, y), \end{aligned} \tag{2.2}$$

where X_2 and Y_2 are homogeneous polynomials in x and y of degree 2 and $\Phi(x, y) = -bx^3 - bmx^2y$. The equilibrium $(0, 0)$ of system (2.2) is an isolated critical point of higher order.

Obviously, system (2.2) is analytic in a neighborhood of the origin. By Theorem 3.10 on page 79 of [18], any orbit of (2.2) tending to the origin must tend to it spirally or along a fixed direction, which depends on the characteristic equation of system (2.2).

In this section, we will show that if a solution orbit of (2.2) tends to the origin then it must tend to it along a fixed direction. We will also determine the number of solution orbits of system (2.2) that tend to $(0, 0)$ along a fixed direction as $t \to +\infty$ or $t \to -\infty$ in the interior of the first quadrant by using the results in [18]. Hereafter, we refer to [18] for results and explanations of several notations involved.

First of all, we introduce the polar coordinates $x = r\cos\theta$, $y = r\sin\theta$ and define

$$G(\theta) = \cos\theta Y_2(\cos\theta, \sin\theta) - \sin\theta X_2(\cos\theta, \sin\theta).$$

Then the characteristic equation of system (2.2) takes the form

$$G(\theta) = \sin\theta\cos\theta[(c - am - dm)\sin\theta + (f - d - a)\cos\theta] = 0. \tag{2.3}$$

Clearly, either $G(\theta) = 0$ has a finite number of real roots $\theta_k (k = 1, 2, \ldots, n)$ or $G(\theta) \equiv 0$. By the results in section II.2 in [18], we know that no orbit of system (2.2) can tend to the critical point $(0, 0)$ spirally. It is a singular case if $G(\theta) \equiv 0$; and if $G(\theta)$ is not identically zero, then there are at most $2(2+1)$ directions $\theta = \theta_i$ along which an orbit of system (2.2) may approach the origin. These directions $\theta = \theta_i$ are given by solutions of the equation (2.3). If the orbits of system (2.2) tend to the origin as a sequence t_n of t tends to $+\infty$ or $-\infty$ along a direction $\theta = \theta_i$, then the direction is called a *characteristic direction*. The orbits of system (2.2) which approach the origin along characteristic directions divide a neighborhood of the origin into a finite number of open regions, called *sectors*. For an analytic system these sectors can be classified into three types called *hyperbolic sectors*, *parabolic sectors*, and *elliptic sectors*, respectively. They are described in the following figure and their definitions are given in [2] and [18], see also [15]. Note that the topological equivalence of a sector to one of the sectors in Figure 2.1 need not preserve the directions of the flow.

In the following, we will discuss three cases according to the number of real roots to the characteristic equation (2.3) in $0 \le \theta \le \frac{\pi}{2}$.

2.1. $f - d - a = 0$ and $c - am - dm = 0$

In this case, $G(\theta) \equiv 0$, which is a singular case.

Performing the Briot-Bouquet transformation $y = ux$, system (2.2) in I^+ is transformed into

$$\begin{aligned} \dot{x} &= ax^2 + (am - c)x^2u - bx^3 - bmx^3u, \\ \dot{u} &= -bx^2(u + mu^2). \end{aligned} \tag{2.4}$$

On the (u, x)-plane system (2.4) can be written as

$$\frac{dx}{du} = \frac{a + (am - c)u - b(1 + mu)x}{-b(u + mu^2)}. \tag{2.5}$$

Equation (2.5) has a general solution as follows

$$x = \frac{a}{b} + ku + \frac{cu}{b} \ln \frac{u}{1 + mu},$$

where k is an arbitrary constant. So the general solution of system (2.2) in I^+ is

$$x = \frac{a}{b} + k\frac{y}{x} + \frac{cy}{bx} \ln \frac{y}{my + x}$$

as $f - d - a = 0$ and $c - am - dm = 0$. The topological structure of the orbits of system (2.1) in the interior of the first quadrant is sketched in Figure 2.2, which consists of an elliptic sector and a parabolic sector.

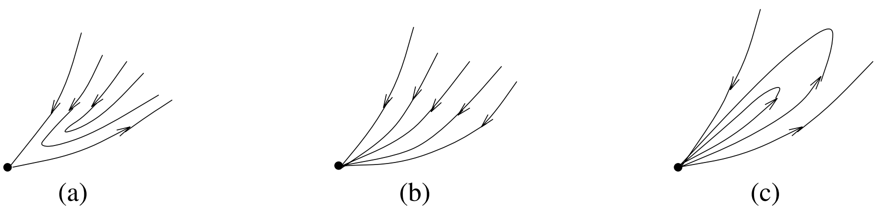

Fig. 2.1. (a) A hyperbolic sector; (b) a parabolic sector; (c) an elliptic sector.

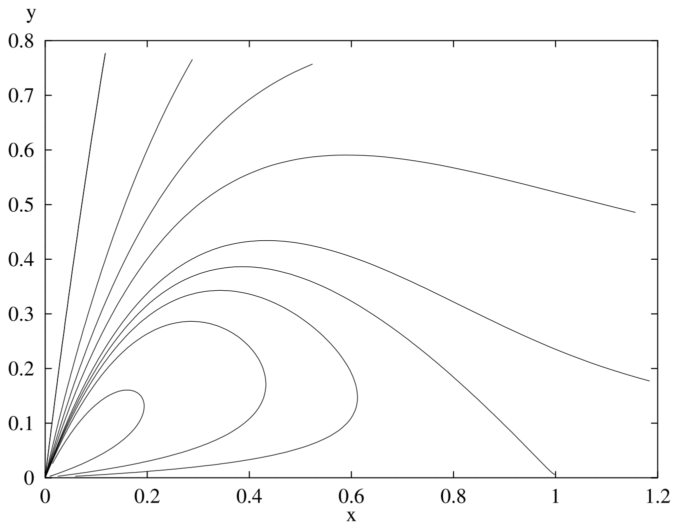

Fig. 2.2. Topological structure of system (2.1) at $(0, 0)$ when $c - am - dm = 0$ and $f - d - a = 0$. This figure was created by XPP (see [6]) with $a = 1, b = 1, c = 2, m = 1, d = 1$, and $f = 2$.

2.2. $(f - d - a)(c - am - dm) = 0$ *but one of them is not zero*

In this case equation (2.3) has two roots in $0 \le \theta \le \frac{\pi}{2}$, $\theta_1 = 0$ and $\theta_2 = \frac{\pi}{2}$.

To determine if there exists an orbit of system (2.2) which tends to the origin along the direction θ_i $(i = 1, 2)$ as t tends to $+\infty$ or $-\infty$, we have to compute the derivatives of $G(\theta)$ and the function $H(\theta)$.

$$\begin{aligned} G'(\theta) &= \sin\theta\cos\theta[(c - am - dm)\cos\theta - (f - d - a)\sin\theta] \\ &\qquad + \cos 2\theta[(c - am - dm)\sin\theta + (f - d - a)\cos\theta], \\ H(\theta) &= \sin\theta Y_2(\cos\theta, \sin\theta) + \cos\theta X_2(\cos\theta, \sin\theta) \\ &= a\cos^3\theta - dm\sin^3\theta + \cos\theta\sin\theta[(f - d)\sin\theta + (am - c)\cos\theta], \\ G''(\theta) &= 2\cos 2\theta[(c - am - dm)\cos\theta - (f - d - a)\sin\theta] \\ &\qquad - 5\sin\theta\cos\theta[(c - am - dm)\sin\theta + (f - d - a)\cos\theta]. \end{aligned} \tag{2.6}$$

2.2.1. $f - d - a \neq 0$ *and* $c - am - dm = 0$

In this case, θ_1 is a simple root of (2.3) and θ_2 is a multiple root with multiplicity 2 of (2.3). We have

Theorem 2.1. *Suppose that* $f - d - a \neq 0$ *and* $c - am - dm = 0$. *Then*

(a) *there exist* $\epsilon_1 > 0$ *and* $r_1 > 0$ *such that*

(i) *if* $f - d - a > 0$, *all orbits of system (2.2) in* $\{(\theta, r) :\ 0 \le \theta < \epsilon_1,\ \ 0 < r < r_1\}$ *tend to* $(0, 0)$ *along* θ_1 *as* $t \to -\infty$;

(ii) *if* $f-d-a<0$, *there exists a unique orbit of system (2.2) in* $\{(\theta,r):\ 0\le\theta<\epsilon_1,\ \ 0<r<r_1\}$ *that tends to* $(0,0)$ *along* θ_1 *as* $t\to-\infty$; *and*

(b) *there exist* $\epsilon_2>0$ *and* $r_2>0$ *such that all orbits of system (2.2) in* $\{(\theta,r):\ 0\le\frac{\pi}{2}-\theta<\epsilon_2,\ \ 0<r<r_2\}$ *tend to* $(0,0)$ *along* θ_2 *as* $t\to+\infty$.

Proof. Since $G'(\theta_1)=f-d-a$ and $H(\theta_1)=a$, if $f-d-a<0$, by Theorem 3.4 on page 68 of [18] there exist $\epsilon_1>0$ and $r_1>0$ such that all orbits of system (2.2) in $\{(\theta,r):\ 0\le\theta<\epsilon_1,\ \ 0<r<r_1\}$ tend to $(0,0)$ along θ_1 as $t\to-\infty$. If $f-d-a<0$, the conclusion follows from Theorem 3.7 on page 70 of [18].

On the other hand, when $c-am-dm=0$, $G'(\theta_2)=0$ and $G''(\theta_2)H(\theta_2)\neq 0$. Thus from Theorem 3.8 on page 75 of [18], there exist $\epsilon_2>0$ and $r_2>0$ such that all orbits of system (2.2) in $\{(\theta,r):\ 0\le\frac{\pi}{2}-\theta<\epsilon_2,\ \ 0<r<r_2\}$ tend to $(0,0)$ along θ_2 as $t\to+\infty$. □

2.2.2. $f-d-a=0$ *and* $c-am-dm\neq 0$

In this case, θ_2 is a simple root of (2.3) and θ_1 is a multiple root with multiplicity 2 of (2.3). Using a similar analysis as in the proof of the above theorem, we have

Theorem 2.2. *Suppose that* $f-d-a=0$ *and* $c-am-dm\neq 0$. *Then*

(a) *there exist* $\epsilon_3>0$ *and* $r_3>0$ *such that all orbits of system (2.2) in* $\{(\theta,r):\ 0\le\theta<\epsilon_3,\ \ 0<r<r_3\}$ *tend to* $(0,0)$ *along* θ_1 *as* $t\to-\infty$*; and*

(b) *there exist* $\epsilon_4>0$ *and* $r_4>0$ *such that*

  (i) *if* $c-am-dm>0$, *all orbits of system (2.2) in* $\{(\theta,r):\ 0\le\frac{\pi}{2}-\theta<\epsilon_4,\ \ 0<r<r_4\}$ *tend to* $(0,0)$ *along* θ_2 *as* $t\to+\infty$;

  (ii) *if* $c-am-dm<0$, *there exists a unique orbit of system (2.2) in* $\{(\theta,r):\ 0\le\frac{\pi}{2}-\theta<\epsilon_4,\ \ 0<r<r_4\}$ *that tends to* $(0,0)$ *along* θ_2 *as* $t\to+\infty$.

2.3. $(f-d-a)(c-am-dm)\neq 0$

In this case, we discuss two subcases because we only consider (2.3) in $0\le\theta\le\frac{\pi}{2}$. (A) If $(f-d-a)(c-am-dm)>0$, then equation (2.3) has two simple roots: $\theta_1=0$ and $\theta_2=\frac{\pi}{2}$. (B) If $(f-d-a)(c-am-dm)<0$, then equation (2.3) has three simple roots: θ_1, θ_2 and $\theta_3=\arctan\frac{a+d-f}{c-am-dm}$.

For the case (A), we have the following theorem according to Theorems 3.4 and 3.7 in [18].

Theorem 2.3. *Assume that* $(f-d-a)(c-am-dm)\neq 0$. *Then*

(a) *there exist* $\epsilon_5>0$ *and* $r_5>0$ *such that*

  (i) *if* $f-d-a>0$, *all orbits of system (2.2) in* $\{(\theta,r):\ 0\le\theta<\epsilon_5,\ \ 0<r<r_5\}$ *tend to* $(0,0)$ *along* θ_1 *as* $t\to-\infty$;

  (ii) *if* $f-d-a<0$, *there exists a unique orbit of system (2.2) in* $\{(\theta,r):\ 0\le\theta<\epsilon_5,\ \ 0<r<r_5\}$ *that tends to* $(0,0)$ *along* θ_1 *as* $t\to-\infty$; *and*

(b) *there exist* $\epsilon_6>0$ *and* $r_6>0$ *such that*

  (i) *if* $c-am-dm>0$, *all orbits of system (2.2) in* $\{(\theta,r):\ 0\le\frac{\pi}{2}-\theta<\epsilon_6,\ \ 0<r<r_6\}$ *tend to* $(0,0)$ *along* θ_2 *as* $t\to+\infty$;

(ii) *if* $c - am - dm < 0$, *there exists a unique orbit of system (2.2) in* $\{(\theta, r) : 0 \le \frac{\pi}{2} - \theta < \epsilon_6,\ \ 0 < r < r_6\}$ *that tends to* $(0, 0)$ *along* θ_2 *as* $t \to +\infty$.

For the case (B), we have the same results for θ_1 and θ_2 as in the above Theorem 2.3. Thus, we only consider θ_3.

Theorem 2.4. *Suppose that* $f - d - a > 0$ *and* $c - am - dm < 0$. *Then*

(a) *there exist* $\epsilon_7 > 0$ *and* $r_7 > 0$ *such that there exists a unique orbit of system (2.2) in* $\{(\theta, r) : 0 \le |\theta - \theta_3| < \epsilon_7,\ \ 0 < r < r_7\}$ *that tends to* $(0, 0)$ *along* θ_3 *as* $t \to -\infty$ *when one of the following conditions holds*
 (i) $a + d < f$ *and* $c \le am$, *or*
 (ii) $a + d < f < \frac{cd}{c-am}$ *and* $am < c < am + dm$; *and*

(b) *there exist* $\epsilon_8 > 0$ *and* $r_8 > 0$ *such that all orbits of system (2.2) in* $\{(\theta, r) : 0 \le |\theta - \theta_3| < \epsilon_8,\ \ 0 < r < r_8\}$ *tend to* $(0, 0)$ *along* θ_3 *as* $t \to +\infty$ *when* $\frac{cd}{c-am} \le f$ *and* $am < c < am + dm$.

Proof. We apply the Briot-Bouquet transformation

$$x = x, \quad y = ux, \quad \text{and} \quad d\tau = xdt$$

to transform (2.2) into

$$\begin{aligned} \frac{dx}{d\tau} &= ax + (am - c)ux + bx^2(1 + mu), \\ \frac{du}{d\tau} &= (f - d - a)u + (c - am - dm)u^2 - bxu(1 + mu). \end{aligned} \tag{2.7}$$

The aim of the transformation is to decompose the relatively complex topological structure near a complex critical point $(0, 0)$ of system (2.2) into simpler topological structures of several simpler critical points of system (2.7). This transformation maps the first, second, third and fourth quadrant in the (x, y)-plane respectively into the first, third, second and fourth quadrant in the (x, u)-plane. It is a topological transformation from $R^2(x, y) \setminus \{x = 0\}$ to $\tilde{R}^2(x, u) \setminus \{x = 0\}$, while its inverse transformation maps the u-axis to the point $O(0, 0)$. Note that by the time scale $d\tau = xdt$, the inverse Briot-Bouquet transformation maps the orbits in the left of the u-axis in the (x, u)-plane to the orbits in the left of the y-axis in the (x, y)-plane with reversed directions. Roughly speaking, the inverse transformation keeps the first and fourth quadrants in the (x, u)-plane fixed, reflects the second and the third quadrants with respect to the negative x-axis, then condenses the u-axis into one point. Therefore, we only consider the equilibria of system (2.7) in the u-axis.

In the u-axis system (2.7) has two equilibria $(0, 0)$ and $(0, \frac{f-d-a}{am+dm-c})$. Obviously, $(0, 0)$ is an unstable node. In the following we consider the equilibrium $(0, \frac{f-d-a}{am+dm-c})$.

Let $x_1 = x$, $x_2 = u - \frac{f-d-a}{am+dm-c}$. Then system (2.7) becomes

$$\frac{dx_1}{d\tau} = \frac{amf - cf + cd}{am + dm - c}x_1 + (am - c)x_1x_2 - \frac{b(mf - c)}{am + dm - c}x_1^2 - bmx_1^2x_2,$$

$$\frac{dx_2}{d\tau} = \frac{b(f-d-a)(mf-c)}{(am+dm-c)^2}x_1 - (f-d-a)x_2$$
$$+\frac{b(2mf-ma-md-c)}{am+dm-c}x_1x_2 + (c-am-dm)x_2^2 + bmx_1^2x_2. \quad (2.8)$$

Equilibrium $(0, 0)$ of system (2.8) is a saddle if any one of the following conditions holds (a) $a+d < f$ and $c \le am$, (b) $a+d < f < \frac{cd}{c-am}$ and $am < c < am+dm$. Therefore, the equilibrium $(0, \frac{f-d-a}{am+dm-c})$ of system (2.7) is a saddle, and there exists a unique separatrix of this equilibrium in the interior of the first quadrant of system (2.7), which tends to $(0, \frac{f-d-a}{am+dm-c})$ as $t \to -\infty$.

By the inverse Briot-Bouquet transformation, there exist $\epsilon_7 > 0$ and $r_7 > 0$ such that there exists a unique orbit of system (2.2) in $\{(\theta, r) :\ 0 \le |\theta - \theta_3| < \epsilon_7,\ \ 0 < r < r_7\}$ which tends to $(0, 0)$ along θ_3 as $t \to -\infty$.

When $f = \frac{cd}{c-am}$ and $am < c < am + dm$, the equilibrium $(0, 0)$ of system (2.8) is a degenerate equilibrium. We obtain, after some elementary but lengthy computations, that the equilibrium $(0, 0)$ of system (2.8) is a saddle-node. Thus, in this case the equilibrium $(0, \frac{f-d-a}{am+dm-c})$ of system (2.7) is a saddle-node, and the stable node part is in the interior of the first quadrant of system (2.7). However, when $\frac{cd}{c-am} < f$ and $am < c < am + dm$, the equilibrium $(0, 0)$ of system (2.8) is a stable node. Hence, the equilibrium $(0, \frac{f-d-a}{am+dm-c})$ of system (2.7) is a stable node. For both cases, we use the inverse Briot-Bouquet transformation to obtain the result: there exist $\epsilon_8 > 0$ and $r_8 > 0$ such that all orbits of system (2.2) in $\{(\theta, r) :\ 0 \le |\theta - \theta_3| < \epsilon_8,\ \ 0 < r < r_8\}$ tend to $(0, 0)$ along θ_3 as $t \to +\infty$. This completes the proof of the theorem. □

Using a similar method as in the proof of Theorem 2.4, we obtain

Theorem 2.5. *Assume that* $f - d - a < 0$ *and* $c - am - dm > 0$. *Then*

(a) *there exist* $\epsilon_9 > 0$ *and* $r_9 > 0$ *such that there exists a unique orbit of system (2.2) in* $\{(\theta, r) :\ 0 \le |\theta - \theta_3| < \epsilon_9,\ \ 0 < r < r_9\}$ *which tends to* $(0, 0)$ *along* θ_3 *as* $t \to +\infty$ *if one of the following conditions holds:*
  (i) $f \le d$ *and* $am + dm < c$, *or*
  (ii) $d < f < \frac{cd}{c-am}$ *and* $am + dm < c$; *and*

(b) *there exist* $\epsilon_{10} > 0$ *and* $r_{10} > 0$ *such that there exists an infinite number of orbits of system (2.2) in* $\{(\theta, r) :\ 0 \le |\theta - \theta_3| < \epsilon_{10},\ \ 0 < r < r_{10}\}$ *which tend to* $(0, 0)$ *along* θ_3 *as* $t \to -\infty$ *when* $\frac{cd}{c-am} \le f < a + d$ *and* $am + dm < c$.

From the above arguments, we can see that the critical point $(0, 0)$ of system (2.1) is not of center type. We have discussed the existence and the number of orbits of system (2.1) which tend to the critical point $(0, 0)$ along fixed directions. However, such information does not provide enough knowledge about the topological structure in a neighborhood in I^+ of the origin, i.e., it does not tell us how many sectors there are and what kinds of sectors they are in the neighborhood. For this purpose, we have to study the behavior of orbits of system (2.1) in the whole I^+.

3. Equilibria of System (2.1) except $(0, 0)$

In this section, we will discuss the existence and stability of equilibria of system (2.1) except $(0, 0)$. System (2.1) always has a boundary equilibrium $(\frac{a}{b}, 0)$ and at most one interior equilibrium. As showed in [13], an unique interior equilibrium of system (2.1) exists if and only if any one of the following conditions holds:

(i) $d < f$ and $c \leq ma$;
(ii) $d < f < \frac{cd}{c-am}$ and $am < c$.

In both cases, system (2.1) has a unique interior equilibrium (x^*, y^*), where

$$x^* = \frac{a}{b} - \frac{c(f-d)}{bmf}, \; y^* = \frac{f-d}{dm}x^*.$$

Next we discuss the stability of the equilibria $(\frac{a}{b}, 0)$ and (x^*, y^*).

Standard and simple arguments show that the equilibrium $(\frac{a}{b}, 0)$ is a saddle when $f > d$, and the positive x-axis is divided by the point $(\frac{a}{b}, 0)$ into two parts. They are two separatrices of the equilibrium and both of them asymptotically approach the equilibrium as $t \to +\infty$. There also exists a unique separatrix in I^+ which tends to $(\frac{a}{b}, 0)$ as $t \to -\infty$. However, when $f < d$ the equilibrium $(\frac{a}{b}, 0)$ is a stable node. When $f = d$ the equilibrium $(\frac{a}{b}, 0)$ is a saddle-node. The phase portraits are sketched in Figure 3.1.

Consider the Jacobian matrix A of system (2.1) at the equilibrium (x^*, y^*), which takes the form of

$$A = \begin{pmatrix} -bx^* + \dfrac{cx^*y^*}{(my^*+x^*)^2} & -\dfrac{c(x^*)^2}{(my^*+x^*)^2} \\ \dfrac{fm(y^*)^2}{(my^*+x^*)^2} & -\dfrac{fmx^*y^*}{(my^*+x^*)^2} \end{pmatrix}.$$

It is easy to see that the determinant of A is always positive and its trace is

$$\begin{aligned} \mathrm{tr}A &= -bx^* + (c - fm)\frac{x^*y^*}{(my^*+x^*)^2} \\ &= \frac{cf^2 + md^2f - amf^2 - dmf^2 - cd^2}{mf^2}. \end{aligned} \tag{3.1}$$

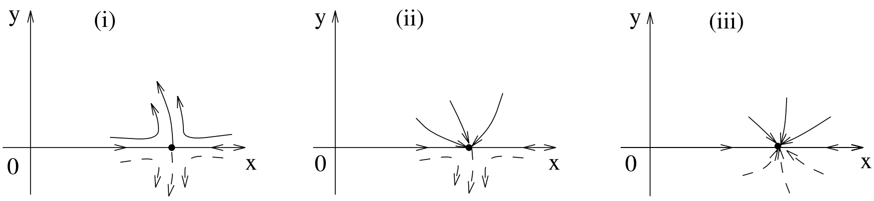

Fig. 3.1. The topological structure of system (2.1) at $(\frac{a}{b}, 0)$ when (i) $f > d$ (a saddle), (ii) $f = d$ (a saddle-node), and (iii) $f < d$ (a stable node).

Theorem 3.1. *Suppose that system (2.1) has a unique interior equilibrium* (x^*, y^*). *Then there are three possibilities:*

(1) (x^*, y^*) *is locally asymptotically stable if any one of the following conditions holds*
  (i) $d < f$ *and* $c \le ma$;
  (ii) $d < f < \frac{cd}{c-am}$ *and* $am < c \le am + dm$;
  (iii) $d < f < \frac{-md^2+\sqrt{\Delta}}{2(c-am-dm)}$ *and* $0 < c-am-dm$, *where* $\Delta = m^2d^4+4cd^2(c-am-dm)$.
(2) (x^*, y^*) *is unstable if*
  (iv) $\frac{-md^2+\sqrt{\Delta}}{2(c-am-dm)} < f < \frac{cd}{c-am}$ *and* $0 < c-am-dm$.
(3) (x^*, y^*) *is nonhyperbolic if*
  (v) $f = \frac{-md^2+\sqrt{\Delta}}{2(c-am-dm)}$ *and* $0 < c-am-dm$.

Proof. It is clear that (x^*, y^*) is locally asymptotically stable (unstable) if the trace $\mathrm{tr}A < 0$ ($\mathrm{trA} > 0$, respectively) since $\det A > 0$. Therefore, we only consider the sign of the following function

$$F = cf^2 + md^2f - amf^2 - dmf^2 - cd^2 = (c-am-dm)f^2 + md^2f - cd^2$$

following (3.1).

Obviously, when the condition (i) holds, we have

$$F < -cd^2 < 0.$$

Hence, (x^*, y^*) is locally asymptotically stable.

If the condition (ii) holds, then we consider three subcases: (a) $d < f \le \frac{c}{m}$ and $am < c < am+dm$, (b) $\frac{c}{m} < f < \frac{cd}{c-am}$ and $am < c < am+dm$, (c) $d < f < \frac{cd}{c-am}$ and $c = am+dm$. In the subcase (a), we have

$$F \le (c-am-dm)f^2 < 0,$$

which implies that (x^*, y^*) is locally asymptotically stable. In the subcase (b), (x^*, y^*) is locally asymptotically stable by Theorem 3.2 in [13]. In the subcase (c), we have

$$F = md^2f - cd^2 = md^2(f-a-d) < 0.$$

Thus, (x^*, y^*) is locally asymptotically stable.

When $c-am-dm > 0$, after some straightforward computations, we can see that

$$d < \frac{-md^2+\sqrt{\Delta}}{2(c-am-dm)} < \frac{cd}{c-am}.$$

Thus, system (2.1) has a unique equilibrium if the condition (iii) is true. We can rewrite F as follows

$$F = (c-am-dm)[f + \frac{md^2+\sqrt{\Delta}}{2(c-am-dm)}][f - \frac{-md^2+\sqrt{\Delta}}{2(c-am-dm)}]. \quad (3.2)$$

When the condition (iii) holds, it is clear that $F < 0$, which yields that (x^*, y^*) is locally asymptotically stable. Summarizing the above arguments, we obtain conclusion (1).

From the above expression (3.2) of F, it is clear that $F > 0$ when the condition (iv) holds. Thus, the equilibrium (x^*, y^*) is unstable.

However, when $f = \frac{-md^2+\sqrt{\Delta}}{2(c-am-dm)}$ and $c - am - dm > 0$, i.e. the condition (v) is true, then $F = 0$, which implies $\mathrm{trA} = 0$. Thus, the equilibrium (x^*, y^*) is not hyperbolic. This proves the theorem. □

From the above theorem, we know that the unique interior equilibrium (x^*, y^*) of system (2.1) is a center type nonhyperbolic equilibrium when $f = \frac{-md^2+\sqrt{\Delta}}{2(c-am-dm)}$ and $c-am-dm > 0$. Hence, system (2.1) can have Hopf bifurcation. To determine the stability of the equilibrium and direction of Hopf bifurcation in this case, we have to compute the Liapunov coefficients of the equilibrium.

For convenience, we reconsider system (2.2). Notice that there are six parameters in (2.2). When $f = \frac{-md^2+\sqrt{\Delta}}{2(c-am-dm)}$ and $c-am-dm > 0$, we nondimensionalize system (2.2) with the substitutions

$$t \to \frac{bd}{(f-d)^2}t, \quad x \to \frac{f-d}{bd}x, \quad y \to \frac{(f-d)^2}{bd^2m}y,$$

then system (2.2) takes the following simpler form

$$\begin{aligned} \frac{dx}{dt} &= x(Ax - By - Cx^2 - Dxy), \\ \frac{dy}{dt} &= y(x-y) \end{aligned} \tag{3.3}$$

with four positive parameters

$$A = \frac{a}{f-d}, \quad B = \frac{c-am}{dm}, \quad C = \frac{1}{d}, \quad D = \frac{f-d}{d^2}.$$

System (3.3) has a unique interior equilibrium (x_0, x_0) which is nonhyperbolic, where $x_0 = \frac{A-B}{C+D}$. Thus,

$$A - 2Cx_0 - Dx_0 - 1 = 0. \tag{3.4}$$

Translating the interior equilibrium (x_0, x_0) of system (3.3) to the origin, system (3.3) can be written as

$$\begin{aligned} \frac{dx}{dt} &= x_0x - (B + Dx_0)x_0y + (1 - Cx_0)x^2 - (B + 2Dx_0)xy - Cx^3 - Dx^2y, \\ \frac{dy}{dt} &= x_0(x-y) + y(x-y). \end{aligned} \tag{3.5}$$

Let $X = x - y$, $Y = y$. Then system (3.5) becomes

$$\begin{aligned}\frac{dX}{dt} &= (1 - B - Dx_0)x_0Y + (1 - Cx_0)X^2 + (1 - 2Cx_0 - B - 2Dx_0)XY \\ &\quad +(1 - Cx_0 - B - 2Dx_0)Y^2 - CX^3 - (3C + D)X^2Y \\ &\quad -(3C + 2D)XY^2 - (C + D)Y^3, \\ \frac{dY}{dt} &= x_0X + XY.\end{aligned} \tag{3.6}$$

By the formula of the first Liapunov coefficient on page 344 in [15], we have the first Liapunov coefficient σ of the equilibrium $(0, 0)$ of system (3.6) as follows

$$\sigma = -\frac{3\pi[(1 - B - Dx_0)(2D + 3BC + 3DCx_0) - (1 - 2Cx_0 - B - 2Dx_0)(D + BC + DCx_0)]}{2(1 - B - Dx_0)x_0(B + Dx_0 - 1)^{\frac{3}{2}}}.$$

Noting equation (3.4), we further obtain that

$$\sigma = \frac{3\pi D(C + D)(B - 1)^2}{2x_0C(1 - B - Dx_0)(B + Dx_0 - 1)^{\frac{3}{2}}} < 0. \tag{3.7}$$

Hence, the origin of system (3.6) is a weak focus of multiplicity one and it is stable.

Theorem 3.2. *If* $f = \frac{-md^2+\sqrt{\Delta}}{2(c-am-dm)}$ *and* $0 < c - am - dm$*, then system (2.1) has a unique interior equilibrium* (x^*, y^*)*, which is a weak stable focus of multiplicity one.*

From Theorems 3.1 and 3.2, we know that system (2.1) undergoes a Hopf bifurcation for some parameter values. The limit cycle created by the Hopf bifurcation will be discussed in the next section.

4. Global dynamics of System (2.1)

In this section, we summarize the results in sections 2 and 3, and classify the global dynamics of system (2.1) depending on all parameters.

Theorem 4.1. *System (2.1) has no interior equilibrium and* $(0, 0)$ *is a global attractor of system (2.1) in* I^+ *if any one of the following conditions holds*

(i) $f - d - a > 0$ *and* $c - ma - dm \geq 0$*;*
(ii) $f - d - a = 0$ *and* $c - am - dm \geq 0$*;*
(iii) $f \geq \frac{cd}{c-am}$ *and* $am + dm > c > am$*;*
(iv) $a + d > f \geq \frac{cd}{c-am}$ *and* $c - am - dm > 0$.

Moreover, the topological structure of the origin in I^+ *consists of an elliptic sector and a parabolic sector. The phase portrait of system (2.1) in one of these cases is sketched in Figure 4.1.*

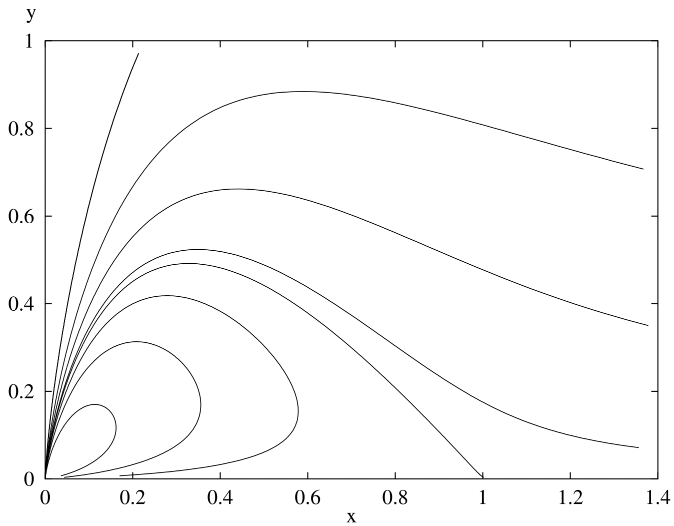

Fig. 4.1. The phase portrait of system (2.1) created by XPP. $(0, 0)$ is a global attractor, $(\frac{a}{b}, 0)$ is a saddle, where $a = 0.5$, $b = 0.5$, $c = 1$, $m = 1$, $d = 0.4$, and $f = 1$.

Indeed, by the sufficient and necessary conditions of the existence of an interior equilibrium of system (2.1) in section 3, we can see that system (2.1) has no interior equilibrium for all cases in Theorem 4.1. Clearly, any case in Theorem 4.1 implies $f > d$. Thus equilibrium $(\frac{a}{b}, 0)$ is a saddle. Note that by theorems in section 2, there exist ϵ_0 and r_0 such that all orbits of system (2.1) in $\{(\theta, r) :\ 0 \le \frac{\pi}{2} - \theta < \epsilon_0,\ \ 0 < r < r_0\}$ tend to $(0, 0)$ along θ_2 as $t \to +\infty$ if one of conditions (i), (ii) and (iv) holds. However, if condition (iii) holds, then there exist $\bar{\epsilon}$ and $\bar{r}$ such that all orbits of system (2.1) in $\{(\theta, r) :\ 0 \le |\theta - \theta_3| < \bar{\epsilon},\ \ 0 < r < \bar{r}\}$ tend to $(0, 0)$ along θ_3 as $t \to +\infty$.

Notice that the conclusion in Theorem 4.1 coincide with the conclusion in Theorem 2.6 in [13].

Theorem 4.2. *If $f \le d$ and $c - am - dm < 0$, then system (2.1) has no interior equilibrium and the equilibrium $(\frac{a}{b}, 0)$ is a global attractor in I^+. The topological structure of the origin in I^+ consists of a hyperbolic sector (see Figure 4.2).*

Proof. Clearly, system (2.1) has no interior equilibrium when $c - am - dm < 0$ and $f \le d$. By Theorem 2.3, there exists a unique orbit of system (2.1) tending to $(0, 0)$ along θ_1 (θ_2) as $t \to -\infty$ ($t \to +\infty$, respectively), i.e. the positive x-axis (y-axis). Moreover, no other orbits tend to $(0, 0)$.

On the other hand, $(\frac{a}{b}, 0)$ is a stable node. Thus the conclusion of the theorem holds. □

In Theorem 2.5 of [13], Kuang and Beretta proved that if $f \le d$ and $c \le am$, then $(\frac{a}{b}, 0)$ is globally asymptotically stable. Clearly, their conclusion is included in Theorem 4.2.

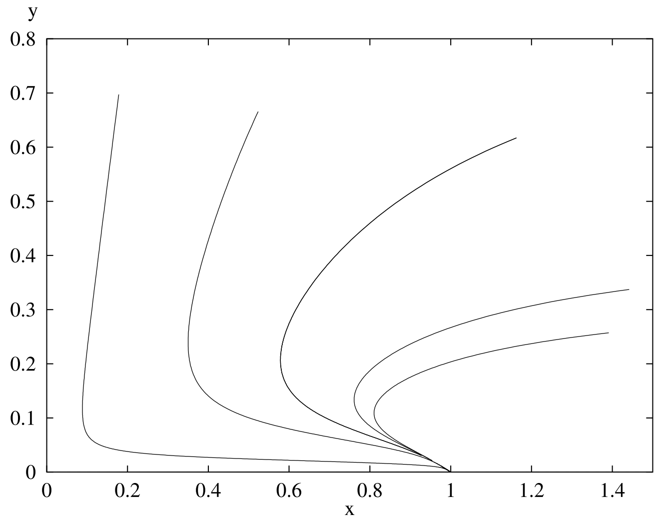

Fig. 4.2. The phase portrait of system (2.1) created by XPP. $(0, 0)$ has a hyperbolic sector and a parabolic sector, $(\frac{a}{b}, 0)$ is a global attractor, where $a = 0.5, b = 0.5, c = 0.8, m = 1, d = 0.4$, and $f = 0.3$.

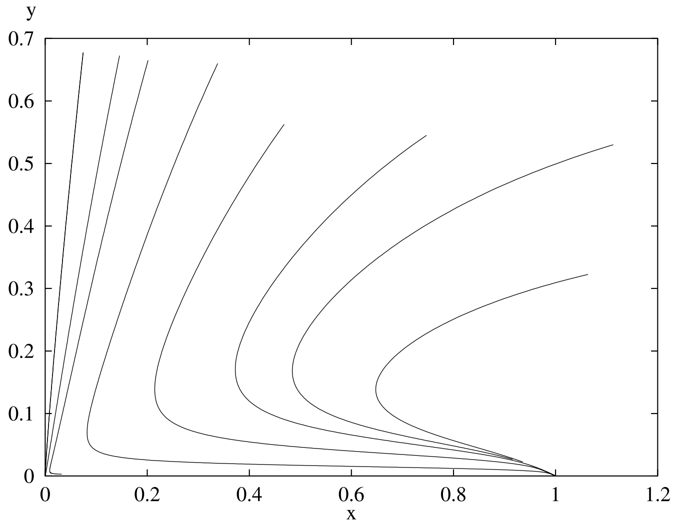

Fig. 4.3. The phase portrait of system (2.1) created by XPP. Both $(0, 0)$ and $(\frac{a}{b}, 0)$ are attractors, where $a = 0.5, b = 0.5, c = 1, m = 1, d = 0.4$, and $f = 0.3$.

Theorem 4.3. *System (2.1) has no interior equilibrium,* $(0, 0)$ *and* $(\frac{a}{b}, 0)$ *are attractors of system (2.1) in* I^+ *if* $f \leq d$ *and* $am + dm \leq c$*. Moreover, the topological structure of the origin in* I^+ *consists of a hyperbolic sector and a parabolic sector (see Figure 4.3).*

Proof. It is clear that $(\frac{a}{b}, 0)$ is a stable node in I^+ and system (2.1) has no interior equilibrium if $f \leq d$ and $am + dm \leq c$.

On the other hand, when $f \leq d$ and $c - am - dm = 0$, there exists an infinite number of orbits (a unique orbit) of system (2.1) tending to $(0, 0)$ along θ_2 (θ_1, respectively) as $t \to +\infty$ ($t \to -\infty$, respectively), and no other orbit tends to $(0, 0)$ as $t \to +\infty$ or $t \to -\infty$ by Theorem 2.1. When $f \leq d$ and $am + dm < c$, there exists an infinite number of orbits (a unique orbit) of system (2.1) tending to $(0, 0)$ along θ_2 (θ_1, θ_3, respectively) as $t \to +\infty$ ($t \to -\infty, t \to +\infty$, respectively), and no other orbit tends to $(0, 0)$ by Theorems 2.3 and 2.5. This completes the proof. □

In Theorem 3.1 of [13], Kuang and Beretta have shown that if system (2.1) has a unique interior equilibrium which is locally asymptotically stable, then system (2.1) has no nontrivial positive periodic solution. In the following we will repeatedly use this conclusion.

Theorem 4.4. *If $d < f < a + d$ and $c - am - dm < 0$, then system (2.1) has a unique interior equilibrium, which is a global attractor. The topological structure of the origin in I^+ consists of a hyperbolic sector (see Figure 4.4).*

Proof. By Theorem 3.1, system (2.1) has a unique interior equilibrium (x^*, y^*), which is locally asymptotically stable. Since $d < f$, $(\frac{a}{b}, 0)$ is a saddle. In I only the positive x-axis and y-axis tend to $(0, 0)$ as $t \to -\infty$ and $t \to +\infty$, respectively, no other orbits approach $(0, 0)$ according to Theorem 2.3. Thus, the conclusion of this theorem is true by Theorem 3.1 in [13]. □

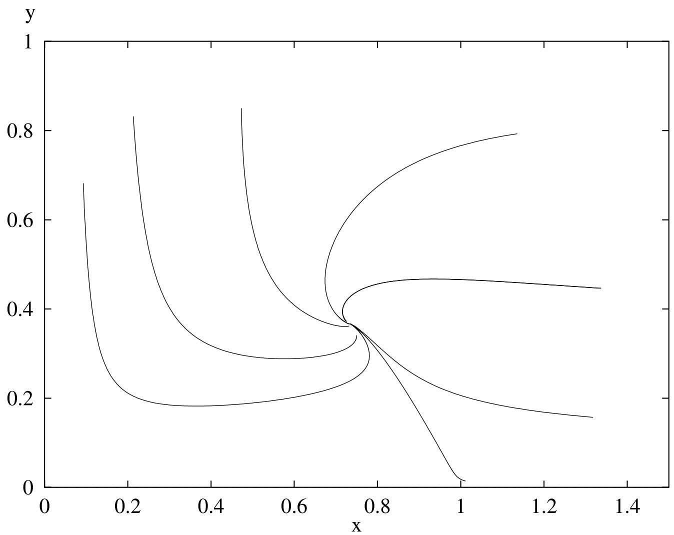

Fig. 4.4. The phase portrait of system (2.1) created by XPP. $(0, 0)$ has a hyperbolic sector, $(\frac{a}{b}, 0)$ is a saddle and (x^*, y^*) is a global attractor, where $a = 0.5$, $b = 0.5$, $c = 0.4$, $m = 1$, $d = 0.4$, and $f = 0.6$.

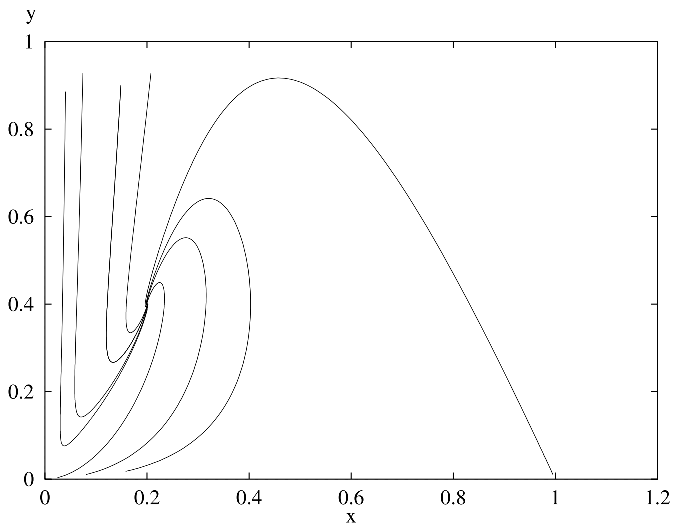

Fig. 4.5. The phase portrait of system (2.1) created by XPP. $(0, 0)$ has a hyperbolic sector and a parabolic sector, $(\frac{a}{b}, 0)$ is a saddle and (x^*, y^*) is a global attractor, where $a = 1, b = 1, c = 1.2, m = 1, d = 1$, and $f = 3$.

Theorem 4.5. *System (2.1) has a unique interior equilibrium, which is a global attractor in I^+ if any one of the following conditions holds*

(i) $f - d - a = 0$ *and* $am + dm > c$;
(ii) $f - d - a > 0$ *and* $am \geq c$;
(iii) $\frac{cd}{c-am} > f > a + d$ *and* $am + dm > c > am$.

Moreover, the topological structure of the origin in I^+ consists of a parabolic sector and a hyperbolic sector (see Figure 4.5).

Proof. In any one of the cases (i), (ii) and (iii), system (2.1) has a unique interior equilibrium (x^*, y^*) and it is locally asymptotically stable by Theorem 3.1. Moreover, $(\frac{a}{b}, 0)$ is a saddle.

On the other hand, in case (i) there exists an infinite number of orbits of system (2.1) tending to $(0, 0)$ along θ_1 as $t \to -\infty$ and a unique orbit of system (2.1) tending to $(0, 0)$ along θ_2 as $t \to +\infty$ (i.e. the positive y-axis) by Theorem 2.1. Hence, (x^*, y^*) is a global attractor in I^+ by Theorem 3.1 in [13].

In cases (ii) and (iii), from Theorem 2.3 the same statements hold for characteristic directions θ_1 and θ_2. Furthermore, there exists a unique orbit of system (2.1) tending to $(0, 0)$ along θ_3 as $t \to -\infty$ by Theorem 2.4. Therefore, (x^*, y^*) is a global attractor in I^+ by Theorem 3.1 in [13]. The proof of the theorem is completed. □

Theorem 4.6. *Suppose that one of the following conditions holds:*

(i) $a + d > f > d$ *and* $c - am - dm = 0$;

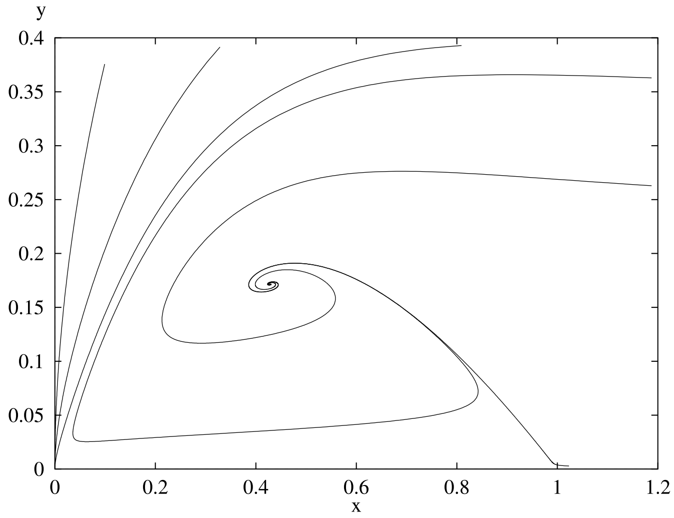

Fig. 4.6. The phase portrait of system (2.1) created by XPP. Both $(0,0)$ and (x^*, y^*) are attractors, a global attractor, and $(\frac{a}{b}, 0)$ is a saddle, where $a = 1, b = 1, c = 2, m = 1, d = 0.5$, and $f = 0.7$.

(ii) $\frac{-md^2+\sqrt{\Delta}}{2(c-am-dm)} \geq f > d$ *and* $c > am + dm$.

Then system (2.1) has a unique interior equilibrium (x^*, y^*) *and no limit cycle, both* $(0,0)$ *and* (x^*, y^*) *are attractors of system (2.1) in* I^+. *Moreover, the topological structure of the origin in* I^+ *consists of a hyperbolic sector and a parabolic sector (see Figure 4.6).*

Proof. In both cases system (2.1) has a unique interior equilibrium (x^*, y^*), which is locally asymptotically stable by Theorem 3.1 and Theorem 3.2. Hence, system (2.1) has no limit cycle according to Theorem 3.1 in [13].

On the other hand, in case (i) there exists an infinite number of orbits (a unique orbit) of system (2.1) tending to $(0,0)$ along θ_2 (θ_1, respectively) as $t \to +\infty$ ($t \to -\infty$, respectively), and no other orbit approaches $(0,0)$ as $t \to +\infty$ or $t \to -\infty$ by Theorem 2.1. In case (ii) from Theorem 2.3 there exists a unique orbit (an infinite number of orbits) of system (2.1) tending to $(0,0)$ along θ_1 (θ_2, respectively) as $t \to -\infty$ ($t \to +\infty$, respectively), and there exists a unique orbit of system (2.1) tending to $(0,0)$ along θ_3 as $t \to +\infty$ by Theorem 2.5. This completes the proof of the theorem. ◻

Theorem 4.7. *Suppose that* $\frac{cd}{c-am} > f > \frac{-md^2+\sqrt{\Delta}}{2(c-am-dm)}$ *and* $c > am + dm$. *Then system (2.1) has a unique unstable interior equilibrium and can have a unique limit cycle in* I^+, *which is stable if it exists. More precisely, for some parameters system (2.1) has a unique stable limit cycle in* I^+ *and there is a parabolic sector in which all orbits of system (2.1) approach* $(0,0)$ *as* $t \to +\infty$ *(see Figure 4.7), and for some other parameters system (2.1) has no limit cycle (see Figure 4.8).*

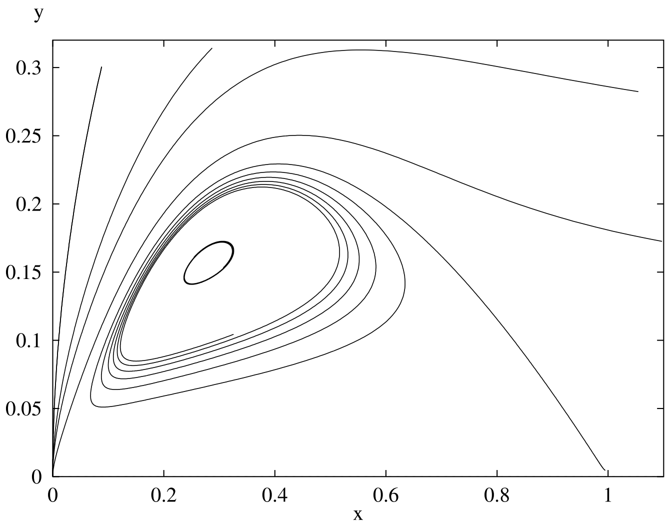

Fig. 4.7. The phase portrait of system (2.1) created by XPP. (0, 0) is an attractor, $(\frac{a}{b}, 0)$ is a saddle, (x^*, y^*) is an unstable focus, and there is a stable limit cycle surrounding (x^*, y^*), where $a = 1, b = 1, c = 2, m = 1, d = 0.5$, and $f = 0.782$.

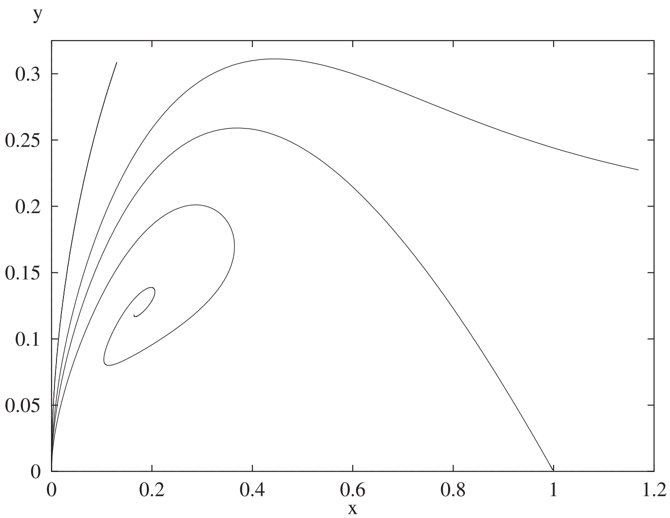

Fig. 4.8. The phase portrait of system (2.1) created by XPP. (0, 0) is an attractor, $(\frac{a}{b}, 0)$ is a saddle, (x^*, y^*) is an unstable focus, and the limit cycle is broken when f increases, where $a = 1, b = 1, c = 2, m = 1, d = 0.5$, and $f = 0.8$.

Proof. When $\frac{cd}{c-am} > f > \frac{-md^2+\sqrt{\Delta}}{2(c-am-dm)}$ and $c > am + dm$, system (2.1) has a unique interior equilibrium (x^*, y^*) which is unstable by Theorem 3.1. However, if $d < f \leq \frac{-md^2+\sqrt{\Delta}}{2(c-am-dm)}$ and $c > am + dm$, then the equilibrium (x^*, y^*) becomes stable by Theorems 3.1 and 3.2. Therefore, a Hopf bifurcation occurs. From (3.7) the first Liapunov number $\sigma < 0$, it follows from Theorem 1 in [15] that the Hopf bifurcation is supercritical and there is a stable limit cycle. The following surface

$$f = \frac{-md^2 + \sqrt{m^2d^4 + 4cd^2(c - am - dm)}}{2(c - am - dm)} \quad \text{and} \quad c - am - dm > 0$$

is called the *Hopf bifurcation surface*.

Hence, there exists a small positive number ϵ such that system (2.1) has a stable limit cycle when $\epsilon + \frac{-md^2+\sqrt{\Delta}}{2(c-am-dm)} > f > \frac{-md^2+\sqrt{\Delta}}{2(c-am-dm)}$ and $c > am + dm$. Denoted this parameter region by **D**. Notice that system (2.1) has at most one limit cycle in I^+ by the Theorem 2.7 of [10]. Thus, system (2.1) has a unique limit cycle which is stable as all parameters are in **D**.

On the other hand, when $\frac{cd}{c-am} > f > \frac{-md^2+\sqrt{\Delta}}{2(c-am-dm)}$ and $c > am + dm$, the equilibrium $(\frac{a}{b}, 0)$ is a saddle and there exists a unique orbit γ_0 of system (2.1) that tends to the equilibrium $(0, 0)$ along the direction θ_3 as $t \to +\infty$ by Theorem 2.5. Let γ be an unstable separatrix of the equilibrium $(\frac{a}{b}, 0)$ in I^+. Then there are three possible relative positions between γ and γ_0 in I^+ as follows

(i) γ_0 is above γ;
(ii) γ_0 coincides with γ;
(iii) γ_0 is below γ.

If all parameters are in **D**, then either case (i) or case (ii) occurs. Otherwise, system (2.1) has at least two limit cycles by Poincare-Bendixson theorem, which contradicts Theorem 2.7 in [10]. If case (i) occurs, then there is a parabolic sector composed of the positive y-axis and γ_0 in which all orbits of system (2.1) approach $(0, 0)$ as $t \to +\infty$ by Theorem 2.5. Therefore, system (2.1) has a unique stable limit cycle for all parameters in **D** and there is a parabolic sector in which all orbits of system (2.1) approach $(0, 0)$ as $t \to +\infty$ (see Figure 4.7). If case (ii) occurs, then system (2.1) has a heteroclinic cycle composed of an interval of the positive x-axis and a heteroclinic orbit connecting $(0, 0)$ and $(\frac{a}{b}, 0)$, and there is a parabolic sector composed of the positive y-axis and the heteroclinic orbit connecting $(0, 0)$ and $(\frac{a}{b}, 0)$ in which all orbits of system (2.1) approach $(0, 0)$ as $t \to +\infty$ by Theorem 2.5.

If case (iii) occurs, then the parameters of system (2.1) must not be in the region **D**. In this case, system (2.1) has no limit cycle. Computer simulation shows the case indeed occurs (see Figure 4.8). This completes the proof of the theorem. □

5. Discussion

In contrast with the traditional prey-dependent predator-prey models, a ratio-dependent model is not well defined at the origin $(0, 0)$ and thus the local stability of $(0, 0)$ cannot be analyzed directly.

In this paper we have considered a class of ratio-dependent models proposed by Arditi and Ginzburg [3]. It has been observed by Jost, Arino and Arditi [11], and Kuang and Beretta [13] that this ratio-dependent model exhibits very rich and complicated dynamics. By redefining the system at the origin $(0, 0)$ and making a transformation in the time variable, we transformed the given model into an

Table 1. Global dynamics of (2.1) in I when $(f-d-a)(c-am-dm) > 0$.

Parameters	(0, 0)	$(\frac{a}{b}, 0)$	(x^*, y^*)	Phase portrait
$f-d-a>0$ $c-am-dm>0$	Global attractor	Saddle	DNE	Fig. 4.1
$f \le d$ $c-am-dm<0$	Hyperbolic sector	Global attractor	DNE	Fig. 4.2
$d<f<d+a$ $c-am-dm<0$	Hyperbolic sector	Saddle	Global attractor	Fig. 4.4

Table 2. Global dynamics of (2.1) in I when $(f-d-a)(c-am-dm) = 0$.

Parameters	(0, 0)	$(\frac{a}{b}, 0)$	(x^*, y^*)	Phase portrait
$f-d-a=0$ $c-am-dm=0$	Global attractor	Saddle	DNE	Fig. 4.1
$f-d-a=0$ $c-am-dm>0$	Global attractor	Saddle	DNE	Fig. 4.1
$f-d-a=0$ $c-am-dm<0$	Hyperbolic sector and parabolic sector	Saddle	Global attractor	Fig. 4.5
$f-d-a>0$ $c-am-dm=0$	Global attractor	Saddle	DNE	Fig. 4.1
$f \le d$ $c-am-dm=0$	Attractor	Attractor	DNE	Fig. 4.3
$d<f<d+a$ $c-am-dm=0$	Attractor	Saddle	Attractor	Fig. 4.6

equivalent polynomial system. The origin (0, 0) is a critical point of high order. We have classified and determined all possible topological structures near the origin (0, 0) and two other equilibria $(\frac{a}{b}, 0)$ and (x^*, y^*) depending on all parameters. Interesting dynamic behavior such as deterministic extinction, existence of multiple attractors, and existence of a limit cycle has been observed.

The global dynamics of the system can been summarized and classified into the following tables by considering three cases: (i) $(f-d-a)(c-am-dm) > 0$; (ii) $(f-d-a)(c-am-dm) = 0$; and (iii) $(f-d-a)(c-am-dm) < 0$.

Remark. After submitting this paper, two preprints, Hsu, Hwang and Kuang [10] and Yang and Ma [17], came to our attention. All the open questions proposed in Kuang and Berreta [13] have been answered positively in these two papers, especially the uniqueness of the limit cycle. The main technique in Hsu, Hwang and Kuang [10] is to transform system (2.1) into a Gause-type predator-prey system by a transformation $u = x/y$ which in turn can be transformed to a Liénard system. Thus, the well-established results on existence and uniqueness of limit cycles for Liénard systems can be applied. It is interesting to notice that

Table 3. Global dynamics of (2.1) in I when $(f-d-a)(c-am-dm)<0$.

Parameters	(0, 0)	$(\frac{a}{b}, 0)$	(x^*, y^*)	Phase portrait
$f-d-a>0$ $c \le am$	Hyperbolic sector and parabolic sector	Saddle	Global attractor	Fig. 4.5
$a+d<f<\frac{cd}{c-am}$ $am<c<am+dm$	Hyperbolic sector and parabolic sector	Saddle	Global attractor	Fig. 4.5
$\frac{cd}{c-am} \le f$ $am<c<am+dm$	Global attractor	Saddle	DNE	Fig. 4.1
$f \le d$ $c-am-dm>0$	Attractor	Attractor	DNE	Fig. 4.3
$d<f<\frac{-md^2+\sqrt{\Delta}}{2(c-am-dm)}$ $c-am-dm>0$	Attractor	Saddle	Attractor	Fig. 4.6
$\frac{-md^2+\sqrt{\Delta}}{2(c-am-dm)}<f<\frac{cd}{c-am}$ $c-am-dm>0$	Attractor	Saddle	Unstable focus Limit cycle	Fig. 4.8 Fig. 4.7
$\frac{cd}{c-am} \le f<a+d$ $c-am-dm>0$	Global attractor	Saddle	DNE	Fig. 4.1

the transformation $u=x/y$ is similar to the Briot-Bouquet transformation $y=ux$ we used in section 2. Some of the techniques and results in Yang and Ma [17] are similar to ours. In comparison, we have provided more detailed information about the topological structures near the equilibria, especially near the origin, and based on that, we are able to determine the global dynamics of the model. We would like to thank Professor Yang Kuang and Professor Zhien Ma for sending us the preprints.

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