

A DENSITY-DEPENDENT PREDATOR-PREY MODEL OF BEDDINGTON-DEANGELIS TYPE

HAIYIN LI, ZHIKUN SHE

ABSTRACT. In this article, we study the dynamics of a density-dependent predator-prey system of Beddington-DeAngelis type. We obtain sufficient and necessary conditions for the existence of a unique positive equilibrium, the global attractiveness of the boundary equilibrium, and the permanence of the system, respectively. Moreover, we derive a sufficient condition for the locally asymptotic stability of the positive equilibrium by the Lyapunov function theory and a sufficient condition for the global attractiveness of the positive equilibrium by the comparison theory.

1. INTRODUCTION

The study of dynamics of predator-prey systems is one of the important subjects in mathematical ecology and mathematical biology. The basic predator-prey model for a prey population density $x(t)$ and a predator population density $y(t)$ is

$$\begin{aligned}x'(t) &= x(t)(a - bx(t)) - f(x, y)y(t) \\y'(t) &= -dy(t) + hf(x, y)y(t)\end{aligned}\tag{1.1}$$

where a is the intrinsic growth rate of the prey, b measures the intensity of intraspecific action of the prey, h denotes the conversion coefficient, d denotes the predator's death rate, and the function $f(x, y)$ is the predator's functional response.

The above basic model has been extensively studied in the literature [7, 8, 14, 17, 22, 23, 24, 26, 27, 28]. Since one of the central goals of ecologists is to understand the relationship between predator and prey, the predator's functional response, as one significant component of the predator-prey relationship, has also been considered [3, 5, 6, 9, 21]. Beddington [3] and DeAngelis [6] originally proposed the predator-prey system with the Beddington-DeAngelis functional response, described by the model

$$\begin{aligned}x'(t) &= x(t)\left(a - bx(t) - \frac{cy(t)}{m_1 + m_2x(t) + m_3y(t)}\right) \\y'(t) &= y(t)\left(-d + \frac{fx(t)}{m_1 + m_2x(t) + m_3y(t)}\right).\end{aligned}\tag{1.2}$$

Skalski and Gilliam [21] further presented the statistical evidence for predator-prey systems that three predator-dependent functional response: Beddington-DeAngelis,

2000 *Mathematics Subject Classification.* 34D23, 92D25.

Key words and phrases. Density dependence; global attractiveness; ω -limit set; permanence.

©2014 Texas State University - San Marcos.

Submitted November 16, 2013. Published September 16, 2014.

Crowley-Martin and Hassell-Varley can provide better description of predator feeding over a range of predator-prey abundances.

Moreover, certain environments confine the predator to be density dependent and there are also considerable evidences that some predator species may be density dependence because of the environmental factors [1, 2]. Further, Kratina [12] showed that predator dependence is important not only at very high predator densities on per capita predation rate but also at low predator densities. So, it is not enough to only require the prey to be density dependent and we also need to take into account realistic levels of predator dependence.

In [18], the following model is used to describe the growth of a prey $x(t)$ and a predator $y(t)$ with density dependence:

$$\begin{aligned} x'(t) &= x(t) \left(a - bx(t) - \frac{cy(t)}{m_1 + m_2x(t) + m_3y(t)} \right) \\ y'(t) &= y(t) \left(-d - ry(t) + \frac{fx(t)}{m_1 + m_2x(t) + m_3y(t)} \right) \end{aligned} \quad (1.3)$$

where $x(t)$ is the prey population density, $y(t)$ is the predator population density, r stands for predator density dependence rate, and the predator consumes prey with functional response of the Beddington-DeAngelis type $\frac{cx(t)y(t)}{m_1 + m_2x(t) + m_3y(t)}$ and contributes to its growth with the rate $\frac{fx(t)y(t)}{m_1 + m_2x(t) + m_3y(t)}$. Note that compared with the system (1.2), the system (1.3) contains not only $bx^2(t)$ (which stands for intraspecific action of prey species) but also $ry^2(t)$ (which stands for intraspecific action of predator species).

In this article, we investigate the dynamics of the model described by the differential equations (1.3). We start with a sufficient and necessary condition for the existence of a unique positive equilibrium by analyzing the corresponding locations of hyperbolic curves while the same condition was provided in [18] only as a sufficient condition.

Then, by using the corresponding characteristic equations of the origin and the boundary equilibrium, we analyze their locally asymptotic stability, respectively. Additionally, we analyze the locally asymptotic stability of the positive equilibrium by constructing a Lyapunov function.

Afterwards, based on a sufficient and necessary condition for the global attractiveness of the boundary equilibrium, we further obtain a sufficient and necessary condition for the permanence of the system (1.3) by investigating types of the limit set [10] instead of making use of the the persistence theory [11, 19, 25]. Note that [18] does not consider the necessary condition for the global attractiveness of the boundary equilibrium and thus can only provide a stronger, sufficient condition for the permanence of the system. Here, the following definition of permanence is used.

Definition 1.1. The system (1.3) is said to be permanent if there exist positive constants δ and Δ with $0 < \delta \leq \Delta$ such that

$$\min\{\liminf_{t \rightarrow +\infty} x(t), \liminf_{t \rightarrow +\infty} y(t)\} \geq \delta, \quad \max\{\limsup_{t \rightarrow +\infty} x(t), \limsup_{t \rightarrow +\infty} y(t)\} \leq \Delta$$

for all solutions $(x(t), y(t))$ of (1.3) with positive initial conditions.

Since the permanence of the system shows that the time evolution of the two species eventually either forms a cyclic loop or attracts to the positive equilibrium,

we finally derive a sufficient condition for assuring the global attractiveness of the positive equilibrium by the comparison theorem.

The rest of this article is organized as follows. In Section 2, we obtain a sufficient and necessary condition for the existence of a unique positive equilibrium and analyze the local stability of the non-negative equilibria of the system (1.3). In Section 3, we present a sufficient and necessary condition for the global attractiveness of the boundary equilibrium. In Section 4, we derive a sufficient and necessary condition for the permanence of the system (1.3). In Section 5, we consider the global attractiveness of the positive equilibrium by using the comparison theorem. We conclude our discussions in Section 6.

2. EQUILIBRIA AND THEIR LOCAL STABILITY

It is clear that for all parameter values, the system (1.3) has the equilibria $E_0(0, 0)$ and $E_1(\frac{a}{b}, 0)$, denoted as the origin and the boundary equilibrium, respectively. For studying the existence of positive equilibria, we analyze the following two equations:

$$\begin{aligned} (a - bx)(m_1 + m_2x + m_3y) - cy &= 0 \\ (-d - ry)(m_1 + m_2x + m_3y) + fx &= 0. \end{aligned} \tag{2.1}$$

For the equation $(a - bx)(m_1 + m_2x + m_3y) - cy = 0$, it is clear that $(a/b, 0)$ and $(-m_1/m_2, 0)$ are on its corresponding curves and if $c - am_3 \neq 0$, $(0, \frac{am_1}{c-am_3})$ is also on its corresponding curves. In addition, when $\frac{c-am_3}{bm_3} \neq \frac{m_1}{m_2}$, this equation is a hyperbolic equation and its two asymptotic lines are $x + \frac{c-am_3}{bm_3} = 0$ and

$$y + \frac{m_2}{m_3}x + \frac{bm_1m_3 - cm_2}{bm_3^2} = 0.$$

Thus, the locations of its corresponding curves can be roughly shown from Figure 1. When $\frac{c-am_3}{bm_3} = \frac{m_1}{m_2}$, the equation is equivalent to $(m_1 + m_2x)(am_2 - bm_2x - bm_3y) = 0$.

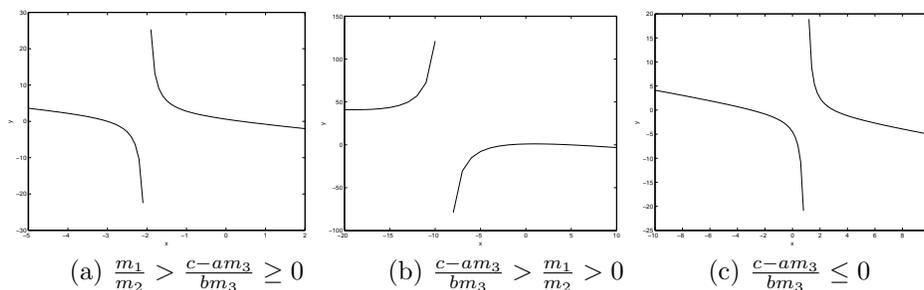


FIGURE 1. Curves of the hyperbolic equation $(a - bx)(m_1 + m_2x + m_3y) - cy = 0$.

For the equation $(-d - ry)(m_1 + m_2x + m_3y) + fx = 0$, it is clear that $(0, -d/r)$ and $(0, -m_1/m_3)$ are on its corresponding curves and if $f - dm_2 \neq 0$, $(\frac{dm_1}{f-dm_2}, 0)$ is also on its corresponding curves. In addition, when $\frac{m_1}{m_3} \neq \frac{dm_2-f}{rm_2}$, this equation is a hyperbolic equation and its two asymptotic lines are $y + \frac{dm_2-f}{rm_2} = 0$ and $y + \frac{m_2}{m_3}x + \frac{rm_1m_2+fm_3}{rm_2} = 0$. Thus, the locations of its corresponding curves can

be roughly seen from Figure 2. When $\frac{m_1}{m_3} = \frac{dm_2-f}{rm_2}$, the equation is equivalent to $(m_1 + m_3y)(dm_3 + rm_2x + rm_3y) = 0$.

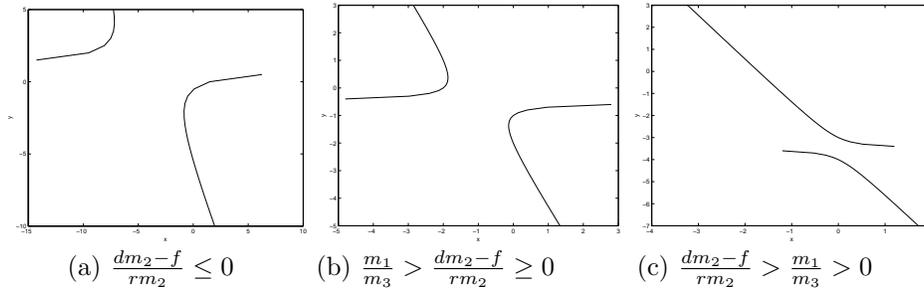


FIGURE 2. Curves of the hyperbolic equation $(a - bx)(m_1 + m_2x + m_3y) - cy = 0$.

Thus, by combining Figures 1 and 2 with the above discussions, we have the following theorem.

Theorem 2.1. *System (1.3) has a unique positive equilibrium $E^*(x^*, y^*)$ if and only if*

$$(f - dm_2)a/b > dm_1. \quad (2.2)$$

Remark 2.2. In [18] it is used $(f - dm_2)a/b > dm_1$ as the sufficient condition of the existence of a unique positive equilibrium.

Remark 2.3. From (2.2), we can easily see that the predator density dependent rate r does not affect the existence of the positive equilibrium.

In the rest of this section, we study the stability of the non-negative equilibria $E_0(0, 0)$, $E_1(\frac{a}{b}, 0)$ and $E^*(x^*, y^*)$, respectively. For this, we first write the system (1.3) as $\bar{X}'(t) = \bar{F}(\bar{X}(t))$, where $\bar{X}(t) = (x(t), y(t))$. Then, for an arbitrary but the fixed point $\bar{X}^* = (x, y)$, we consider its corresponding characteristic equation as follows.

Let $G = (\frac{\partial \bar{F}}{\partial \bar{X}(t)})_{\bar{X}^*}$, then

$$G = \begin{bmatrix} a - 2bx - cq'_x & -cq'_y \\ fq'_x & -d - 2ry + fq'_y \end{bmatrix}_{\bar{X}^*},$$

where

$$q(x, y) = \frac{xy}{m_1 + m_2x + m_3y}, \quad q'_x = \frac{y(m_1 + m_3y)}{(m_1 + m_2x + m_3y)^2},$$

$$q'_y = \frac{x(m_1 + m_2x)}{(m_1 + m_2x + m_3y)^2}.$$

Thus, the characteristic equation of (1.3) at the point \bar{X}^* is

$$|G - \lambda I| = \begin{vmatrix} a - 2bx - cq'_x - \lambda & -cq'_y \\ fq'_x & -d - 2ry + fq'_y - \lambda \end{vmatrix} = P(\lambda, \tau) = 0,$$

where

$$P(\lambda) = \lambda^2 + P_1\lambda + P_0, \quad P_1 = -a + 2bx + cq'_x - R,$$

$$P_0 = (a - 2bx)R + cq'_x(d + 2ry), \quad R = fq'_y - d - 2ry.$$

Based on the characteristic equation of the point E_0 , we have:

Theorem 2.4. *The equilibrium $E_0(0, 0)$ is unstable.*

Proof. The characteristic equation of (1.3) at the point E_0 is

$$|G - \lambda I|_{(0,0)} = (\lambda - a)(\lambda + d) = 0.$$

Clearly, $\lambda = -d$ is a negative eigenvalue and $\lambda = a$ is a positive eigenvalue, implying that E_0 is an unstable saddle. \square

Additionally, based on the characteristic equation of the point E_1 , we have:

Theorem 2.5. *The equilibrium $E_1(\frac{a}{b}, 0)$ is*

- (i) *unstable if $(f - dm_2)a/b > dm_1$;*
- (ii) *locally asymptotically stable if $(f - dm_2)a/b < dm_1$.*

Proof. Since the characteristic equation of (1.3) at the point E_1 is $(\lambda + a)[\lambda - (\frac{af}{m_1b + m_2a} - d)] = 0$, it follows that $\lambda = -a$ and $\lambda = \frac{af}{m_1b + m_2a} - d$ are two eigenvalues.

(i) If $(f - dm_2)a/b > dm_1$, $\lambda = \frac{af}{m_1b + m_2a} - d$ is positive and E_1 is a unstable saddle.

(ii) If $(f - dm_2)a/b < dm_1$, then $\lambda = \frac{af}{m_1b + m_2a} - d$ is negative, implying that E_1 is a locally asymptotically stable node. \square

Remark 2.6. If $(f - dm_2)a/b = dm_1$, we can easily prove that $E_1(\frac{a}{b}, 0)$ is linearly neutrally stable. But, whether $E_1(\frac{a}{b}, 0)$ is stable when $(f - dm_2)a/b = dm_1$ is unknown. However, we can prove that when $(f - dm_2)a/b = dm_1$, $E_1(\frac{a}{b}, 0)$ is globally attractive, which will be discussed in Section 3.

Further, instead of considering the negativeness of the real parts of the eigenvalues [18], we analyze the locally asymptotically stable analysis of $E^*(x^*, y^*)$ by constructing a Lyapunov function for its linearization as follows.

Let

$$\begin{aligned} x(t) &= x^* + u(t) \\ y(t) &= y^* + v(t), \end{aligned}$$

then the linearization of (1.3) is

$$\begin{aligned} u'(t) &= Au(t) - Cv(t) \\ v'(t) &= -Dv(t) + Fu(t), \end{aligned} \tag{2.3}$$

where

$$\begin{aligned} A &= a - 2bx^* - \frac{cy^*(m_1 + m_3y^*)}{(m_1 + m_2x^* + m_3y^*)^2}, & C &= \frac{cx^*(m_1 + m_2x^*)}{(m_1 + m_2x^* + m_3y^*)^2} \\ D &= d + 2ry^* - \frac{fx^*(m_1 + m_2x^*)}{(m_1 + m_2x^* + m_3y^*)^2}, & F &= \frac{fy^*(m_1 + m_3y^*)}{(m_1 + m_2x^* + m_3y^*)^2}. \end{aligned} \tag{2.4}$$

Clearly, C and F are positive. Therefore, by the construction of a Lyapunov function, we have the following result for the positive equilibrium $E^*(x^*, y^*)$.

Theorem 2.7. *If (2.2) holds and*

$$|F - C| < \min\{2D, -2A\}, \quad (2.5)$$

then the equilibrium $(0, 0)$ of the system (2.3) is locally asymptotically stable, implying that the positive equilibrium $E^(x^*, y^*)$ of (1.3) is locally asymptotically stable.*

Proof. For proving the locally asymptotic stability of the equilibrium $(0, 0)$ of the system (2.3), it is sufficient to consider the existence of a strict Lyapunov function.

Letting $W(t) = u^2(t) + v^2(t)$, the time derivative of $W(t)$ is

$$W'(t) = 2Au^2(t) - 2Dv^2(t) + 2(F - C)u(t)v(t).$$

Clearly, $W(t) \geq 0$ and $W(t) = 0$ if and only if $u(t) = v(t) = 0$. In addition, if $u(t) = v(t) = 0$, then $W'(t) = 0$. Moreover,

$$\begin{aligned} W'(t) &\leq 2Au^2(t) - 2Dv^2(t) + 2|F - C||u(t)||v(t)| \\ &\leq [2A + |F - C|]u^2(t) + (-2D + |F - C|)v^2(t). \end{aligned}$$

From (2.2) and (2.5), we have that: if $u^2(t) + v^2(t) > 0$, then $W'(t) < 0$. Thus, $W(t)$ is a strict Lyapunov function. Due to the Lyapunov stability theorem [16], the equilibrium $(0, 0)$ of the system (2.3) is locally asymptotically stable, implying that the positive equilibrium $E^*(x^*, y^*)$ of the system (1.3) is locally asymptotically stable. \square

3. GLOBAL ATTRACTIVENESS OF THE BOUNDARY EQUILIBRIUM

From Theorem 2.5, if $(f - dm_2)a/b < dm_1$, E_1 is locally attractive. However, for the qualitative analysis, it is far from enough. So, in this section, we try to derive a sufficient and necessary condition for assuring the global attractiveness of E_1 . For this, the following lemma is first introduced.

Lemma 3.1. *Let $S = \{(x, y) : x > 0, y > 0\}$ and $\bar{S} = \{(x, y) : x \geq 0, y \geq 0\}$. Then, the sets S and \bar{S} are both invariant sets.*

Proof. Since $x = 0$ and $y = 0$ are both solutions to the system (1.3), due to the uniqueness of the solution to the system (1.3), the lemma directly holds. \square

Then, based on Lemma 3.1, we have the following result on the global attractiveness of E_1 .

Theorem 3.2. *For any solution $(x(t), y(t))$ of (1.3) with $x(0) > 0$ and $y(0) > 0$, $\lim_{t \rightarrow +\infty} (x(t), y(t)) = (\frac{a}{b}, 0)$ if and only if*

$$(f - dm_2)a/b \leq dm_1. \quad (3.1)$$

Proof. For proving the necessity, we consider the following two cases:

Case 1: $(f - dm_2)a/b < dm_1$. First, we want to prove that $\lim_{t \rightarrow +\infty} y(t) = 0$. Due to Lemma 3.1, $x'(t) \leq ax(t) - bx^2(t)$. Then, by considering the comparison equation

$$p'(t) = ap(t) - bp^2(t), \quad p(0) = x(0) > 0,$$

we have that $x(t) \leq p(t)$ for all $t \geq 0$, and $\lim_{t \rightarrow +\infty} p(t) = \frac{a}{b}$. Thus, there exists a sufficiently small positive constant ε with $(f - dm_2)(\frac{a}{b} + \varepsilon) < dm_1$ such that for

this ε , there exists a $T_\varepsilon > 0$ such that $x(t) < \frac{a}{b} + \varepsilon$ for all $t > T_\varepsilon$. Substituting it into the second equation of the system (1.3), we get that for all $t > T_\varepsilon$,

$$y'(t) \leq \left[\frac{(f - dm_2)(\frac{a}{b} + \varepsilon) - dm_1}{m_1 + m_2(\frac{a}{b} + \varepsilon)} \right] y(t) - ry^2(t).$$

So, let us consider the comparison equation

$$q'(t) = \left[\frac{(f - dm_2)(\frac{a}{b} + \varepsilon) - dm_1}{m_1 + m_2(\frac{a}{b} + \varepsilon)} \right] q(t) - rq^2(t), \quad q(T_\varepsilon) = y(T_\varepsilon) > 0,$$

whose solution is

$$q(t) = \frac{Fq'(T_\varepsilon)e^{F(t-T_\varepsilon)}}{1 + rq'(T_\varepsilon)e^{F(t-T_\varepsilon)}},$$

where

$$F = \frac{(f - dm_2)(\frac{a}{b} + \varepsilon) - dm_1}{m_1 + m_2(\frac{a}{b} + \varepsilon)}, \quad q'(T_\varepsilon) = \frac{q(T_\varepsilon)}{F - rq(T_\varepsilon)}.$$

Clearly, by the comparison theorem, we have that $y(t) \leq q(t)$ for all $t \geq T$. In addition, since $(f - dm_2)(\frac{a}{b} + \varepsilon) < dm_1$, then $F < 0$, implying that $\lim_{t \rightarrow +\infty} q(t) = 0$ and thus $\lim_{t \rightarrow +\infty} y(t) = 0$.

Second, we want to prove that $x(t) \rightarrow \frac{a}{b}$ as $t \rightarrow +\infty$, that is, to prove that for any $\varepsilon_1 \in (0, \frac{a}{b})$, there exists a $T_0 > 0$ such that for all $t > T_0$, $-\varepsilon_1 < x(t) - \frac{a}{b} < \varepsilon_1$.

Since $\lim_{t \rightarrow +\infty} y(t) = 0$, from Lemma 3.1, for any given $\varepsilon_1 \in (0, \frac{a}{b})$, there exists a $T_1 > 0$ such that for all $t \geq T_1$, $0 < y(t) < \frac{bm_1}{2c}\varepsilon_1$. Thus, for all $t \geq T_1$, we have

$$\left(a - \frac{b\varepsilon_1}{2}\right)x(t) - bx^2(t) \leq x'(t) \leq ax(t) - bx^2(t). \tag{3.2}$$

Let us consider the comparison equation

$$\tilde{p}'(t) = \left(a - \frac{b\varepsilon_1}{2}\right)\tilde{p}(t) - b\tilde{p}^2(t), \quad \tilde{p}(T_1) = x(T_1) > 0.$$

Since $a > b\varepsilon_1$, we have $\lim_{t \rightarrow +\infty} \tilde{p}(t) = \frac{a}{b} - \frac{\varepsilon_1}{2}$. In addition, we have that for all $t \geq T_1$, $\tilde{p}(t) \leq x(t) \leq p(t)$.

Since $\lim_{t \rightarrow +\infty} p(t) = \frac{a}{b}$, for the above ε_1 , there exists a $T_2 > 0$ such that for all $t > T_2$, $p(t) \leq \frac{a}{b} + \varepsilon_1$. Similarly, since $\lim_{t \rightarrow +\infty} \tilde{p}(t) = \frac{a}{b} - \frac{\varepsilon_1}{2}$, for the above ε_1 , there exists a $T_3 > 0$ such that for all $t > T_3$, $\tilde{p}(t) - \frac{a}{b} + \frac{\varepsilon_1}{2} > -\frac{\varepsilon_1}{2}$. Thus, letting $T_0 = \max\{T_1, T_2, T_3\}$, for all $t > T_0$, $-\varepsilon_1 < x(t) - \frac{a}{b} < \varepsilon_1$, implying that $\lim_{t \rightarrow +\infty} x(t) = \frac{a}{b}$.

(2) $(f - dm_2)a/b = dm_1$. First, we want to prove that $\lim_{t \rightarrow +\infty} y(t) = 0$. Similarly, for an arbitrary $\varepsilon_2 > 0$, there exists $T_{\varepsilon_2} > 0$ such that $x(t) < \frac{a}{b} + \varepsilon_2$ for all $t > T_{\varepsilon_2}$. Thus, due to Lemma 3.1, for all $t > T_{\varepsilon_2}$,

$$\begin{aligned} y'(t) &< -dy(t) - ry^2(t) + \frac{fx(t)}{m_1 + m_2x(t)}y(t) \\ &< y(t)\left(\frac{f(\frac{a}{b} + \varepsilon_2)}{m_1 + m_2(\frac{a}{b} + \varepsilon_2)} - d\right) - ry^2(t) \\ &= \frac{\varepsilon_2(f - dm_2)}{m_1 + m_2(\frac{a}{b} + \varepsilon_2)}y(t) - ry^2(t). \end{aligned}$$

So, let us consider the comparison equation

$$\tilde{q}'(t) = \frac{\varepsilon_2(f - dm_2)}{m_1 + m_2(\frac{a}{b} + \varepsilon_2)}\tilde{q}(t) - r\tilde{q}^2(t), \quad \tilde{q}(T_{\varepsilon_2}) = y(T_{\varepsilon_2}) > 0,$$

whose solution is $\tilde{q}(t) = \frac{F\tilde{q}'(T_{\varepsilon_2})e^{F(t-T_{\varepsilon_2})}}{1+r\tilde{q}'(T_{\varepsilon_2})e^{F(t-T_{\varepsilon_2})}}$, where $F = \frac{\varepsilon_2(f-dm_2)}{m_1+m_2(\frac{a}{b}+\varepsilon_2)}$ and $\tilde{q}'(T) = \frac{\tilde{q}(T_{\varepsilon_2})}{F-r\tilde{q}'(T_{\varepsilon_2})}$. Clearly, by the comparison theorem, we have that $y(t) \leq \tilde{q}(t)$ for all $t \geq T_{\varepsilon_2}$. In addition, since $(f-dm_2)a/b = dm_1$, then $F > 0$, implying that $\lim_{t \rightarrow +\infty} \tilde{q}(t) = \frac{\varepsilon_2(f-dm_2)}{r(m_1+m_2(\frac{a}{b}+\varepsilon_2))}$.

Thus, for the above ε_2 , there exists a $T' > 0$ such that for all $t \geq T'$,

$$\tilde{q}(t) - \frac{\varepsilon_2(f-dm_2)}{r(m_1+m_2(\frac{a}{b}+\varepsilon_2))} < \varepsilon_2.$$

Letting $T'_0 = \max\{T_{\varepsilon_2}, T'_1\}$, then for all $t > T'_0$, $y(t) < \frac{\varepsilon_2(f-dm_2)}{r(m_1+m_2(\frac{a}{b}+\varepsilon_2))} + \varepsilon_2 < \frac{f-dm_2+r(m_1+m_2\frac{a}{b})}{r(m_1+m_2\frac{a}{b})}\varepsilon_2$, implying that $\lim_{t \rightarrow +\infty} y(t) = 0$. The proof of $\lim_{t \rightarrow +\infty} x(t) = \frac{a}{b}$ is similar to the case $(f-dm_2)a/b < dm_1$.

For proving the sufficiency, we assume that $(f-dm_2)a/b > dm_1$ and try to derive a contradiction. Due to the assumption that $(f-dm_2)a/b > dm_1$, system (1.3) has a unique positive equilibrium (x^*, y^*) , which is also a solution to (1.3), contradicting with $\lim_{t \rightarrow +\infty} (x^*, y^*) = (\frac{a}{b}, 0)$. Thus, condition (3.1) must hold. \square

Remark 3.3. In [18] it is only provided $f < dm_2$ as a sufficient condition for the globally asymptotic stability of $E_1(\frac{a}{b}, 0)$.

Remark 3.4. From Theorems 2.5 and 3.2, we can directly derive that $E_1(\frac{a}{b}, 0)$ is a saddle if and only if $(f-dm_2)a/b > dm_1$.

4. PERMANENCE ANALYSIS

From Theorem 3.2, $(f-dm_2)a/b \leq dm_1$ is a sufficient condition for the predator to be extinctive. In this section, we will like to derive a sufficient and necessary condition for the permanence (or equivalently, the extinction).

Firstly, we introduce the following boundedness result for (1.3).

Lemma 4.1. *All solutions of (1.3) with positive initial conditions are bounded for $t \geq 0$.*

Proof. Due to Lemma 3.1, for all $t > 0$, $x'(t) \leq ax(t) - bx^2(t)$. Similar to the proof of Theorem 3.2, there exists a $T > 0$ such that for all $t > T$, $x(t) \leq \frac{a}{b} + 1$, implying that $x(t)$ is bounded for all $t \geq 0$.

Letting $\omega(t) = \frac{f}{c}x(t) + y(t)$, we have

$$\frac{d\omega(t)}{dt} \leq -dy(t) + \frac{af}{c}x(t) = -d\omega(t) + \frac{(a+d)f}{c}x(t).$$

Clearly, there exist $M > 0$ and $T_1 > 0$ such that for all $t \geq T_1$,

$$\frac{d\omega(t)}{dt} \leq M - d\omega(t).$$

Let $\frac{dp(t)}{dt} = M - dp(t)$ with $p(T_1) = \omega(T_1)$, then $\omega(t) \leq p(t)$ for all $t \geq T_1$ and $\lim_{t \rightarrow +\infty} p(t) \leq \frac{M}{d}$. Thus, there exists a $T_2 > \max\{T, T_1\}$ such that for all $t > T_2$, $\omega(t) \leq p(t) \leq \frac{M}{d} + 1$, implying that $y(t)$ is bounded for all $t \geq 0$. \square

Secondly, based on Lemma 4.1 and [16, Lemma 4.1], we have the following property about the ω -limit set.

Lemma 4.2. *For any point in $S = \{(x, y) : x > 0, y > 0\}$, its ω -limit set is nonempty, compact, connected, and invariant.*

Thirdly, by Lemma 4.1, Lemma 4.2 and Poincaré-Bendixson theorem [10], we have the following theorem describing the possible types of the ω -limit set of any initial point in $S = \{(x(0), y(0)) : x(0) > 0, y(0) > 0\}$.

Theorem 4.3. *If $(f - dm_2)a/b > dm_1$, then for any initial point in S , its ω -limit set consists of either only the positive equilibrium E^* or a closed orbit.*

Proof. For any point (x_0, y_0) in S , let $(x(t), y(t))$ be the orbit of the system (1.3) with $(x(0), y(0)) = (x_0, y_0)$. By Lemma 4.2 and Poincaré-Bendixson theorem [10],

- (a) the ω -limit set of (x_0, y_0) consists of a single point p which is a equilibrium point such that $\lim_{t \rightarrow +\infty} (x(t), y(t)) = p$, or
- (b) the ω -limit set of (x_0, y_0) is a closed orbit, or
- (c) the ω -limit set of (x_0, y_0) consists of equilibrium points together with their connecting orbits. Each such orbit approaches an equilibrium point as $t \rightarrow +\infty$ and $t \rightarrow -\infty$.

In addition, it is clear that if $(f - dm_2)a/b > dm_1$, system (1.3) has only three equilibria E_0 , E_1 and E^* in the first quadrant. Moreover, by the proof of Theorem 2.4, E_0 is a saddle; by the proof of Theorem 2.5, if $(f - dm_2)a/b > dm_1$, E_1 is also a saddle.

So, for the above case (a), the ω -limit set consists of only the equilibrium E^* . Moreover, we can prove that the above case (c) cannot occur as follows.

First, we can prove that the ω -limit set cannot contain E_0 and E^* together. Otherwise, there exists an orbit $\gamma_0(t)$ connecting E_0 and E^* . Since E_0 is a saddle, $\lim_{t \rightarrow +\infty} \gamma_0(t) = E_0$, contradicting with the fact that $(0, y(t))$ is the unique orbit of the system (1.3) with $\lim_{t \rightarrow +\infty} (0, y(t)) = E_0$.

Second, we assume that the ω -limit set consists of E_0 and E_1 together with their connecting orbit $(x(t), 0)$ with $0 < x(t) < a/b$, $\lim_{t \rightarrow -\infty} (x(t), 0) = E_0$ and $\lim_{t \rightarrow +\infty} (x(t), 0) = E_1$, and try to derive a contradiction as follows.

Since E_0 is a saddle, there exists a constant $\delta > 0$ such that the orbit $(x(t), y(t))$ infinitely enters and then leaves the region $\{(x, y) : x^2 + y^2 \leq \delta\}$. Let t_n be the n -th time instant for the orbit to enter the region. Due to Lemma 4.1, $\{(x(t_n), y(t_n))\}$ is a bounded sequence. Thus, there exist a subsequence $\{(x(t_{n_k}), y(t_{n_k}))\}$ and a (\bar{x}, \bar{y}) such that $\lim_{k \rightarrow +\infty} (x(t_{n_k}), y(t_{n_k})) = (\bar{x}, \bar{y})$ and $\bar{y} \neq 0$, contradicting with the assumption that the ω -limit set consists of E_0 and E_1 together with their connecting orbit $(x(t), 0)$.

Third, we can similarly prove that the ω -limit set cannot consist of E_1 and E^* together with their connecting orbit.

Fourth, the ω -limit set cannot consist of E_0 and a homoclinic orbit since $(0, y(t))$ is the unique orbit of the system (1.3) with $\lim_{t \rightarrow +\infty} (0, y(t)) = E_0$.

Fifth, the ω -limit set cannot consist of E_1 and a homoclinic orbit since $(x(t), 0)$ with $0 < x(t) < a/b$ is the unique orbit of the system (1.3) with $\lim_{t \rightarrow +\infty} (x(t), 0) = E_1$.

Sixth, assume that the ω -limit set contains E^* and a homoclinic orbit. Then, there exists at least one positive equilibrium inside the region enclosed by the homoclinic orbit, contradicting with the result that E^* is the unique positive equilibrium.

Thus, we have proved that if $(f - dm_2)a/b > dm_1$, then for any point in S , its ω -limit set consists of either only the positive equilibrium E^* or a closed orbit. \square

Finally, based on Theorems 4.3 and 3.2 and Definition 1.1, we have the following result for the permanence of the system (1.3).

Theorem 4.4. *System (1.3) is permanent if and only if $(f - dm_2)a/b > dm_1$ (i.e., positive equilibria exist).*

Proof. Due to Theorem 4.3 and Definition 1.1, if $(f - dm_2)a/b > dm_1$, then the system (1.3) is permanent. In addition, due to Theorem 3.2 and Definition 1.1, if $(f - dm_2)a/b \leq dm_1$, the system (1.3) is not permanent. Thus, the sufficiency and necessity are both proved. \square

Remark 4.5. By Theorem 4.4, the predator density dependent rate r does not affect the permanence of the system (1.3).

5. PERMANENT COEXISTENCE TO THE POSITIVE EQUILIBRIUM

From Theorems 4.3 and 4.4, the permanence of the system shows that the time evolution of the two species eventually either forms a cyclic loop or attracts to the positive equilibrium. In this section, we try to use the comparison theorem to provide a sufficient condition for the global asymptotic stability of $E^*(x^*, y^*)$.

Let the initial point be in the set $S = \{(x, y) : x > 0, y > 0\}$. We need the following preparations by iteratively making use of the comparison theorem.

Similar to the proof in Theorem 3.2, for an arbitrary sufficiently small $\varepsilon'_1 > 0$, there exists a T_1 such that for all $t \geq T_1$,

$$x(t) < \frac{a}{b} + \varepsilon'_1. \quad (5.1)$$

Let $A_1 = \frac{a}{b} + \varepsilon'_1$. In addition, from the first equation of the system (1.3), we can also obtain that: for all $t > 0$,

$$x'(t) > ax(t) - bx^2(t) - \frac{c}{m_3}x(t).$$

When $a > \frac{c}{m_3}$, for any given $\varepsilon'_{1,B} > 0$ with $\varepsilon'_{1,B} < \min\{\varepsilon'_1, \frac{1}{b}(a - \frac{c}{m_3})\}$, there exists a $T_2 > T_1$ such that for all $t > T_2$,

$$x(t) > \frac{1}{b}(a - \frac{c}{m_3}) - \varepsilon'_{1,B} > 0. \quad (5.2)$$

Let $B_1 = \frac{1}{b}(a - \frac{c}{m_3}) - \varepsilon'_{1,B}$.

From the second equation of the system (1.3), we can obtain that: for all $t > 0$, $y'(t) < y(t)[\frac{f}{m_2} - d - ry(t)]$. Due to the condition (2.2), $f > dm_2$ directly holds. Thus, similar to the proof of the second case in Theorem 3.2, for the above ε'_1 , there exists a $T_3 > T_2$ such that for all $t > T_3$,

$$y(t) < \frac{1}{r}(\frac{f}{m_2} - d) + \varepsilon'_1. \quad (5.3)$$

Let $C_1 = \frac{1}{r}(\frac{f}{m_2} - d) + \varepsilon'_1$. In addition, by using the inequalities (5.2) and (5.3) for the second equation of (1.3), we also obtain that: for all $t > T_3$

$$y'(t) > y(t)[-d - ry(t) + \frac{fB_1}{m_1 + m_2B_1 + m_3C_1}].$$

If $\frac{fB_1}{m_1+m_2B_1+m_3C_1} > d$, similar to the proof of the second case in Theorem 3.2, for any given $\varepsilon'_{1,D} > 0$ with $\varepsilon'_{1,D} < \min\{\varepsilon'_1, \frac{1}{r}(\frac{fB_1}{m_1+m_2B_1+m_3C_1} - d)\}$, there exists a $T_4 > T_3$ such that for all $t > T_4$,

$$y(t) > \frac{1}{r} \left(\frac{fB_1}{m_1 + m_2B_1 + m_3C_1} - d \right) - \varepsilon'_{1,D} > 0. \quad (5.4)$$

Let $D_1 = \frac{1}{r} \left(\frac{fB_1}{m_1+m_2B_1+m_3C_1} - d \right) - \varepsilon'_{1,D}$. Therefore, for system (1.3), we have

$$B_1 < x(t) < A_1, \quad D_1 < y(t) < C_1, \quad t \geq T_4.$$

Provided that $a > \frac{c}{m_3}$ and $\frac{fB_1}{m_1+m_2B_1+m_3C_1} > d$, by using (5.1) and (5.4) in the first equation of (1.3), we obtain

$$x'(t) < ax(t) - bx^2(t) - \frac{cD_1x(t)}{m_1 + m_2A_1 + m_3D_1}, \quad t > T_4.$$

If $a > \frac{c}{m_3}$ holds, then $a > \frac{cD_1}{m_1+m_2A_1+m_3D_1}$. Similarly, for the above ε'_1 , there exists a $T_5 > T_4$ such that for all $t > T_5$,

$$x(t) < \frac{1}{b} \left(a - \frac{cD_1}{m_1 + m_2A_1 + m_3D_1} \right) + \varepsilon'_1. \quad (5.5)$$

Let $A_2 = \frac{1}{b} \left(a - \frac{cD_1}{m_1+m_2A_1+m_3D_1} \right) + \varepsilon'_1$. Clearly, $A_2 < A_1$. In addition, by using (5.2) and (5.3) in the first equation of (1.3), we have

$$x'(t) > ax(t) - bx^2(t) - \frac{cx(t)C_1}{m_1 + m_2B_1 + m_3C_1}, \quad t > T_4.$$

When $a > \frac{c}{m_3}$ holds, then $a > \frac{cC_1}{m_1+m_2B_1+m_3C_1}$. Similarly, for any given $\varepsilon'_{2,B} > 0$ with $\varepsilon'_{2,B} < \min\{\varepsilon'_1, \varepsilon'_{1,B}, \frac{1}{b} \left(a - \frac{cC_1}{m_1+m_2B_1+m_3C_1} \right)\}$, there exists a $T_6 > T_5$ such that for all $t > T_6$,

$$x(t) > \frac{1}{b} \left(a - \frac{cC_1}{m_1 + m_2B_1 + m_3C_1} \right) - \varepsilon'_{2,B} > 0. \quad (5.6)$$

Let $B_2 = \frac{1}{b} \left(a - \frac{cC_1}{m_1+m_2B_1+m_3C_1} \right) - \varepsilon'_{2,B}$. Clearly, $B_2 > B_1$.

Moreover, provided that $a > \frac{c}{m_3}$ and $\frac{fB_1}{m_1+m_2B_1+m_3C_1} > d$, by using the inequalities (5.1) and (5.4) in the second equation of the system (1.3), we obtain

$$y'(t) < y(t) \left[\frac{fA_1}{m_1 + m_2A_1 + m_3D_1} - d - ry(t) \right], \quad t > T_4.$$

If $\frac{fB_1}{m_1+m_2B_1+m_3C_1} > d$ holds, then $\frac{fA_1}{m_1+m_2A_1+m_3D_1} > d$. Similarly, for the above ε'_1 , there exists a $T_7 > T_6$ such that for all $t > T_7$,

$$y(t) < \frac{1}{r} \left(\frac{fA_1}{m_1 + m_2A_1 + m_3D_1} - d \right) + \varepsilon'_1, \quad (5.7)$$

Let $C_2 = \frac{1}{r} \left(\frac{fA_1}{m_1+m_2A_1+m_3D_1} - d \right) + \varepsilon'_1$. So $C_2 < C_1$. In addition, by using (5.2) and (5.3) in the second equation of (1.3), we have

$$y'(t) > y(t) \left[-d - ry(t) + \frac{fB_1}{m_1 + m_2B_1 + m_3C_1} \right], \quad t > T_4.$$

Similarly, for any given $\varepsilon'_{2,D} > 0$, $\varepsilon'_{2,D} < \min\{\varepsilon'_1, \varepsilon'_{1,D}, \frac{1}{r} \left(\frac{fB_1}{m_1+m_2B_1+m_3C_1} - d \right)\}$, there exists a $T_8 > T_7$ such that for all $t > T_8$,

$$y(t) > \frac{1}{r} \left(\frac{fB_1}{m_1 + m_2B_1 + m_3C_1} - d \right) - \varepsilon'_{2,D}, \quad (5.8)$$

Let $D_2 = \frac{1}{r} \left(\frac{fB_1}{m_1+m_2B_1+m_3C_1} - d \right) - \varepsilon'_{2,D}$. So it has $D_2 > D_1$.

Thus, combining the above discussions, we have

$$B_1 < B_2 < x(t) < A_2 < A_1, \quad D_1 < D_2 < y(t) < C_2 < C_1, \quad t \geq T_8.$$

By repeating the above procedure, we can get five sequences $\{T_n\}_{n=1}^{+\infty}$, $\{A_n\}_{n=1}^{\infty}$, $\{C_n\}_{n=1}^{\infty}$, $\{B_n\}_{n=1}^{\infty}$ and $\{D_n\}_{n=1}^{\infty}$. Here, by defining $\Delta(x, y)$ to be $m_1 + m_2x + m_3y$, then for all $n \geq 2$, A_n , C_n , B_n and D_n have the following expressions

$$\begin{aligned} A_n &= \frac{1}{b} \left(a - \frac{cD_{n-1}}{\Delta(A_{n-1}, D_{n-1})} \right) + \varepsilon'_1, & B_n &= \frac{1}{b} \left(a - \frac{cC_{n-1}}{\Delta(B_{n-1}, C_{n-1})} \right) - \varepsilon'_{n,B}, \\ C_n &= \frac{1}{r} \left(\frac{fA_{n-1}}{\Delta(A_{n-1}, D_{n-1})} - d \right) + \varepsilon'_1, & D_n &= \frac{1}{r} \left(\frac{fB_{n-1}}{\Delta(B_{n-1}, C_{n-1})} - d \right) - \varepsilon'_{n,D}, \end{aligned}$$

respectively, satisfying

$$\begin{aligned} 0 < \varepsilon'_{n,B} < \min\{\varepsilon'_1, \varepsilon'_{n-1,B}, \frac{1}{b} \left(a - \frac{cC_{n-1}}{\Delta(B_{n-1}, C_{n-1})} \right)\} \\ 0 < \varepsilon'_{n,D} < \min\{\varepsilon'_1, \varepsilon'_{n-1,D}, \frac{1}{r} \left(\frac{fB_{n-1}}{\Delta(B_{n-1}, C_{n-1})} - d \right)\} \end{aligned} \quad (5.9)$$

$$0 < B_1 < B_2 < \cdots < B_n < x(t) < A_n < \cdots < A_2 < A_1, \quad t \geq T_{4n}$$

$$0 < D_1 < D_2 < \cdots < D_n < y(t) < C_n < \cdots < C_2 < C_1, \quad t \geq T_{4n}.$$

Clearly, $\{A_n\}$ and $\{C_n\}$ are bounded decreasing sequences and $\{B_n\}$ and $\{D_n\}$ are bounded increasing sequences. Thus, there exist \bar{A} , \bar{C} , \bar{B} and \bar{D} such that $\lim_{t \rightarrow +\infty} A_n = \bar{A}$, $\lim_{t \rightarrow +\infty} C_n = \bar{C}$, $\lim_{t \rightarrow +\infty} B_n = \bar{B}$ and $\lim_{t \rightarrow +\infty} D_n = \bar{D}$. In addition, from the formula (5.9), $\bar{A} \geq \bar{B}$ and $\bar{C} \geq \bar{D}$.

Further, from the expressions of A_n , C_n , B_n and D_n , we obtain

$$\begin{aligned} A_n - B_n &= \varepsilon'_1 + \varepsilon'_{n,B} + \left(cm_1(C_{n-1} - D_{n-1}) + cm_2[A_{n-1}(C_{n-1} - D_{n-1}) \right. \\ &\quad \left. + D_{n-1}(A_{n-1} - B_{n-1}) \right) / (b\Delta(B_{n-1}, C_{n-1})\Delta(A_{n-1}, D_{n-1})). \end{aligned}$$

Thus, when $n \rightarrow +\infty$, we have

$$\bar{A} - \bar{B} = \frac{cm_1(\bar{C} - \bar{D}) + cm_2[\bar{A}(\bar{C} - \bar{D}) + \bar{D}(\bar{A} - \bar{B})]}{b\Delta(\bar{B}, \bar{C})\Delta(\bar{A}, \bar{D})} + \varepsilon'_1 + \varepsilon'_{n,B}. \quad (5.10)$$

Similarly, we can obtain

$$\begin{aligned} C_n - D_n &= \varepsilon'_1 + \varepsilon'_{n,D} + \left(fm_1(A_{n-1} - B_{n-1}) + fm_3[A_{n-1}(C_{n-1} - D_{n-1}) \right. \\ &\quad \left. + D_{n-1}(A_{n-1} - B_{n-1}) \right) / (r\Delta(B_{n-1}, C_{n-1})\Delta(A_{n-1}, D_{n-1})). \end{aligned}$$

Thus, when $n \rightarrow +\infty$, we have

$$\bar{C} - \bar{D} = \frac{f(m_1 + m_3\bar{D})(\bar{A} - \bar{B}) + (\varepsilon'_1 + \varepsilon'_{n,D})r\Delta(\bar{B}, \bar{C})\Delta(\bar{A}, \bar{D})}{r\Delta(\bar{B}, \bar{C})\Delta(\bar{A}, \bar{D}) - fm_3\bar{A}}. \quad (5.11)$$

Putting (5.11) in (5.10), we have

$$\bar{A} - \bar{B} \leq \left| \frac{2 \left(\frac{cr(m_1+m_2\bar{A})}{b[r\Delta(\bar{B}, \bar{C})\Delta(\bar{A}, \bar{D}) - fm_3\bar{A}] + 1} \right)}{1 - \frac{c}{b\Delta(\bar{B}, \bar{C})\Delta(\bar{A}, \bar{D})} \left[\frac{f(m_1+m_2\bar{A})(m_1+m_3\bar{D})}{r\Delta(\bar{B}, \bar{C})\Delta(\bar{A}, \bar{D}) - fm_3\bar{A}} + m_2\bar{D} \right]} \right| \varepsilon'_1.$$

Then, by the arbitrariness of ε'_1 , we have $\bar{A} = \bar{B}$.

Similarly, by equation (5.11) and the relation $\bar{A} = \bar{B}$, we have

$$\bar{C} - \bar{D} \leq \left| \frac{2r\Delta(\bar{B}, \bar{C})\Delta(\bar{A}, \bar{D})}{r\Delta(\bar{B}, \bar{C})\Delta(\bar{A}, \bar{D}) - fm_3\bar{A}} \right| \varepsilon'_1.$$

Then, by the arbitrariness of ε'_1 , we have $\bar{C} = \bar{D}$.

Combining the above preparations, we can prove the following theorem.

Theorem 5.1. *If (2.2) and the following condition*

$$am_3 > c, \quad \frac{\frac{f}{bm_3}(am_3 - c)}{m_1 + \frac{m_2}{bm_3}(am_3 - c) + \frac{m_3}{rm_2}(f - dm_2)} > d \tag{5.12}$$

hold, then for any solution $(x(t), y(t))$ of (1.3) with the positive initial condition in S , $\lim_{t \rightarrow +\infty} (x(t), y(t)) = E^*$; this implies that the positive equilibrium E^* of (1.3) is globally attractive.

Proof. The condition (5.12) can assure that $a > \frac{c}{m_3}$ and $\frac{fB_1}{m_1 + m_2B_1 + m_3C_1} > d$. Thus, provided that the condition (2.2) holds, from the above preparations and the formula (5.9), for any solution $(x(t), y(t))$ of the system (1.3) with the positive initial condition in S , there exist \bar{A} and \bar{C} such that $\lim_{t \rightarrow +\infty} (x(t), y(t)) = (\bar{A}, \bar{C})$.

Since (\bar{A}, \bar{C}) is the unique ω -limit point of $(x(0), y(0))$, due to the property of the ω -limit set, (\bar{A}, \bar{C}) must be an equilibrium in the set $\bar{S} = \{(x, y) : x \geq 0, y \geq 0\}$. Further, due to Theorem 2.4, the condition (2.2) and Theorem 3.2, this equilibrium must be the positive equilibrium E^* . \square

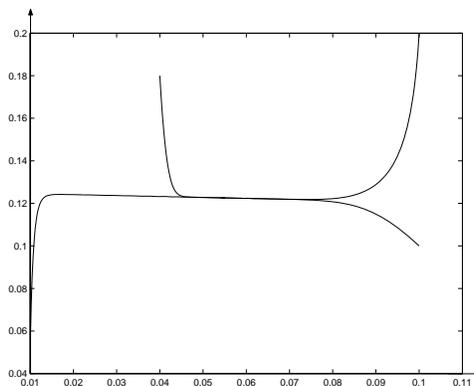


FIGURE 3. Four phase diagrams of system (5.13).

Example 5.2. Let $a = 2, b = 16, c = 1, d = 0.01, r = 3, f = 2, m_1 = 1, m_2 = 2$ and $m_3 = 3$, then system (1.3) becomes

$$\begin{aligned} x' &= x \left[2 - 16x - \frac{y}{1 + 2x + 3y} \right], \\ y' &= y \left[-\frac{1}{100} - 3y + \frac{2x}{1 + 2x + 3y} \right]. \end{aligned} \tag{5.13}$$

Clearly, $(f - dm_2)a/b - dm_1 \approx 0.238, am_3 - c = 5, \frac{\frac{f}{bm_3}(am_3 - c)}{m_1 + \frac{m_2}{bm_3}(am_3 - c) + \frac{m_3}{rm_2}(f - dm_2)} - d \approx 0.102$. Thus, the conditions (2.2) and (5.12) hold. By Theorem 5.1, the positive

equilibrium point $E^* = (0.123, 0.055)$ of (5.13) is globally attractive, which can also be seen from Figure 3. Note that in Figure 3, the four phase diagrams start from initial points $(0.2, 0.1)$, $(0.05, 0.01)$, $(0.1, 0.1)$ and $(0.18, 0.04)$, respectively, and all approach $E^* = (0.123, 0.055)$ as $t \rightarrow +\infty$.

Remark 5.3. The conditions for global attractiveness of the positive equilibrium provided in Theorem 5.1 depend only on parameters, while the conditions in [18] depend on parameters and on the positive equilibrium (x^*, y^*) . That additionally need requires solving numerically for (x^*, y^*) in equations (2.1).

6. CONCLUSION

In this paper, we further investigated the dynamics of a density-dependent predator-prey system developed by Li and Takeuchi [18] and obtained the following results:

- (1) The system has a unique positive equilibrium if and only if $(f - dm_2)a/b > dm_1$;
- (2) The boundary equilibrium $E_1(\frac{a}{b}, 0)$ is a saddle if and only if $(f - dm_2)a/b > dm_1$. Moreover, $E_1(\frac{a}{b}, 0)$ is global attractive if and only if $(f - dm_2)a/b \leq dm_1$;
- (3) The system is permanent if and only if $(f - dm_2)a/b > dm_1$.

In addition, we have provided a sufficient condition for locally asymptotic stability of $E^*(x^*, y^*)$ by constructing a Lyapunov function and a sufficient condition for global attractiveness of $E^*(x^*, y^*)$ by making use of the comparison theorem.

Further, we derived that the predator density dependent rate r does not affect the existence of a positive equilibrium and the permanence (or equivalently, the extinction) of the system (1.3). However, whether r will affect locally asymptotic stability of $E^*(x^*, y^*)$ and global attractiveness of $E^*(x^*, y^*)$ is still an unsolved problem, which will be our future work. It is also interesting to:

- (1) provide weaker conditions for global attractiveness of the positive equilibrium;
- (2) derive conditions to assure the (unique) existence of periodic orbits [4, 15, 13];
- (3) analyze bifurcations [13, 19, 20, 28] about the stability of the positive equilibrium.

Acknowledgments. This work was supported by grants NSFC-11422111, NSFC-11290141, NSFC-11371047, SKLSDE-2013ZX-10, and by the Innovation Foundation of BUAA for PhD Graduates.

REFERENCES

- [1] D. D. Bainov, P. S. Simeonov; *Systems with impulse effect: stability theory and applications*, Ellis Horwood Limited, Chichester, 1989.
- [2] D. D. Bainov, P. S. Simeonov; *Impulsive differential equations: periodic solutions and applications*, Longman Scientific and Technical, New York, 1993.
- [3] J. R. Beddington; *Mutual interference between parasites or predators and its effect on searching efficiency*, J. Animal Ecol. 44(1975), 331–340.
- [4] R. S. Cantrell, C. Cosner; *On the dynamics of predator-prey models with the Beddington-DeAngelis functional response*, J. Math. Anal. Appl. 257(2001), 206–222.
- [5] J. Cui, Y. Takeuchi; *Permanence, extinction and periodic solution of predator-prey system with Beddington-DeAngelis functional response*, J. Math. Anal. Appl. 317(2006), 464–474.

- [6] D. L. DeAngelis, R. A. Goldstein, R. V. O'Neil; *A model of trophic interaction*, Ecology 56(1975), 881–892.
- [7] Z. Du and Z. Feng, *Periodic solutions of a neutral impulsive predator-prey model with Beddington-DeAngelis functional response with delays*, J. Comput. Appl. Math. 258(2014), 87–98.
- [8] Z. Du, X. Chen and Z. Feng, *Multiple positive periodic solutions to a predator-prey model with Leslie-Gower Holling-type II functional response and harvesting terms*, Discrete Contin. Dyn. Syst. Ser. S 7(2014), 1203–1214.
- [9] M. Fan, Y. Kuang; *Dynamics of a nonautonomous predator-prey system with the Beddington-DeAngelis functional response*, J. Math. Anal. Appl. 295(2004), 15–39.
- [10] W. Hahn; *Stability of motion*, Springer, 1967.
- [11] J. K. Hale, P. Waltman; *Persistence in infinite-dimensional systems*, SIAM J. Math. Anal. 20(1989), 388–395.
- [12] S. B. Hsu, S. P. Hubbell, P. Waltman; *Competing predators*, SIAM J. Appl. Math. 35(1978), 617–625.
- [13] S. B. Hsu, S. P. Hubbell, P. Waltman; *A contribution to the theory of competing predators*, Ecological Monogr. 35(1978), 617–625.
- [14] G. Huang, W. Ma, Y. Takeuchi; *Global analysis for delay virus dynamics model with Beddington-DeAngelis functional response*, Appl. Math. Lett. 24(2011), 1199–1203.
- [15] T. Hwang; *Uniqueness of limit cycles of the predator-prey system with Beddington-DeAngelis functional response*, J. Math. Anal. Appl. 290(2004), 113–122.
- [16] H. K. Khalil; *Nonlinear systems (third edition)*, Prentice Hall, 2002.
- [17] Y. Kuang, E. Beretta; *Global qualitative analysis of a ratio-dependent predator-prey system*, J. Math. Biol. 36(1998), 389–406.
- [18] H. Li, Y. Takeuchi; *Dynamics of the density dependent predator-prey system with Beddington-DeAngelis functional response*, J. Math. Anal. Appl. 374(2011), 644–654.
- [19] S. Liu, E. Beretta; *A stage-structured predator-prey model of Beddington-DeAngelis type*, SIAM J. Appl. Math. 66(2006), 1101–1129.
- [20] Z. Liu, R. Yuan; *Stability and bifurcation in a delayed predator-prey system with Beddington-DeAngelis functional response*, J. Math. Anal. Appl. 296(2004), 521–537.
- [21] G. T. Skalski, J. F. Gilliam; *Functional responses with predator interference: Viable alternatives to the Holling type II model*, Ecology, 82(2001), 3083–3092.
- [22] X. Song, L. Chen; *Optimal harvesting and stability for a predator-prey system with stage structure*, Acta Math. Appl. Sini. Eng ser. 18(3)(2002), 423–430.
- [23] G. Sun, Z. Jin, Q. Liu, B. Li; *Rich dynamics in a predator-prey with both noise and periodic force*, Biosystems 100(2010), 14–22.
- [24] Z. Teng; *Uniform persistence of the periodic predator-prey Lotka-Volterra systems*, Appl. Anal. 72(3-4)(1998), 339–352.
- [25] H. R. Thieme; *Persistence under relaxed point-dissipativity (with application to an endemic model)*, SIAM J. Math. Anal. 24(1993), 407–435.
- [26] W. Wang, J. Sun; *On the predator-prey system with Holling-(n+1) functional response*, Acta Math. Sini. Eng ser. 23(2007), 1–6.
- [27] D. Xiao, H. Zhu; *Multiple focus and hopf bifurcations in a predator prey system with non-monotonic functional response*, SIAM J. Appl. Math. 66(3)(2006), 802–819.
- [28] H. Zhu, S. Campbell, G. Wolkowicz; *Bifurcation analysis of a predator-prey system with nonmonotonic functional response*, SIAM J. Appl. Math. 63(2002), 636–682.

HAIYIN LI

LMIB AND SCHOOL OF MATHEMATICS AND SYSTEMS SCIENCE, BEIHANG UNIVERSITY, BEIJING, CHINA.

DEPARTMENT OF MATHEMATICS AND INFORMATION, HENAN UNIVERSITY OF ECONOMICS AND LAW, ZHENGZHOU, CHINA

E-mail address: lihaiyin2013@163.com

ZHIKUN SHE

SKLSDE, LMIB AND SCHOOL OF MATHEMATICS AND SYSTEMS SCIENCE, BEIHANG UNIVERSITY, BEIJING, CHINA

E-mail address: zhikun.she@buaa.edu.cn