On the Dynamics of Two-consumers-one-resource Competing Systems with Beddington-DeAngelis Functional Response

Sze-Bi Hsu*[1], Shigui Ruan†[2], and Ting-Hui Yang‡[3]

[1]*Department of Mathematics and The National Center for Theoretical Science, National Tsing-Hua University, Hsinchu 30013, Taiwan, Republic of China*

[2]*Department of Mathematics, University of Miami, Coral Gables, FL 33124-4250, USA*

[3]*Department of Mathematics, Tamkang University, 151 Ying-chuan Road, New Taipei City 25137, Taiwan, Republic of China*

March 16, 2013

Abstract

In this paper we study a two-consumers-one-resource competing system with Beddington-DeAngelis functional response. The two consumers competing for a renewable resource have intraspecific competition among their own populations. Firstly we investigate the extinction and uniform persistence of the predators, local and global stability of the equilibria, and existence of Hopf bifurcation at the positive equilibrium. Then we compare the dynamic behavior of the system with and without interference effects. Analytically we study the competition of two identically species with different interference effects. We also study the relaxation oscillation in the case of interference effects. Finally we present extensive numerical simulations to understand the interference effects on the competition outcomes.

*Research was partially supported by National Council of Science, Republic of China.

†Research was partially supported by National Science Foundation (DMS-1022728).

‡Research was partially supported by National Council of Science, Republic of China.

1 Introduction

In this paper we study a two-consumers-one-resource system with Beddington-DeAngelis functional response. The two consumers (predators) competing for a renewable resource (prey) have interference competition among their own populations. The mathematical model takes the following system of three nonlinear ordinary differential equations Beddington [2], DeAngelis et al. [8], Huisman and De Boer [14]:

$$\begin{aligned} \frac{dx}{dt} &= rx(1-\frac{x}{K}) - \frac{m_1 x}{a_1 + x + b_1 y_1} y_1 - \frac{m_2 x}{a_2 + x + b_2 y_2} y_2, \\ \frac{dy_1}{dt} &= (\frac{e_1 m_1 x}{a_1 + x + b_1 y_1} - d_1) y_1, \\ \frac{dy_2}{dt} &= (\frac{e_2 m_2 x}{a_2 + x + b_2 y_2} - d_2) y_2 \end{aligned} \tag{1.1}$$

with initial values $x(0) = x_0 > 0$, $y_1(0) = y_{10} > 0$, $y_2(0) = y_{20} > 0$.

In (1.1) $x(t)$, $y_1(t)$, and $y_2(t)$ represent the population density of prey and two predators respectively at time t. In the absence of predation, the prey grows logistically with intrinsic growth rate r and carrying capacity K. The i-th predator consumes the prey according to the Beddington-DeAngelis functional response $\frac{m_i x y_i}{a_i + x + b_i y_i}$ and its growth rate is $\frac{e_i m_i x y_i}{a_i + x + b_i y_i}$, where e_i is the conversion efficiency coefficient ; m_i is the maximal consumption rate; a_i is the half-satuation constant and b_i measures the intraspecific interference among the population of i-th predator; d_i is the death rate.

Note that if $b_1 = b_2 = 0$ then system (1.1) is reduced to a system with Holling type II functional responses:

$$\begin{aligned} \frac{dx}{dt} &= rx(1-\frac{x}{K}) - \frac{m_1 x}{a_1 + x} y_1 - \frac{m_2 x}{a_2 + x} y_2, \\ \frac{dy_1}{dt} &= (\frac{e_1 m_1 x}{a_1 + x} - d_1) y_1, \\ \frac{dy_2}{dt} &= (\frac{e_2 m_2 x}{a_2 + x} - d_2) y_2. \end{aligned} \tag{1.2}$$

Hsu, Hubbel and Waltman [12, 13], Butler and Waltman [5], Keener [17], Muratri and Rinaldi [19], Smith [20], Liu, Xiao and Yi [18], among others, have showed that system (1.2) exhibits coexistence in the sense of Armstrong and McGehee [1], that is, for appropriate parameter values and suitable initial population densities $(x(0), y(0), z(0))$, the model does predicts coexistence of the two predators via a locally attracting periodic orbit. However, system (1.2) cannot be uniformly persistent. The case when $b_1 = 0$ and $b_2 \neq 0$ was studied in Catrell, Cosner and Ruan [7].

This paper is organized as follows. In Section 2, we study existence and stability of equilibria in system (1.1), including the semi-trivial equilibria(i.e., with survival of only one predator species) and the positive equilibrium (with the coexistence of both competing predators). Sufficient conditions for the uniform persistence of the system are obtained. In Section 3, we construct a Lyapunov function to establish the global stability of the positive equilibrium. We also have similar extinction results as those in [13]. In Section 4, we consider the competition of two identical predators with different interference effects. In Section 5, we study relaxation oscillations to system (1.1) with $r \gg 1$ and $b_i = O(\varepsilon^{1+\mu_i})$ where $\varepsilon = 1/r$ and $\mu_i > 0$, $i = 1, 2$. Numerical simulations are presented to explain the obtained results.

2 Local Analysis

2.1 Subsystems

Consider the following predator-prey system which is a subsystem of (1.1):

$$\begin{cases} \dfrac{dx}{dt} = rx(1 - \dfrac{x}{K}) - \dfrac{mx}{a + x + by}y, \\ \dfrac{dy}{dt} = (\dfrac{emx}{a + x + by} - d)y, \\ \quad x(0) > 0, y(0) > 0. \end{cases} \tag{2.1}$$

With the scaling:

$$t \to rt, \quad x \to x/K, \quad y \to by/K \tag{2.2}$$

the system (2.1) becomes

$$\begin{cases} \dfrac{dx}{dt} = x(1-x) - \dfrac{sxy}{x+y+A}, \\ \dfrac{dy}{dt} = \delta y(-D + \dfrac{x}{x+y+A}), \end{cases} \tag{2.3}$$

where

$$s = \frac{m}{br}, \quad \delta = \frac{me}{r}, \quad D = \frac{d}{me}, \quad A = \frac{a}{K}.$$

From the analysis in Cantrell and Cosner [6] and Hwang [15, 16], we have the following results about the asymptotic behavior of the solutions of (2.3). The first result is about the extinction of predator.

Proposition 2.1. *If* $em \leq d$ *or* $K \leq \lambda = \frac{a}{(\frac{me}{d})-1}$*, then the equilibrium* $(1, 0)$ *of system* (2.3) *is globally asymptotically stable, or equivalently the equilibrium* $(K, 0)$ *of system* (2.1) *is globally asymptotically stable.*

Now we assume that

(H1) $K > \lambda > 0$.

Under the assumption (H1), there exist three equilibria $(0, 0)$, $(1, 0)$ and (x_*, y_*), where x_* and y_* are positive and satisfy

$$\begin{cases} 1 - x_* - \dfrac{sy_*}{x_* + y_* + A} = 0, \\ \dfrac{x_*}{x_* + y_* + A} = D. \end{cases} \tag{2.4}$$

Obviously, we have

$$s > \frac{sy_*}{x_* + y_* + A} = 1 - x_*$$

and from (2.4) it follows that

$$\begin{cases} y_* = \dfrac{(1 - x_*)(x_* + A)}{x_* + s - 1}, \\ x_*^2 + (s - 1 - Ds)x_* - DAs = 0. \end{cases} \tag{2.5}$$

From the second equation of (2.5), we have

$$x_* + s - 1 > x_* + s - 1 - Ds = \frac{DAs}{x_*}, \ y_* > 0 \ .$$

The variational matrix of system (2.3) is given by

$$J(x,y)=\begin{bmatrix} 1-2x-\frac{sy}{x+y+A}+\frac{sxy}{(x+y+A)^2} & \frac{-sx}{x+y+A}+\frac{sxy}{(x+y+A)^2} \\ \frac{\delta y(y+A)}{(x+y+A)^2} & \frac{\delta x}{x+y+A}-\frac{\delta xy}{(x+y+A)^2}-D\delta \end{bmatrix}. \tag{2.6}$$

From Hwang [15, 16], we have the following result.

Proposition 2.2. *Let the assumption* (H1) *hold.*

(i) *If* $tr\big(J(x_*,y_*)\big)<0$ *then the equilibrium* (x_*,y_*) *of system* (2.3) *is globally asymptotically stable.*

(ii) *If* $tr\big(J(x_*,y_*)\big)>0$ *then there exists a unique limit cycle for system* (2.3).

Furthermore,

(1) *If* $s\le\max\{\delta,\frac{D\delta}{1+D}+\frac{1}{1-D^2}\}$ *or equivalently*

$$b\ge\min\{\frac{1}{e},\frac{m^2e^2-d^2}{de(me-d)+mre^2}\} \tag{2.7}$$

then $tr\big(J(x_*,y_*)\big)\le 0$.

(2) *If* $s>\max\{\delta,\frac{D\delta}{1+D}+\frac{1}{1-D^2}\}$ *or equivalently*

$$0\le b<\min\{\frac{1}{e},\frac{m^2e^2-d^2}{de(me-d)+mre^2}\} \tag{2.8}$$

then there exists $0<A_*<\frac{1-D}{D}$ *such that* $tr\big(J(x_*,y_*)\big)<0$ (>0) *if and only of* $A>A_*$ $(A<A_*)$.

Remark 2.1. In the above (ii), if we set $K_*=a/A_*$, then the prey and predator coexist in equilibrium if the carrying capacity K satisfies $\lambda<K<K_*$ and the prey and predator populations exhibit periodic oscillation if $K>K_*$.

Let $\bar{x}=Kx_*$, $\bar{y}=\frac{K}{b}y_*$. From (2.3), $(\bar{x},\bar{y})$ is a positive equilibrium of system (2.1). We summarize the results for system (2.1) in Table I.

Table I: Stability of equilibria for system (2.1)

Conditions	Stability of equilibrium
$em \leq d$ or $K \leq \lambda$	$(K, 0)$ is globally asymptotically stable
$K > \lambda$ and $b \geq \min\{\frac{1}{e}, \frac{m^2e^2-d^2}{de(me-d)+mre^2}\}$	$(\bar{x}, \bar{y})$ is globally asymptotically stable
$\lambda < K < K_*$ and $b < \min\{\frac{1}{e}, \frac{m^2e^2-d^2}{de(me-d)+mre^2}\}$	$(\bar{x}, \bar{y})$ is globally asymptotically stable
$K > K_* > \lambda$ and $b < \min\{\frac{1}{e}, \frac{m^2e^2-d^2}{de(me-d)+mre^2}\}$	$(\bar{x}, \bar{y})$ is an unstable focus and there exists a unique limit cycle

2.2 Equilibria Analysis and Uniform Persistence

In this section, we shall find all equilibria of system (1.1) and determine their stabilities. Consider

$$\begin{aligned}
\frac{dx}{dt} &= rx(1 - \frac{x}{K}) - \frac{m_1 x}{a_1 + x + b_1 y_1} y_1 - \frac{m_2 x}{a_2 + x + b_2 y_2} y_2 := f(x, y_1, y_2), \\
\frac{dy_1}{dt} &= (\frac{e_1 m_1 x}{a_1 + x + b_1 y_1} - d_1) y_1 := g(x, y_1), \\
\frac{dy_2}{dt} &= (\frac{e_2 m_2 x}{a_2 + x + b_2 y_2} - d_2) y_2 := h(x, y_2).
\end{aligned}$$

Then the Jacobian matrix of system (1.1) takes the form

$$J(x, y_1, y_2) = \begin{bmatrix} f_x & f_{y_1} & f_{y_2} \\ g_x & g_{y_1} & 0 \\ h_x & 0 & h_{y_2} \end{bmatrix} \tag{2.9}$$

where

$$\begin{aligned}
f_x &= r(1-\frac{x}{K}) - \frac{m_1 y_1}{a_1+x+b_1 y_1} - \frac{m_2 y_2}{a_2+x+b_2 y_2} + \\
&\quad x(-\frac{r}{K} + \frac{m_1 y_1}{(a_1+x+b_1 y_1)^2} + \frac{m_2 y_2}{(a_2+x+b_2 y_2)^2}),\\
f_{y_1} &= -\frac{m_1 x(a_1+x)}{(a_1+x+b_1 y_1)^2},\\
f_{y_2} &= -\frac{m_2 x(a_2+x)}{(a_2+x+b_2 y_2)^2},\\
g_x &= \frac{e_1 m_1 y_1 (a_1+b_1 y_1)}{(a_1+x+b_1 y_1)^2},\\
g_{y_1} &= \frac{e_1 m_1 x}{a_1+x+b_1 y_1} - d_1 - \frac{b_1 e_1 m_1 x y_1}{(a_1+x+b_1 y_1)^2} = \frac{e_1 m_1 x(a_1+x)}{(a_1+x+b_1 y_1)^2} - d_1,
\end{aligned}$$

$$\begin{aligned}
h_x &= \frac{e_2 m_2 y_2 (a_2+b_2 y_2)}{(a_2+x+b_2 y_2)^2},\\
h_{y_2} &= \frac{e_2 m_2 x}{a_2+x+b_2 y_2} - d_2 - \frac{b_2 e_2 m_2 x y_2}{(a_2+x+b_2 y_2)^2} = \frac{e_2 m_2 x(a_2+x)}{(a_2+x+b_2 y_2)^2} - d_2.
\end{aligned}$$

We now consider the equilibria and periodic solutions on the boundary.
(a) $E_0 = (0,0,0)$. The trivial equilibrium E_0 always exists and is a saddle with a two-dimensional stable manifold $\{(x,y,z) : x = 0, y_1 > 0, y_2 > 0\}$ and a one-dimensional unstable manifold $\{(x,y,z) : y_1 = 0, y_2 = 0\}$.
(b) $E_K = (K,0,0)$. The semi-trivial equilibrium E_K always exists. The Jacobian matrix at E_K is given by

$$J(E_K) = \begin{bmatrix} -r & * & * \\ 0 & \frac{e_1 m_1 K}{a_1+K} - d_1 & 0 \\ 0 & 0 & \frac{e_2 m_2 K}{a_2+K} - d_2 \end{bmatrix}.$$

Then E_K is asymptotically stable if

$$\frac{e_1 m_1 K}{a_1+K} - d_1 < 0 \qquad \text{and} \qquad \frac{e_2 m_2 K}{a_2+K} - d_2 < 0\ .$$

We note that $\frac{e_i m_i K}{a_i+K} - d_i < 0$ if and only if

$$e_i m_i \le d_i \quad \text{or} \quad K < \lambda_i = \frac{a_i}{(\frac{e_i m_i}{d_i}) - 1}\ ,$$

where λ_i is the break-even density for the i-th predator where there is no intraspecific competition within the population of the i-th predator. If $K > \lambda_1$ and $K > \lambda_2$ then E_K is a saddle with a one-dimensional stable manifold $\{(x, y_1, y_2) : x > 0, y_1 = y_2 = 0\}$.

Actually, we can verify the global asymptotical stability of E_K under a weaker condition in the following lemma.

Lemma 2.3. *If* $e_i m_i \leq d_i$ *then* $\limsup_{t\to\infty} y_i(t) = 0$ *for* $i = 1, 2$.

Proof. We only prove the case of $i = 1$. By the first equation of (1.1), we know that $\limsup_{t\to\infty} x(t) \leq K$. So we assume $x(t) \leq K$ for t large enough. It is easy to see that

$$e_1 m_1 K \leq d_1 K < d_1(a_1 + K).$$

Let $\mu = d_1 - \frac{e_1 m_1 K}{a_1+K} > 0$. According to the monotonicity of the function $\frac{e_1 m_1 x}{a+x}$ with respect to x, we have

$$\frac{\dot{y}_1}{y_1} = \frac{e_1 m_1 x}{a_1 + x + b y_1} - d_1 < \frac{e_1 m_1 x}{a_1 + x} - d_1 \leq \frac{e_1 m_1 K}{a_1 + K} - d_1 = -\mu.$$

This implies that $\limsup_{t\to\infty} y_1(t) = 0$. We complete the proof. □

From now on we always assume that

(H2) $e_1 m_1 > d_1$ and $e_2 m_2 > d_2$.

Hence $\frac{e_i m_i K}{a_i+K} - d_i < 0$ if and only if $K < \lambda_i$ if **(H2)** holds.
(c) $E_1 = (\bar{x}_1, \bar{y}_1, 0)$. The semi-trivial equilibrium E_1 is a boundary equilibrium on the (x, y_1)-plane, where $\bar{x}_1$, $\bar{y}_1$ are obtained by restricting to the system of the first predator y_1 and the prey x. The Jacobian matrix at E_1 is given by

$$J(E_1) = \begin{bmatrix} \bar{x}_1\left(-\frac{r}{K} + \frac{m_1\bar{y}_1}{(a_1+\bar{x}_1+b_1\bar{y}_1)^2}\right) & -\frac{m_1\bar{x}_1(a_1+\bar{x}_1)}{(a_1+\bar{x}_1+b_1\bar{y}_1)^2} & -\frac{m_2\bar{x}_1}{a_2+\bar{x}_1} \\ \frac{e_1 m_1\bar{y}_1(a_1+b_1\bar{y}_1)}{(a_1+\bar{x}_1+b_1\bar{y}_1)^2} & -\frac{b_1 e_1 m_1\bar{x}_1\bar{y}_1}{(a_1+\bar{x}_1+b_1\bar{y}_1)^2} & 0 \\ 0 & 0 & \frac{e_2 m_2\bar{x}_1}{a_2+\bar{x}_1} - d_2 \end{bmatrix}.$$

We note that the top left 2×2 submatrix is exactly the Jacobian matrix J in (2.6) for the subsystem (2.1) at the equilibrium (x_*, y_*), where a, b, e, m, d are replaced by a_1, b_1, e_1, m_1, d_1 (The conditions are presented in Table I). And $\frac{e_2 m_2 \bar{x}_1}{a_2+\bar{x}_1} - d_2 < 0$ if and only if $\bar{x}_1 < \lambda_2$ under the assumption **(H2)**. There are four cases for the stability of E_1.

Table II: Stability of equilibrium E_1 for system (1.1)

Conditions		Stability of equilibrium E_1
$K > \lambda_1$ and $b_1 \geq \min\{\frac{1}{e_1}, \frac{m_1^2 e_1^2 - d_1^2}{d_1 e_1 (m_1 e_1 - d_1) + m_1 r e_1^2}\}$	$\bar{x}_1 < \lambda_2$ ($\bar{x}_1 > \lambda_2$)	E_1 is globally asymptotically stable (E_1 is a saddle with a one-dimensional unstable manifold W_1^u and a two-dimensional stable manifold on the (x, y_1) plane.)
$\lambda_1 < K < K_*$ and $b_1 < \min\{\frac{1}{e_1}, \frac{m_1^2 e_1^2 - d_1^2}{d_1 e_1 (m_1 e_1 - d_1) + m_1 r e_1^2}\}$		
$K > K_* > \lambda_1$ and $b_1 < \min\{\frac{1}{e_1}, \frac{m_1^2 e_1^2 - d_1^2}{d_1 e_1 (m_1 e_1 - d_1) + m_1 r e_1^2}\}$	$\bar{x}_1 < \lambda_2$ ($\bar{x}_1 > \lambda_2$)	E_1 is an unstable focus and there exists a unique limit cycle (E_1 is a repeller)

Case A1: The equilibrium E_1 is asymptotically stable in $\mathbb{R}^3$ if $(\bar{x}_1, \bar{y}_1)$ is an asymptotically stable equilibrium for system (2.1) with a, b, e, m, d replaced by a_1, b_1, e_1, m_1, d_1 (The conditions are presented in Table I) and $\frac{e_2 m_2 \bar{x}_1}{a_2 + \bar{x}_1} - d_2 < 0$.

Case A2: If $(\bar{x}_1, \bar{y}_1)$ is an asymptotically stable equilibrium for system (2.1) and $\bar{x}_1 > \lambda_2$, then E_1 is a saddle with a one-dimensional unstable manifold W_1^u and a two-dimensional stable manifold on the (x, y_1) plane.

Case A3: If $(\bar{x}_1, \bar{y}_1)$ is an unstable focus for system (2.1) and $\bar{x}_1 < \lambda_2$, then E_1 is a saddle with a one-dimensional stable manifold W_1^s and a unique limit cycle Γ_1 on the (x, y_1) plane.

Case A4: If $(\bar{x}_1, \bar{y}_1)$ is an unstable focus for system (2.1) and $\bar{x}_1 > \lambda_2$, then E_1 is a repeller.

We summarize the results on local stability of the boundary equilibrium E_1 for system (1.1) in Table II.

(d) $E_2 = (\bar{x}_2, 0, \bar{y}_2)$. Similar to the above case (c), the Jacobian matrix at E_2 is given by

$$J(E_1) = \begin{bmatrix} \bar{x}_2(-\frac{r}{K} + \frac{m_2\bar{y}_2}{(a_2+\bar{x}_2+b_2\bar{y}_2)^2}) & -\frac{m_1\bar{x}_2}{a_1+\bar{x}_2} & -\frac{m_2\bar{x}_2(a_2+\bar{x}_2)}{(a_2+\bar{x}_2+b_2\bar{y}_2)^2} \\ 0 & \frac{e_1m_1\bar{x}_2}{a_1+\bar{x}_2} - d_1 & 0 \\ \frac{e_2m_2\bar{y}_2(a_2+b_2\bar{y}_2)}{(a_2+\bar{x}_2+b_2\bar{y}_2)^2} & 0 & -\frac{b_2e_2m_2\bar{x}_2\bar{y}_2}{(a_2+\bar{x}_2+b_2\bar{y}_2)^2} \end{bmatrix}.$$

We note that the 2×2 submatrix gotten by deleting the second row and second column of above matrix is exactly the Jacobian matrix J in (2.6) for the subsystem (2.1) at the equilibrium (x_*, y_*) where a, b, e, m, d are replaced by a_2, b_2, e_2, m_2, d_2. We have four cases:

Case B1: The equilibrium E_2 is asymptotically stable in $\mathbb{R}^3$ if $(\bar{x}_2, \bar{y}_2)$ is an asymptotically stable equilibrium for system (2.1) with a, b, e, m, d replaced by a_2, b_2, e_2, m_2, d_2 and $\bar{x}_2 < \lambda_1$.

Case B2: If $(\bar{x}_2, \bar{y}_2)$ is an asymptotically stable equilibrium for system (2.1) and $\bar{x}_2 > \lambda_1$, then E_2 is a saddle with a one-dimensional unstable manifold W_2^u and a two-dimensional stable manifold on the (x, y_2) plane

Case B3: If $(\bar{x}_2, \bar{y}_2)$ is an unstable focus for the system (2.1) and $\bar{x}_2 < \lambda_1$, then E_2 is a saddle with a one-dimensional stable manifold W_2^s and a unique limit cycle Γ_2 on the (x, y_2) plane.

Case B4: If $(\bar{x}_2, \bar{y}_2)$ is an unstable focus for system (2.1) and $\bar{x}_2 > \lambda_1$, then E_2 is a repeller.

Similarly, we summarize the results on local stability of the boundary equilibrium E_2 for system (1.1) in Table III.

(e) $E_{\Gamma_1} = (\phi_1, \psi_1, 0)$. If the condition in Proposition 2.2 (ii) is satisfied, then the equilibrium $\bar{E} = (\bar{x}_1, \bar{y}_1)$ on the (x, y_1) plane is unstable and there is a unique stable limit cycle Γ_1 on the (x, y_1) plane, denoted by $(\phi_1(t), \psi_1(t))$. Consequently, $E_{\Gamma_1} = (\phi_1, \psi_1, 0)$ is a boundary periodic solution for system (1.1). Since E_{Γ_1} is stable restricted to the (x, y_1) plane, we only need to discuss its stability in the y_2-axis direction.

Table III: Stability of equilibrium E_2 for system (1.1)

<table>
<tr><th colspan="2">Conditions</th><th>Stability of equilibrium E_2</th></tr>
<tr><td>$K > \lambda_2$
and
$b_2 \geq \min\{\frac{1}{e_2}, \frac{m_2^2 e_2^2 - d_2^2}{d_2 e_2(m_2 e_2 - d_2) + m_2 r e_2^2}\}$</td><td rowspan="2">$\bar{x}_2 < \lambda_1$
$(\bar{x}_2 > \lambda_1)$</td><td rowspan="2">E_2 is globally asymptotically stable (E_2 is a saddle with a one-dimensional unstable manifold W_2^u and a two-dimensional stable manifold on the (x, y_2) plane.)</td></tr>
<tr><td>$\lambda_2 < K < K_*$
and
$b_2 < \min\{\frac{1}{e_2}, \frac{m_2^2 e_2^2 - d_2^2}{d_2 e_2(m_2 e_2 - d_2) + m_2 r e_2^2}\}$</td></tr>
<tr><td>$K > K_* > \lambda_2$
and
$b_1 < \min\{\frac{1}{e_1}, \frac{m_1^2 e_1^2 - d_1^2}{d_1 e_1(m_1 e_1 - d_1) + m_1 r e_1^2}\}$</td><td>$\bar{x}_2 < \lambda_1$

$(\bar{x}_2 > \lambda_1)$</td><td>E_2 is an unstable focus and there exists a unique limit cycle
(E_2 is a repeller)</td></tr>
</table>

The stability of E_{Γ_1} is determined by the Floquet multipliers of the variational system

$$\dot{\Phi}(t) = J(\phi_1, \psi_1, 0)\Phi(t), \quad \Phi(0) = I \tag{2.10}$$

where $J(x, y_1, y_2)$ is defined in (2.9) and I is the 3×3 identity matrix. Let ω_1 be the period of the periodic solution (ϕ_1, ψ_1). Then the Floquet multiplier corresponding to the y_2-direction is given by

$$\exp[\frac{1}{\omega_1} \int_0^{\omega_1} (\frac{m_2 e_2 \phi_1(t)}{a_2 + \phi_1(t)} - d_2)\ dt].$$

Thus E_{Γ_1} is stable if

$$d_2 > \int_0^{\omega_1} \frac{m_2 e_2 \phi_1(t)}{a_2 + \phi_1(t)}\ dt \tag{2.11}$$

and unstable if

$$d_2 < \int_0^{\omega_1} \frac{m_2 e_2 \phi_1(t)}{a_2 + \phi_1(t)}\ dt\ . \tag{2.12}$$

(f) Similarly, if the boundary periodic solution $E_{\Gamma_2} = (\phi_2(t), 0, \psi_2(t))$ with period ω_2 exists then it is stable if

$$d_1 > \int_0^{\omega_2} \frac{m_1 e_1 \phi_2(t)}{a_1 + \phi_2(t)}\ dt \tag{2.13}$$

and unstable if

$$d_1 < \int_0^{\omega_2} \frac{m_1 e_1 \phi_2(t)}{a_1 + \phi_2(t)}\, dt\ . \tag{2.14}$$

We now have the following results on the uniform persistence of system (1.1). (Bulter et. al [4], Butler and Waltman [3], Freedman et. al [9], Smith and Thieme [21]).

Theorem 2.4. *Assume one of the following cases holds:*

(i) *Let* **Case A2** *and* **Case B2** *holds, i.e.,* E_1 *and* E_2 *are unstable in the* y_2*-axis and the* y_1*-axis direction, respectively.*

(ii) *Let* **Case A2***,* **Case B4** *and* (2.14) *hold, i.e.,* E_1 *and* E_{Γ_2} *are unstable in the* y_2*-axis and the* y_1*-axis direction, respectively.*

(iii) *Let* **Case B2***,* **Case A4** *and* (2.12) *hold, i.e.,* E_2 *and* E_{Γ_1} *are unstable in the* y_1*-axis and the* y_2*-axis direction, respectively.*

(iv) *Let* **Case A4***,* (2.12)*,* **Case B4** *and* (2.14) *hold, i.e.,* E_{Γ_1} *and* E_{Γ_2} *are unstable in the* y_2*-axis and the* y_1*-axis direction, respectively.*

Then system (1.1) *is uniformly persistent.*

(g) $E_c = (x_c, y_{1c}, y_{2c})$. From the 2nd and 3rd equations of (1.1), x_c, y_{1c}, y_{2c} satisfy

$$\frac{e_i m_i x}{a_i + x + b_i y_i} = d_i \tag{2.15}$$

for $i = 1, 2$ or

$$y_{1c} = M_1(x_c - \lambda_1) > 0, \quad y_{2c} = M_2(x_c - \lambda_2) > 0 \tag{2.16}$$

where we use the notations $M_1 = \frac{e_1 m_1 - d_1}{d_1 b_1}$ and $M_2 = \frac{e_2 m_2 - d_2}{d_2 b_2}$ for simplifying. Assume that

(H3) $0 < \lambda_1 < \lambda_2 < K$.

From the first equation of (1.1), x_c satisfies the equation

$$rx(1-\frac{x}{K})-\frac{d_1}{e_1}M_1(x-\lambda_1)-\frac{d_2}{e_2}M_2(x-\lambda_2)=0.$$

Let

$$F(x)=rx(1-\frac{x}{K})-\frac{d_1}{e_1}M_1(x-\lambda_1)-\frac{d_2}{e_2}M_2(x-\lambda_2).$$

Then $F(K)<0$, $F(0)>0$, $F(\lambda_1)>0$, and

$$F(\lambda_2)=r\lambda_2(1-\frac{\lambda_2}{K})-\frac{d_1}{e_1}M_1(\lambda_2-\lambda_1).$$

Hence if

$$F(\lambda_2)>0 \tag{2.17}$$

then $E_c=(x_c,y_{1c},y_{2c})$ exists and is unique. If

$$F(\lambda_2)<0 \tag{2.18}$$

then E_c does not exist. Rewrite

$$F(x)=(-\frac{r}{K})x^2+x\big(r-\frac{d_1}{e_1}M_1-\frac{d_2}{e_2}M_2\big)+\big(\frac{d_1}{e_1}M_1\lambda_1+\frac{d_2}{e_2}M_2\lambda_2\big).$$

Then x_c is the unique positive root of $F(x)=0$,

$$x_c=\frac{K(B+\sqrt{B^2+4rC/K})}{2r} \tag{2.19}$$

where $B=r-\frac{d_1}{e_1}M_1-\frac{d_2}{e_2}M_2$ and $C=\frac{d_1}{e_1}M_1\lambda_1+\frac{d_2}{e_2}M_2\lambda_2$. The condition (2.17) for the existence of E_c is equivalent to

$$K>\lambda_2\big(1-\frac{d_1}{re_1\lambda_2}M_1(\lambda_2-\lambda_1)\big)^{-1}=\tilde{K}>0 \tag{2.20}$$

or $x_c>\lambda_2$. We note that in (2.20) we need

$$r>\frac{d_1}{e_1}M_1(1-\frac{\lambda_1}{\lambda_2}) \tag{2.21}$$

The Jacobian matrix of the system (1.1) at E_c takes the form

$$J(E_c)=\begin{bmatrix} f_x^* & f_{y_1}^* & f_{y_2}^* \\ g_x^* & g_{y_1}^* & 0 \\ h_x^* & 0 & h_{y_2}^* \end{bmatrix}$$

where

$$
\begin{aligned}
f_x^* &= x_c\Big(-\frac{r}{K} + \frac{m_1 y_{1c}}{(a_1+x_c+b_1y_{1c})^2} + \frac{m_2 y_{2c}}{(a_2+x_c+b_2y_{2c})^2}\Big)\\
f_{y_1}^* &= -\frac{m_1 x_c (a_1+x_c)}{(a_1+x_c+b_1y_{1c})^2} < 0\\
f_{y_2}^* &= -\frac{m_2 x_c (a_2+x_c)}{(a_2+x_c+b_2y_{2c})^2} < 0\\
g_x^* &= \frac{e_1 m_1 y_{1c}(a_1+b_1y_{1c})}{(a_1+x_c+b_1y_{1c})^2} > 0\\
g_{y_1}^* &= -\frac{b_1 e_1 m_1 x_c y_{1c}}{(a_1+x_c+b_1y_{1c})^2} < 0\\
h_x^* &= \frac{e_2 m_2 y_{2c}(a_2+b_2y_{2c})}{(a_2+x_c+b_2y_{2c})^2} > 0\\
h_{y_2}^* &= -\frac{b_2 e_2 m_2 x_c y_{2c}}{(a_2+x_c+b_2y_{2c})^2} < 0\ .
\end{aligned}
\tag{2.22}
$$

The characteristic polynomial of $J(E_c)$ is given by

$$
\lambda^3 + \alpha_1\lambda^2 + \alpha_2\lambda + \alpha_3 = 0
$$

where

$$
\begin{aligned}
\alpha_1 &= -(f_x^* + g_{y_1}^* + h_{y_2}^*),\\
\alpha_2 &= f_x^* g_{y_1}^* + f_x^* h_{y_2}^* + g_{y_1}^* h_{y_2}^* - f_{y_2}^* h_x^* - f_{y_1}^* g_x^*\ ,\\
\alpha_3 &= f_{y_1}^* g_x^* h_{y_2}^* + f_{y_2}^* g_{y_1}^* h_x^* - f_x^* g_{y_1}^* h_{y_2}^*\ .
\end{aligned}
$$

By Routh-Hurwitz criterion we have the following result on the local stability of E_c.

Proposition 2.5. *Assume that*

$$
\alpha_1 > 0, \alpha_3 > 0, \ \textit{and} \ \ \alpha_1\alpha_2 > \alpha_3
$$

then E_c is locally asymptotically stable.

Remark 2.2. If $f_x^* < 0$, then $\alpha_1 > 0$ and $\alpha_2 > 0$. From equations (2.22), (2.15), and (2.16), $f_x^* < 0$ if and only if

$$
\begin{aligned}
\frac{r}{K} x_c &> \frac{m_1 x_c y_{1c}}{(a_1+x_c+b_1y_{1c})^2} + \frac{m_2 x_c y_{2c}}{(a_2+x_c+b_2y_{2c})^2}\\
&= \Big(\frac{d_1}{e_1 m_1}\Big)\frac{m_1 y_{1c}}{a_1+x_c+b_1y_{1c}} + \Big(\frac{d_2}{e_2 m_2}\Big)\frac{m_2 y_{2c}}{a_2+x_c+b_2y_{2c}}\ .
\end{aligned}
$$

Then

$$\begin{aligned}
&(\frac{d_1}{e_1 m_1})\frac{m_1 y_{1c}}{a_1 + x_c + b_1 y_{1c}} + (\frac{d_2}{e_2 m_2})\frac{m_2 y_{2c}}{a_2 + x_c + b_2 y_{2c}} \\
&\leq \max\{\frac{d_1}{e_1 m_1}, \frac{d_2}{e_2 m_2}\}\Big(\frac{m_1 y_{1c}}{a_1 + x_c + b_1 y_{1c}} + \frac{m_2 y_{2c}}{a_2 + x_c + b_2 y_{2c}}\Big) \\
&= \max\{\frac{d_1}{e_1 m_1}, \frac{d_2}{e_2 m_2}\} r(1 - \frac{x_c}{K}).
\end{aligned}$$

If

$$\frac{r}{K} x_c > \max\{\frac{d_1}{e_1 m_1}, \frac{d_2}{e_2 m_2}\} r(1 - \frac{x_c}{K})$$

or equivalent

$$\frac{\bar{M}}{1 + \bar{M}} K < x_c < K,$$

where $\bar{M} = \max\{\frac{d_1}{e_1 m_1}, \frac{d_2}{e_2 m_2}\}$, then $f_x^* < 0$.

2.3 Hopf Bifurcation

In this section, we will verify that the Hopf bifurcation indeed occurs. It is obvious that if $b_1 e_1 \geq 1$ and $b_2 e_2 \geq 1$, then α_1 and α_3 are positive for all $K > 0$ from the expressions of α_1 and α_3

$$
\begin{aligned}
\alpha_1 &= -(f_x^* + g_{y_1}^* + h_{y_2}^*),\\
&= \frac{r x_c}{K} - \frac{m_1\, x_c\, y_{1c}}{(b_1\, y_{1c} + x_c + a_1)^2} - \frac{m_2\, x_c\, y_{2c}}{(b_2\, y_{2c} + x_c + a_2)^2} + \frac{b_1\, e_1\, m_1\, x_c\, y_{1c}}{(b_1\, y_{1c} + x_c + a_1)^2} +\\
&\quad \frac{b_2\, e_2\, m_2\, x_c\, y_{2c}}{(b_2\, y_{2c} + x_c + a_2)^2}\ ,\\
\alpha_3 &= f_{y_1}^* g_x^* h_{y_2}^* + f_{y_2}^* g_{y_1}^* h_x^* - f_x^* g_{y_1}^* h_{y_2}^*\\
&= \frac{b_2\, e_1\, e_2\, {m_1}^2\, m_2\, {x_c}^2\ (x_c + a_1)\ y_{1c}\ (b_1\, y_{1c} + a_1)\ y_{2c}}{(b_1\, y_{1c} + x_c + a_1)^4\, (b_2\, y_{2c} + x_c + a_2)^2} +\\
&\quad \frac{b_1\, e_1\, e_2\, m_1\, {m_2}^2\, {x_c}^2\ (x_c + a_2)\ y_{1c}\, y_{2c}\ (b_2\, y_{2c} + a_2)}{(b_1\, y_{1c} + x_c + a_1)^2\, (b_2\, y_{2c} + x_c + a_2)^4} +\\
&\quad \frac{b_1 b_2 e_1 e_2 m_1 m_2 {x_c}^2 y_{1c} y_{2c}\ \left(\frac{r\, x_c}{K} - \frac{m_2\, x_c\, y_{2c}}{(b_2\, y_{2c} + x_c + a_2)^2} - \frac{m_1\, x_c\, y_{1c}}{(b_1\, y_{1c} + x_c + a_1)^2}\right)}{(b_1\, y_{1c} + x_c + a_1)^2\, (b_2\, y_{2c} + x_c + a_2)^2}\\
&= \frac{a_1 b_2\, e_1\, e_2\, {m_1}^2\, m_2\, {x_c}^2\, y_{1c}\, y_{2c}}{(b_1\, y_{1c} + x_c + a_1)^3\, (b_2\, y_{2c} + x_c + a_2)^2} + \frac{a_2 b_1\, e_1\, e_2\, m_1\, {m_2}^2\, {x_c}^2\, y_{1c}\, y_{2c}}{(b_1\, y_{1c} + x_c + a_1)^2\, (b_2\, y_{2c} + x_c + a_2)^3} +\\
&\quad \frac{r b_1 b_2 e_1 e_2 m_1 m_2 {x_c}^3 y_{1c} y_{2c}}{K\, (b_1\, y_{1c} + x_c + a_1)^2\ (b_2\, y_{2c} + x_c + a_2)^2} > 0\ .
\end{aligned}
$$

Hence, by Proposition 2.5, the positive equilibrium E_c will lose its stability if $\alpha_1\alpha_2 - \alpha_3 \le 0$. We take K as the bifurcation parameter. It is easy to see that x_c, y_{1c}, and y_{2c} are functions of K by the equations (2.19) and (2.16). The expression of $\alpha_1\alpha_2 - \alpha_3$ has the form,

$$
\begin{aligned}
\alpha_1\alpha_2 - \alpha_3 &= -(f_x^* + g_{y_1}^* + h_{y_2}^*)(f_x^* g_{y_1}^* + f_x^* h_{y_2}^* + g_{y_1}^* h_{y_2}^* - f_{y_2}^* h_x^* - f_{y_1}^* g_x^*) -\\
&\quad (f_{y_1}^* g_x^* h_{y_2}^* + f_{y_2}^* g_{y_1}^* h_x^* - f_x^* g_{y_1}^* h_{y_2}^*)\\
&= -(f_x^*)^2 g_{y_1} - (f_x^*)^2 h_{y_2} - (g_{y_1}^*)^2 h_{y_2} + f_{y_1}^* g_x^* g_{y_1}^* - g_{y_1}^* (h_{y_2}^*)^2 + f_{y_2}^* h_x^* h_{y_2}^* +\\
&\quad f_x^* \big(f_{y_2}^* h_x^* + f_{y_1}^* g_x^* - (g_{y_1}^*)^2 - 2 g_{y_1}^* h_{y_2}^* - (h_{y_2}^*)^2\big)\ .
\end{aligned}
$$

In the last formula, we have two classes

$$
-(f_x^*)^2 g_{y_1} - (f_x^*)^2 h_{y_2} - (g_{y_1}^*)^2 h_{y_2} + f_{y_1}^* g_x^* g_{y_1}^* - g_{y_1}^* (h_{y_2}^*)^2 + f_{y_2}^* h_x^* h_{y_2}^*
$$

and

$$
f_x^* \big(f_{y_2}^* h_x^* + f_{y_1}^* g_x^* - (g_{y_1}^*)^2 - 2 g_{y_1}^* h_{y_2}^* - (h_{y_2}^*)^2\big)\ .
$$

All terms of the first class are positive and all term of another one are negative except for the function f_x^*. So we should clarify the behavior of f_x^* as a function of K.

By the representation of x_c, (2.19), it is easy to see that if $B = r - \frac{d_1}{e_1}M_1 - \frac{d_2}{e_2}M_2 > 0$ then $\lim_{K\to 0^+} x_c(K) = 0$, $\lim_{K\to 0^+} x_c(K)/K > 0$, $\lim_{K\to\infty} x_c(K) = \infty$, and $\lim_{K\to\infty} x_c(K)/K = B/r > 0$. These implies $\lim_{K\to 0^+} f_x^*(K) < 0$. But the restriction of K, (2.20), it is required that $f_c^*(\tilde{K}) < 0$. It is easy to see that $\frac{d_1}{e_1}M_1 + \frac{d_2}{e_2}M_2 > \frac{d_1}{e_1}M_1(1-\frac{\lambda_1}{\lambda_2})$ which is the restriction of r to guarantee the existence of E_c in (2.21), so we assume $r > \frac{d_1}{e_1}M_1 + \frac{d_2}{e_2}M_2$. A necessary condition for the occurrence of Hopf bifurcation is $\lim_{K\to\infty} f_x^*(K) > 0$. Easy computation shows that

$$\lim_{k\to\infty} f_c^*(K) = -r + \frac{d_1M_1}{e_1} + \frac{d_2M_2}{e_2} + \frac{m_1M_1}{(1+b_1M_1)^2} + \frac{m_2M_2}{(1+b_2M_2)^2}.$$

Hence we assume

(H4) $0 < r - \dfrac{d_1}{e_1}M_1 - \dfrac{d_2}{e_2}M_2 < \dfrac{m_1M_1}{(1+b_1M_1)^2} + \dfrac{m_2M_2}{(1+b_2M_2)^2}$.

Proposition 2.6. *Assume the assumption* **(H4)** *holds and*

(i) $b_1e_1 \geq 1$ *and* $b_2e_2 \geq 1$,

(ii) *there is a* $K^* > 0$ *such that* $\alpha_1(K^*)\alpha_2(K^*) = \alpha_3(K^*)$ *and*

$$\frac{d}{dK}\Big|_{K=K^*} \alpha_1(K)\alpha_2(K) < \frac{d}{dK}\Big|_{K=K^*} \alpha_3(K),$$

then the positive equilibrium E_c is locally stable when $K < K^*$ and loses its stability when $K = K^*$. When $K > K^*$, E_c becomes unstable and a family of periodic solutions bifurcates from E_c.

3 Global Stability of Coexistence State; Extinction

Using the Lyapunov function constructed in Hsu [10, 11] we give sufficient conditions for the global stability of the positive equilibrium E_c.

First we note that

Lemma 3.1. *The solutions of* (1.1) *are positive and bounded for* $t \geq 0$. *Furthermore, for any* $\varepsilon > 0$, *there exists* $T_0 > 0$ *such that*

$$x(t) \leq K + \varepsilon,$$
$$x(t) + \frac{1}{e_1}y_1(t) + \frac{1}{e_2}y_2(t) \leq (\frac{r}{d_{min}} + 1)(K + \varepsilon)$$

for $t \geq T_0$ *where* $d_{min} = \min\{d_1, d_2\}$.

Proof. From (1.1) it followings that

$$\begin{aligned} x'(t) + \frac{1}{e_1}y_1'(t) + \frac{1}{e_2}y_2'(t) &= rx(1 - \frac{x}{K}) - \frac{d_1}{e_1}y_1 - \frac{d_2}{e_2}y_2 \\ &\leq rx - \frac{d_1}{e_1}y_1 - \frac{d_2}{e_2}y_2 \\ &\leq (r + d_{min})x - d_{min}(x + \frac{1}{e_1}y_1 + \frac{1}{e_2}y_2). \end{aligned}$$

Obviously from the first equation of (1.1) and differential inequality, we have

$$x(t) \leq K + \varepsilon \quad \text{for all } t \geq T_0, \text{ for some } T_0.$$

Then

$$\begin{aligned} &\big(x + \frac{1}{e_1}y_1 + \frac{1}{e_2}y_2\big)' \\ &\quad \leq (r + d_{min})(K + \varepsilon) - d_{min}(x + \frac{1}{e_1}y_1 + \frac{1}{e_2}y_2) \end{aligned}$$

Then we have

$$x(t) + \frac{1}{e_1}y_1(t) + \frac{1}{e_2}y_2(t) \leq (\frac{r}{d_{min}} + 1)(K + \varepsilon) \quad \text{for } t \geq T_0.$$

□

Theorem 3.2. *Let the assumption* **(H3)** *hold. Assume* E_c *exists, i.e.,* (2.20) *and* (2.21) *hold. If*

$$K < \frac{1}{\max\{1/a_1, 1/a_2\}} + x_c \tag{3.1}$$

then the positive equilibrium E_c *is globally stable.*

Proof. Choose a Lyapunov function as follows

$$V(x, y_1, y_2) = \int_{x_c}^{x} \frac{\xi - x_c}{\xi} d\xi + \alpha \int_{y_{1c}}^{y_1} \frac{\xi - y_{1c}}{\xi} d\xi + \beta \int_{y_{2c}}^{y_2} \frac{\xi - y_{2c}}{\xi} d\xi ,$$

where α and β are positive constants to be determined. Along the trajectories of the system (1.1) we have

$$\begin{aligned}
\frac{dV}{dt} &= (x - x_c)\Big(r(1 - \frac{x}{K}) - \frac{m_1 y_1}{a_1 + x + b_1 y_1} - \frac{m_2 y_2}{a_2 + x + b_2 y_2}\Big) \\
&\quad + \alpha(y_1 - y_{1c})\big(\frac{m_1 e_1 x}{a_1 + x + b_1 y_1} - d_1\big) + \beta(y_2 - y_{2c})\big(\frac{m_2 e_2 x}{a_2 + x + b_2 y_2} - d_2\big) \\
&= (x - x_c)\Big\{ - \frac{r}{K}(x - x_c) - \big(\frac{m_1 y_1}{a_1 + x + b_1 y_1} - \frac{m_1 y_{1c}}{a_1 + x_c + b_1 y_{1c}}\big) - \\
&\qquad \big(\frac{m_2 y_2}{a_2 + x + b_2 y_2} - \frac{m_2 y_{2c}}{a_2 + x_c + b_2 y_{2c}}\big)\Big\} \\
&\quad + \alpha(y_1 - y_{1c})\big(\frac{m_1 e_1 x}{a_1 + x + b_1 y_1} - \frac{m_1 e_1 x_c}{a_1 + x_c + b_1 y_{1c}}\big) \\
&\quad + \beta(y_2 - y_{2c})\big(\frac{m_2 e_2 x}{a_2 + x + b_2 y_2} - \frac{m_2 e_2 x_c}{a_2 + x_c + b_2 y_{2c}}\big) \\
&= (x - x_c)\Big\{ - \frac{r}{K}(x - x_c) - \frac{m_1\big((a_1 + x_c)(y_1 - y_{1c}) - y_{1c}(x - x_c)\big)}{(a_1 + x + b_1 y_1)(a_1 + x_c + b_1 y_{1c})} \\
&\qquad - \frac{m_2\big((a_2 + x_c)(y_2 - y_{2c}) - y_{2c}(x - x_c)\big)}{(a_2 + x + b_2 y_2)(a_2 + x_c + b_2 y_{2c})}\Big\} \\
&\quad + \alpha(y_1 - y_{1c})\frac{m_1 e_1\big((a_1 + b_1 y_{1c})(x - x_c) - b_1 x_c(y_1 - y_{1c})\big)}{(a_1 + x + b_1 y_1)(a_1 + x_c + b_1 y_{1c})} \\
&\quad + \beta(y_2 - y_{2c})\frac{m_2 e_2\big((a_2 + b_2 y_{2c})(x - x_c) - b_2 x_c(y_2 - y_{2c})\big)}{(a_2 + x + b_2 y_2)(a_2 + x_c + b_2 y_{2c})}.
\end{aligned}$$

Choose $\alpha = \frac{a_1 + x_c}{e_1(a_1 + b_1 y_{1c})}$ and $\beta = \frac{a_2 + x_c}{e_2(a_2 + b_2 y_{2c})}$. Therefore,

$$\begin{aligned}
\frac{dV}{dt} &= (x - x_c)^2\Big\{ - \frac{r}{K} + \frac{m_1 y_{1c}}{(a_1 + x + b_1 y_1)(a_1 + x_c + b_1 y_{1c})} \\
&\qquad\qquad + \frac{m_2 y_{2c}}{(a_2 + x + b_2 y_1)(a_2 + x_c + b_2 y_{2c})}\Big\} \\
&\quad - \frac{\alpha b_1 x_c (y_1 - y_{1c})^2}{(a_1 + x + b_1 y_1)(a_1 + x_c + b_1 y_{1c})} - \frac{\beta b_2 x_c (y_2 - y_{2c})^2}{(a_2 + x + b_2 y_2)(a_2 + x_c + b_2 y_{2c})} .
\end{aligned}$$

The coefficients of $(y_1 - y_{1c})^2$ and $(y_2 - y_{2c})^2$ are negative. The coefficient of $(x - x_c)^2$

is

$$
\begin{aligned}
& -\frac{r}{K} + \frac{m_1 y_{1c}}{(a_1+x+b_1y_1)(a_1+x_c+b_1y_{1c})} + \frac{m_2 y_{2c}}{(a_2+x+b_2y_1)(a_2+x_c+b_2y_{2c})} \\
\le & -\frac{r}{K} + \frac{m_1 y_{1c}}{a_1(a_1+x_c+b_1y_{1c})} + \frac{m_2 y_{2c}}{a_2(a_2+x_c+b_2y_{2c})} \\
\le & -\frac{r}{K} + \max\{\frac{1}{a_1}, \frac{1}{a_2}\} r(1-\frac{x_c}{K}) \\
= & -\frac{r}{K}\big(1-\max\{\frac{1}{a_1}, \frac{1}{a_2}\}(K-x_c)\big).
\end{aligned}
$$

If (3.1) is satisfied, then $dV/dt \le 0$ and $dV/dt = 0$ if and only if $x = x_c$, $y_1 = y_{1c}$, and $y_2 = y_{2c}$. The largest invariant set of $\{dV/dt = 0\}$ is $\{(x_c, y_{1c}, y_{2c})\}$. Therefore, Lemma 3.1 and LaSalle's Invariant Principle imply that $E_c = (x_c, y_{1c}, y_{2c})$ is globally stable. Thus we complete the proof. □

Remark 3.1. Under the assumption (H2) and (2.20), (2.21), E_c exists and $x_c > \lambda_2$. Let $\tilde{K} = \lambda_2(1 - \frac{1}{re\lambda_2}\frac{me_1-d_1}{b_1}(\lambda_2-\lambda_1))^{-1}$. If r is sufficient large then

$$\tilde{K} < \frac{1}{\max\{1/a_1, 1/a_2\}} + \lambda_2 < \frac{1}{\max\{1/a_1, 1/a_2\}} + x_c\ .$$

Thus the condition (3.1) is feasible when r is sufficiently large.

The following extinction result for system (1.1) is similar to Lemma 4.7 and Theorem 3.6 of Hsu, Hubbell and Waltman [13] for system (1.2).

Theorem 3.3. *Let the assumption* **(H3)** *hold.*

(i) *If* $a_1 \ge a_2$ *or*

(ii) *if* $a_1 < a_2$ *but* $\delta_1 > \delta_2$ *where* $\delta_i = m_i e_i/d_i$, $i = 1, 2$

(iii) *if* $a_1 < a_2$, $\delta_1 < \delta_2$ *but* $K < \frac{a_2\delta_1 - a_1\delta_2}{\delta_2-\delta_1}$

then $\lim_{t\to\infty} y_2(t) = 0$ *for any* $b_1 > 0$ *and* $b_2 > 0$ *sufficiently small.*

Proof. Let $\xi > 0$. Then

$$
\begin{aligned}
\xi\frac{y_2'(t)}{y_2(t)} - \frac{y_1'(t)}{y_1(t)} &= \xi[\frac{e_1m_1x}{a_1+x+b_1y_1} - d_1] - [\frac{e_2m_2x}{a_2+x+b_2y_2} - d_2] \\
&\le \xi[\frac{e_1m_1x}{a_1+x} - d_1] - [\frac{e_2m_2x}{a_2+x} - d_2] + [\frac{e_2m_2x}{a_2+x} - \frac{e_2m_2x}{a_2+x+b_2y_2}] \qquad (3.2)
\end{aligned}
$$

Let

$$P_\xi(x) = \xi[\frac{e_1 m_1 x}{a_1 + x} - d_1] - [\frac{e_2 m_2 x}{a_2 + x} - d_2]$$
$$= \xi(e_1 m_1 - d_1)\frac{(x - \lambda_1)}{a_1 + x} - (e_2 m_2 - d_2)\frac{x - \lambda_2}{a_2 + x}.$$

Under the assumption **(H3)** and (i) or (ii), from Lemma 4.7 [13], we can choose $\xi^* > 0$ such that

$$P_{\xi^*}(x) \leq -\zeta < 0 \quad \text{for all } 0 \leq x \leq K + \varepsilon, \text{ for some } \zeta > 0.$$

Consider the third term in (3.2)

$$\begin{aligned} 0 <& \frac{e_2 m_2 x}{a_2 + x} - \frac{e_2 m_2 x}{a_2 + x + b_2 y_2} \\ =& \frac{e_2 m_2 x b_2 y_2}{(a_2 + x)(a_2 + x + b_2 y_2)} \\ =& b_2 \frac{e_2 m_2 x}{a_2 + x} \frac{y_2}{a_2 + x + b_2 y_2} \\ <& b_2 \frac{e_2 m_2 (K + \varepsilon)}{a_2 + (K + \varepsilon)} \cdot \frac{1}{a_2} (y_2)_{max} < b_2 \Delta \end{aligned}$$

where $\Delta = \frac{e_2^2 m_2 (K+\varepsilon)^2}{a_2(a_2+K+\varepsilon)}(\frac{r}{d_{min}} + 1)$. We note that from the bound in Lemma 3.1 Δ is independent of b_2. Hence for $b_2 > 0$ sufficiently small satisfying $b_2\Delta - \zeta < 0$, we have

$$\xi^* \frac{y_2'(t)}{y_2(t)} - \frac{y_1'(t)}{y_1(t)} \leq b_2 \Delta - \zeta < 0.$$

Then $y_2(t) \to 0$ as $t \to \infty$.

If **(H3)** and (iii) hold then

$$\begin{aligned} \frac{y_2'(t)}{d_2 y_2(t)} - \frac{y_1'(t)}{d_1 y_1(t)} =& \frac{\delta_1 x}{a_1 + x + b_1 y_1} - \frac{\delta_2 x}{a_2 + x + b_2 y_2} \\ \leq& \frac{\delta_1 x}{a_1 + x} - \frac{\delta_2 x}{a_2 + x} + (\frac{\delta_2 x}{a_2 + x} - \frac{\delta_2 x}{a_2 + x + b_2 y_2}). \end{aligned}$$

Let $P(x) = \frac{\delta_1 x}{a_1 + x} - \frac{\delta_2 x}{a_2 + x}$. Then from (iii) and the proof of Theorem 3.6 in [13],

$$P(x) \leq -\zeta < 0, \quad \text{for all } 0 \leq x \leq K + \varepsilon \text{ for some } \zeta > 0.$$

Similarly,

$$0 < \frac{\delta_2 x}{a_2 + x} - \frac{\delta_2 x}{a_2 + x + b_2 y_2} < b_2 \tilde{\Delta}$$

where $\tilde{\Delta} = \frac{\delta_2 e_2 (K+\varepsilon)^2}{a_2(a_2+K+\varepsilon)}\left(\frac{r}{d_{min}} + 1\right)$. Then the similar arguments as above yields

$$\lim_{t\to\infty} y_2(t) = 0.$$

This completes the proof. □

4 Competition of Two Identical Species with Different Interference Effects

In this section we consider two identical predators competing for a shared prey with difference in predator interference effects $b_1 \neq b_2$. The equations are the following:

$$\begin{aligned} x' &= rx(1 - \frac{x}{K}) - \frac{mxy_1}{a + x + b_1 y_1} - \frac{mxy_2}{a + x + b_2 y_2}\ , \\ {y_1}' &= (\frac{emx}{a + x + b_1 y_1} - d)y_1\ , \\ {y_2}' &= (\frac{emx}{a + x + b_2 y_2} - d)y_2\ , \end{aligned} \tag{4.1}$$

with initial conditions $x(0) > 0$, $y_1(0) > 0$, $y_2(0) > 0$. Let

$$K > \lambda_1 = \lambda_2 = a/(\frac{em}{d} - 1). \tag{4.2}$$

Assume $b_2 > b_1$. Then

$$\begin{aligned} {y_1}' &= (\frac{emx}{a + x + b_1 y_1} - d)y_1 \\ &> (\frac{emx}{a + x + b_2 y_1} - d)y_1\ . \end{aligned}$$

Thus, if $y_1(0) \geq y_2(0)$ then $y_1(t) > y_2(t)$ for all $t \geq 0$. If $y_1(0) < y_2(0)$ then either there exists $t_0 > 0$ such that $y_1(t_0) = y_2(t_0)$ or $y_1(t) < y_2(t)$ for all $t \geq 0$. If $y_1(t_0) = y_2(t_0)$ then

$$y_1(t) > y_2(t) \quad \text{for all } t \ \geq t_0. \tag{4.3}$$

If $y_1(t) < y_2(t)$ for all $t \geq 0$ then

$$\frac{{y_1}'}{y_1} = \frac{emx}{a + x + b_1 y_1} - d > \frac{emx}{a + x + b_2 y_2} - d = \frac{{y_2}'}{y_2}.$$

We have

$$\frac{y_1(t)}{y_1(0)} > \frac{y_2(t)}{y_2(0)}. \tag{4.4}$$

Thus, we have either $y_1(t_0) > y_2(t_0)$ for some $t_0 > 0$ or $y_2(0)y_1(t) > y_1(0)y_2(t)$ for all $t \geq 0$. If $y_1(t) \to 0$ as $t \to \infty$ then $y_2(t) \to 0$ as $t \to \infty$. Hence we obtain a contradiction to the assumption (4.2). Hence

$$\limsup_{t\to\infty} y_1(t) > 0. \tag{4.5}$$

On the other hand, assume $y_2(t) \to 0$ as $t \to \infty$. Let **Case A1** hold. Then $x(t) \to \bar{x}_1$ and $y_1(t) \to \bar{y}_1$ as $t \to \infty$ and $\frac{em\bar{x}_1}{a+\bar{x}_1+b_1\bar{y}_1} = d$. Thus

$$\frac{em\bar{x}_1}{a + \bar{x}_1} - d > 0\ . \tag{4.6}$$

Let **Case A3** hold. Then $(x(t), y_1(t)) \to (\phi_1(t), \psi_1(t))$ as $t \to \infty$ and

$$\int_0^{\omega_1} \Big(\frac{em\phi_1(t)}{a + \phi_1(t) + b_1\psi_1(t)} - d\Big)\ dt = 0.$$

Hence

$$\int_0^{\omega_1} \Big(\frac{em\phi_1(t)}{a + \phi_1(t)} - d\Big)\ dt > 0\ . \tag{4.7}$$

However, (4.6) and (4.7) imply that E_1 and E_{Γ_1} are unstable in the y_2-axis direction respectively. Thus the assumption $y_2(t) \to 0$ as $t \to \infty$ leads to a contradiction. Hence we have the following results.

Theorem 4.1. *For system* (4.1)*, if* (4.2) *holds then* $\limsup_{t\to\infty} y_1(t) > 0$ *and* $\limsup_{t\to\infty} y_2(t) > 0$.

5 Relaxation Oscillations

Consider system (1.1) with a large prey intrinsic growth rate, i.e., $r \gg 1$. Let $\varepsilon = 1/r$. Then $0 < \varepsilon \ll 1$, With the scaling:

$$x \to x/K, \quad a_1 \to a_1/K, \quad a_2 \to a_2/K, \quad y_1 = y_1/(Kr), \quad y_2 = y_2/(Kr),$$

system (1.1) becomes

$$\begin{aligned}
\varepsilon x' &= x(1-x) - \frac{m_1 x y_1}{a_1 + x + (\frac{b_1}{\varepsilon})y_1} - \frac{m_2 x y_2}{a_2 + x + (\frac{b_2}{\varepsilon})y_2} \\
{y_1}' &= (\frac{e_1 m_1 x}{a_1 + x + (\frac{b_1}{\varepsilon})y_1} - d_1)y_1 \\
{y_2}' &= (\frac{e_2 m_2 x}{a_2 + x + (\frac{b_2}{\varepsilon})y_2} - d_2)y_2
\end{aligned} \tag{5.1}$$

Assume $b_1 = b_1(\varepsilon)$, $b_2 = b_2(\varepsilon)$ such that

$$b_i(\varepsilon) = O(\varepsilon^{1+\mu_i}) \text{ as } \varepsilon \to 0 \tag{5.2}$$

for some $\mu_i > 0$, $i = 1, 2$. Under the assumption (5.2) we apply the geometric singular perturbation method as in Liu, Xiao, and Yi [18] to prove the existence of periodic solutions.

Setting $\varepsilon = 0$ in (5.1) results in the so-called limiting slow system

$$\begin{aligned}
xF(x, y_1, y_2) &= x\big(1 - x - \frac{m_1 y_1}{a_1 + x} - \frac{m_2 y_2}{a_2 + x}\big), \\
{y_1}' &= (\frac{e_1 m_1 x}{a_1 + x} - d_1)y_1, \\
{y_2}' &= (\frac{e_2 m_2 x}{a_2 + x} - d_2)y_2,
\end{aligned} \tag{5.3}$$

which is generally defined on the slow manifold $S_0 = \{(x, y_1, y_2) : xF(x, y_1, y_2) = 0, x \geq 0, y_1 \geq 0, y_2 \geq 0\}$. Orbits or parts of orbits of the system (5.3) on S_0 are called the *slow orbits* of system (5.1) and the variables y_1, y_2 are called slow variables. For system (5.3), the slow manifold S_0 consists of two portions S_1 and S_2, where $S_1 = \{(x, y, z) \in S_0 : x = 0\}$, $S_2 = \{(x, y_1, y_2) : F(x, y_1, y_2) = 0\}$.

In term of the fast time scale $\tau = t/\varepsilon$, system (5.1) becomes

$$
\begin{aligned}
\frac{dy_1}{d\tau} &= \varepsilon y_1\Big(\frac{e_1 m_1 x}{a_1 + x + (\frac{b_1}{\varepsilon})y_1} - d_1\Big),\\
\frac{dy_2}{d\tau} &= \varepsilon y_2\Big(\frac{e_2 m_2 x}{a_2 + x + (\frac{b_2}{\varepsilon})y_2} - d_2\Big),\\
\frac{dx}{d\tau} &= x\Big(1 - x - \frac{m_1 y_1}{a_1 + x + (\frac{b_1}{\varepsilon})y_1} - \frac{m_2 y_2}{a_2 + x + (\frac{b_2}{\varepsilon})y_2}\Big).
\end{aligned}
\tag{5.4}
$$

The system (5.5) is referred to as the fast system. Its limit, the limiting fast system, is obtained by setting $\varepsilon = 0$:

$$
\frac{dy_1}{d\tau} = 0, \quad \frac{dy_2}{d\tau} = 0, \quad \frac{dx}{d\tau} = xF(x, y_1, y_2). \tag{5.5}
$$

The orbits of system (5.5) are parallel to the x-axis and their directions are characterized by the sign of $xF(x, y_1, y_2)$. We refer to these orbits as *fast orbits* of system (5.1) and the variable x is the fast variable.

A continuous and piecewise smooth curve is said to be a *limiting orbit* of system (5.1) if it is the union of a finitely many fast and slow orbits with compatible orientations. A limiting orbit is called a *limiting periodic orbit* if it is a simple closed curve and contains no equilibrium of system (5.1). A periodic orbit of system (5.1) is called a *relaxation oscillation* if its limiting as $\varepsilon \to 0$ is a limiting periodic orbit consisting of both fast and slow orbits.

In the following theorem, we first prove that under the assumption (5.2) there is no positive equilibrium for system (5.1). Then following the methods in Liu, Xiao, and Yi [18] we construct a limiting periodic orbit consisting of both fast and slow orbits. By the theorem of geometric singular perturbation method, there exists a stable relaxation oscillation.

Theorem 5.1. *Let* **(H3)** *and* (5.2) *hold. Assume that the relaxation cycle* Γ_1^ε *on the* (x, y_1)*-plane is unstable in the* y_2*-axis direction and the relaxation cycle* Γ_2^ε *on the* (x, y_2)*-plane is unstable in the* y_1*-axis direction. Then there is at least one stable relaxation oscillation in the positive octant of* $\mathbb{R}^3$*.*

Proof. If $E_c^\varepsilon = (x_c^\varepsilon, y_{1c}^\varepsilon, y_{2c}^\varepsilon)$ exists then from (2.16) and (5.2), $y_{1c}^\varepsilon \to \infty$ as $\varepsilon \to 0$. Thus the equilibrium E_c^ε is not on the surface S_0 and the limiting periodic orbit does not contain E_c^ε. From Theorem 3.4 in [18], there exists a stable relaxation oscillation in the positive octant of $\mathbb{R}^3$. We complete the proof. □

Table IV: Parameter Values in the General Case.

$r = 2.0$	$a_1 = 3$	$b_1 = 0.6$	$d_1 = 0.4$	$e_1 = 0.6$	$m_1 = 1.5$
$K = *$	$a_2 = 6$	$b_2 = 2.0$	$d_2 = 0.45$	$e_2 = 0.7$	$m_2 = 1.5$

6 Numerical Simulations

Choose the values of parameters as in Table II and calculate the values $\lambda_1 = \frac{a_1 d_1}{e_1 m_1 - d_1} = 2.4$ and $\lambda_2 = \frac{a_2 d_2}{e_2 m_2 - d_2} = 4.5$. Now, using K (the carrying capacity of the resource) as a bifurcation parameter, increase K from 4.5 to 80 and calculate $f_x^*(K)$ as a function of K in (2.22). We can see that f_x^* is monotonically increasing from negative to positive (see the first graph of Fig. I). The values of functions α_1, α_3, and $\alpha_1\alpha_2 - \alpha_3$ are also calculated (see the 2nd - 4th graphs of Fig. I). The dynamics of solutions with respect to the capacity K are illustrated in Figure II(a)-(e).

(i) $0 < K = 2 < \lambda_1$. The semi-trivial equilibrium E_K is globally asymptotically stable, (see Fig. II:(a))

(ii) $\lambda_1 < K = 3 < \lambda_2$. The semi-trivial equilibrium E_1 is globally asymptotically stable, (see Fig. II:(b))

(iii) $\lambda_2 < K = 10$. The solution converges to the positive equilibrium E_c as $t \to \infty$. We can see that the positive equilibrium is asymptotically stable, (see Fig. II:(c))

(iv) $K = 75$. The positive equilibrium E_c loses its stability and a periodic solution bifurcates from it. (see Fig. II:(d))

Next, we do some numerical simulations of system (1.1) with interference effects, i.e., $b_1 \neq 0$ and $b_2 \neq 0$. In order to compare the differences of solutions of system (1.1) with or without interference effects, we choose the same parameters as those in Fig. 3 of [12] in Table III. We plot limit cycles of the population of predator 1 against that of predator 2 in Fig III. Fig III (a) is for $b_1 = 0$, $b_2 = 0$, (b) is for $b_1 = 0$, $b_2 = 1$, and (c) is for $b_1 = 1$, $b_2 = 0$. All above three limit cycles

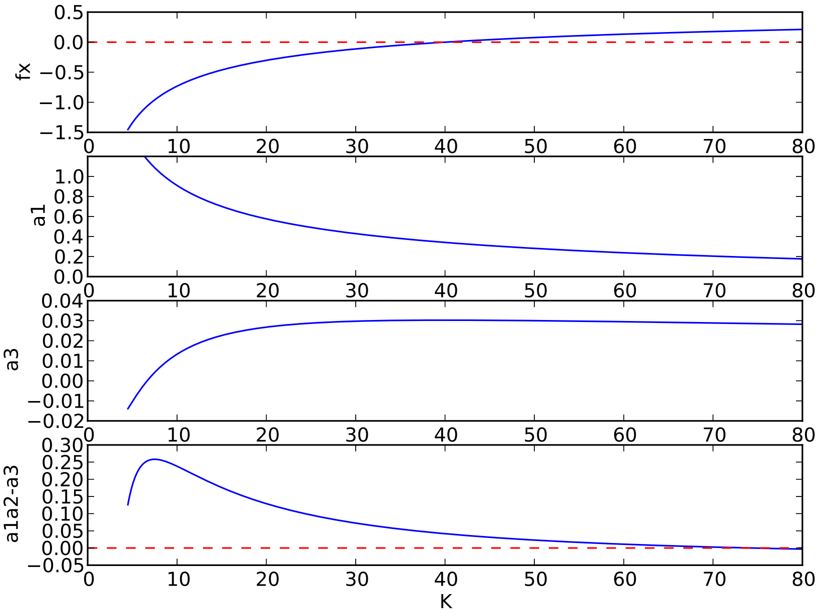

Figure I: The graphs of $f_x^*(K)$, $\alpha_1(K)$, $\alpha_3(K)$ and $\alpha_1(K)\alpha_2(K) - \alpha_3(K)$ in terms of K as K increases from 4.5 to 80.

are plotted in a graph showed in (d). With the same parameters, we compute the numerical solutions of (1.1) with various parameters b_1 and b_2. Fig III (e) and (f) show the numerical results where b_1, b_2 are varied from 0 to 10 with step-size 0.1 in (e) and b_1, b_2 are varied from 0 to 1 with step-size 0.01 in (e). The white region represents that the solutions are periodic and the black region means that the solutions approach a positive equilibrium.

Table V: Parameter Values for the Case with Interference.

$r = 20 \cdot \ln 2$	$a_1 = 200$	$d_1 = \ln 2/2$	$e_1 = 0.1$	$m_1 = 10 \cdot \ln 2$
$K = 1100$	$a_2 = 500$	$d_2 = \ln 2$	$e_2 = 1.4$	$m_2 = 2 \cdot \ln 2$

.

7 Discussion

In this paper we have studied the competition system (1.1) of two predators competing for a renewable resource (the prey) with functional responses of Beddington-DeAngelis Type. In the governing equations (1.1) the parameters b_i $(i = 1, 2)$, measuring the effect of interference, is the intra-specific competition coefficient among the population of the ith predator. The purpose of this paper is to determine the outcome of competition for system (1.1), namely, under what conditions the competitive exclusion holds and under what conditions coexistence of two competing species occurs.

In [15, 16], Hwang gave a complete classification for the behavior of the solutions of the predator-prey system with Beddington-DeAngelis functional response (2.1). The trajectory of the solution of (2.1) either converges to a positive equilibrium or approaches a unique limit cycle (see Table I). We note that (2.1) is a subsystem of (1.1). A complete understanding of the predator-prey system (2.1) will help us to study the behavior of the solutions of the competition system (1.1).

Without the interference effects, that is, $b_i = 0, i = 1, 2$, system (1.1) reduces to system (1.2), the classical model of two competing predators for a renewable resource with Holling-type II functional responses [12, 13]. In this paper we want to explore the differences between systems (1.1) and (1.2). For system (1.2), Hsu, Hubbell and Waltman [13] gave some analytic results about the competitive exclusion of the two competitors. In [12] they did extensive numerical simulations to indicate the possibility of coexistence of two competing predators and interpreted the results by the r-strategy and K-strategy. Note that Butler and Waltman [5] proved a coexistence result by using the bifurcation technique from a limit cycle in the (x, y_1) plane. However, their result is only local (not global) and the system is not uniformly persistent. Liu, Xiao, and Yi [18] and Muratori and Rinaldi [19] considered the case where the intrinsic growth rate of the prey is large and used geometric singular perturbation method to establish the coexistence of two predators in the form of stable relaxation oscillations. When the intrinsic growth rate of the prey is not large, the problem of coexistence remains open.

In this paper, based on the knowledge on the predator-prey subsystem (2.1), we first proved some uniform persistent results in Theorem 2.4. We may interpret the persistent results as the invasion of another species to the subsystem (2.1) which is in the form of equilibrium or limit cycle. In order to compare systems (1.1) and (1.2), our basic assumption is **(H3)** which states the species 1 has a smaller break-even population density. The major difference between systems (1.1) and (1.2) is that system (1.2) has no interior equilibrium while system (1.1) may or may not have an interior equilibrium. A necessary and sufficient condition is given in (2.20) for the existence and uniqueness of the interior equilibrium E_c for system (1.1). The condition (2.20) holds when the carrying capacity K is sufficient large and the intrinsic growth rate r is sufficient large (see (2.21)). When the interior equilibrium E_c exists, in Proposition 2.6 we proved that under some condition **(H4)** Hopf bifurcation occurs at some carrying capacity K^* and a family of periodic solutions bifurcates from E_c. This indicates the possibility of coexistence. In Theorem 3.2, under condition (3.1) , we presented a result for the global stability of E_c. The condition (3.1) holds when the intrinsic growth rate r is sufficient large. In Theorem 3.3, we presented an extinction result for system (1.1), which is a generalization of the extinction result in [13] for system (1.2). The result states that under assumption **(H3)**, if species 2 has larger half saturation constant then for any interference measure $b_2 > 0$ and for sufficient small $b_1 > 0$, species 2 becomes extinct as time goes to infinity. In Section 4 we proposed a question: if two predators are identical except having different interference effects, what do we anticipate for the competition outcomes? In Theorem 4.1 we proved that two species must coexist. Assume species 2 has larger interference effect among its population, i.e. $b_2 > b_1$. Intuitively species 1 is a better competitor. However species 2 is identical to species 1 in every aspect, thus species 2 is able to invade the subsystem of predator 1 and prey. Hence it is impossible for species to become extinct and we have coexistence.

The above discussion explores the difference between system (1.1) and (1.2). When system (1.1) has no interior equilibrium, we conjecture that system (1.1) should be similar to system (1.2). In Section 5, we proved that if the interference effects b_1 and b_2 are smaller in comparison with the inverse of intrinsic growth rate r which is very large (see condition (5.2)), then species 1 and 2 coexist in the form of stable relaxation oscillations. In Section 6 we presented some numerical results.

Our first numerical results (Fig. II) showed that Hopf bifurcation occurs at some carrying capacity K^*. If $K < K^*$ the interior equilibrium is global asymptotically stable. When $K > K^*$, the two species coexists in the form of periodic oscillations. In the second numerical study we assumed that the two species coexist when there is no interference effects, i.e. $b_1 = b_2 = 0$. Then we considered the effect of the interference. The study shows that solutions converge either to an interior equilibrium or to a periodic orbit. Therefore, interference effects seem not to change the outcome of competition.

Acknowledgement

Research of this paper was partially performed when the second author (SR) was visiting the National Center for Theoretical Sciences (NCTS), Hsinchu, the kind hospitality and professional assistance of the staff and members of NCTS is greatly appreciated.

References

[1] R. A. Armstrong and R. McGehee. Competitive exclusion. *American Naturalist*, 115(2):151–170, 1980.

[2] J. R. Beddington. Mutual interference between parasites or predators and its effect on searching efficiency. *The Journal of Animal Ecology*, 44(1):331, 1975.

[3] G. Butler. Persistence in dynamical systems. *J Differential Equations*, 63(2):255–263, 1986.

[4] G. Butler, H. I. Freedman, and P. Waltman. Uniformly persistent systems. *Proceedings of the American Mathematical Society*, 96(3):425–430, 1986.

[5] G. J. Butler and P. Waltman. Bifurcation from a limit cycle in a two predator-one prey ecosystem modeled on a chemostat. *Journal of Mathematical Biology*, 12(3):295–310, 1981.

[6] R. S. Cantrell and C. Cosner. On the Dynamics of Predator–Prey Models with the Beddington–DeAngelis Functional Response. *Journal of Mathematical Analysis and Applications*, 257(1):206–222, 2001.

[7] R. S. Cantrell, C. Cosner, and S. Ruan. Intraspecific interference and consumer-resource dynamics. *Discrete and Continuous Dynamical Systems-Series B*, 4(3):527–546, 2004.

[8] D. L. DeAngelis, R. A. Goldstein, and R. V. O'neill. A model for tropic interaction. *Ecology*, 56(4):881–892, 1975.

[9] H. I. Freedman, S. Ruan, and M. Tang. Uniform persistence and flows near a closed positively invariant set. *Journal of Dynamics and Differential Equations*, 6(4):583–600, 1994.

[10] S. B. Hsu. Limiting Behavior for Competing Species. *SIAM Journal on Applied Mathematics*, 34(4):760–763, 1978.

[11] S.-B. Hsu. A survey of constructing Lyapunov functions for mathematical models in population biology. *Taiwanese Journal of Mathematics*, 9(2):151–173, 2005.

[12] S. B. Hsu, S. P. Hubbell, and P. Waltman. A Contribution to the Theory of Competing Predators. *Ecological Monographs*, 48(3):337–349, 1978.

[13] S. B. Hsu, S. P. Hubbell, and P. Waltman. Competing predators. *SIAM Journal on Applied Mathematics*, 35(4):617–625, 1978.

[14] G. Huisman and R. J. DeBoer. A formal derivation of the "Beddington" functional response. *Journal of theoretical biology*, 185(3):389–400, 1997.

[15] T.-W. Hwang. Global analysis of the predator-prey system with Beddington-DeAngelis functional response. *Journal of Mathematical Analysis and Applications*, 281(1):395–401, 2003.

[16] T.-W. Hwang. Uniqueness of limit cycles of the predator-prey system with Beddington-DeAngelis functional response. *Journal of Mathematical Analysis and Applications*, 290(1):113–122, 2004.

[17] J. P. Keener. Oscillatory coexistence in the chemostat: a codimension two unfolding. *SIAM Journal on Applied Mathematics*, 43(5):1005–1018, 1983.

[18] W. Liu, D. Xiao, and Y. Yi. Relaxation oscillations in a class of predator-prey systems. *Journal of Differential Equations*, 188(1):306–331, 2003.

[19] S. Muratori and S. Rinaldi. Remarks on competitive coexistence. *SIAM Journal on Applied Mathematics*, 49(5):1462–1472, 1989.

[20] H. L. Smith. The interaction of steady state and Hopf bifurcations in a two-predator-one-prey competition model. *SIAM Journal on Applied Mathematics*, 42(1):27–43, 1982.

[21] H. L. Smith and H. R. Thieme. *Dynamical systems and population persistence*, volume 118 of *Graduate Studies in Mathematics*. American Mathematical Society, Providence, RI, 2011.

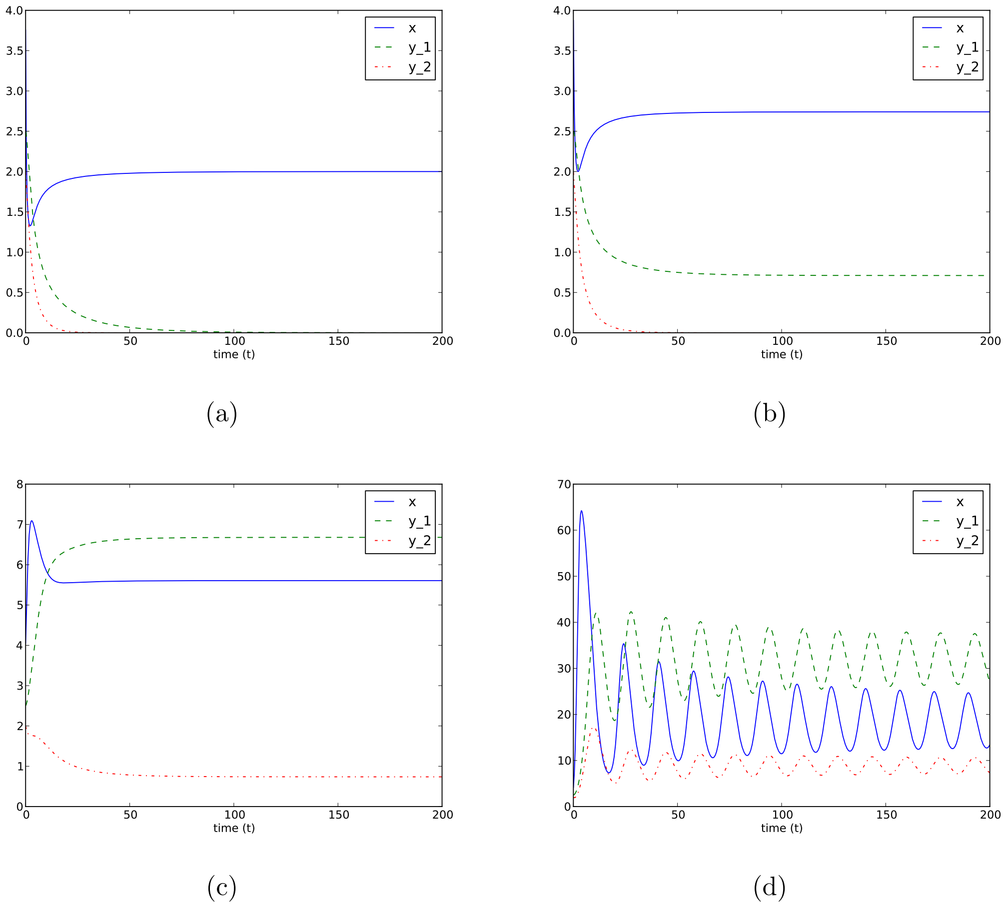

Figure II: The parameters are given in Table II. In Fig II (a), $K = 2$, $E_K = (K, 0, 0)$ is globally asymptotically stable. In Fig II (b), $K = 3$, $E_1 = (\bar{x}_1, \bar{y}_1, 0)$ is globally asymptotically stable. In Fig II (c), $K = 10$, $E_c = (x_c, y_{1c}, y_{2c})$ is globally asymptotically stable. In Fig II (d), $K = 75$, the periodic solution exist. Hopf bifurcation occurs between $K = 70$ and $K = 75$.

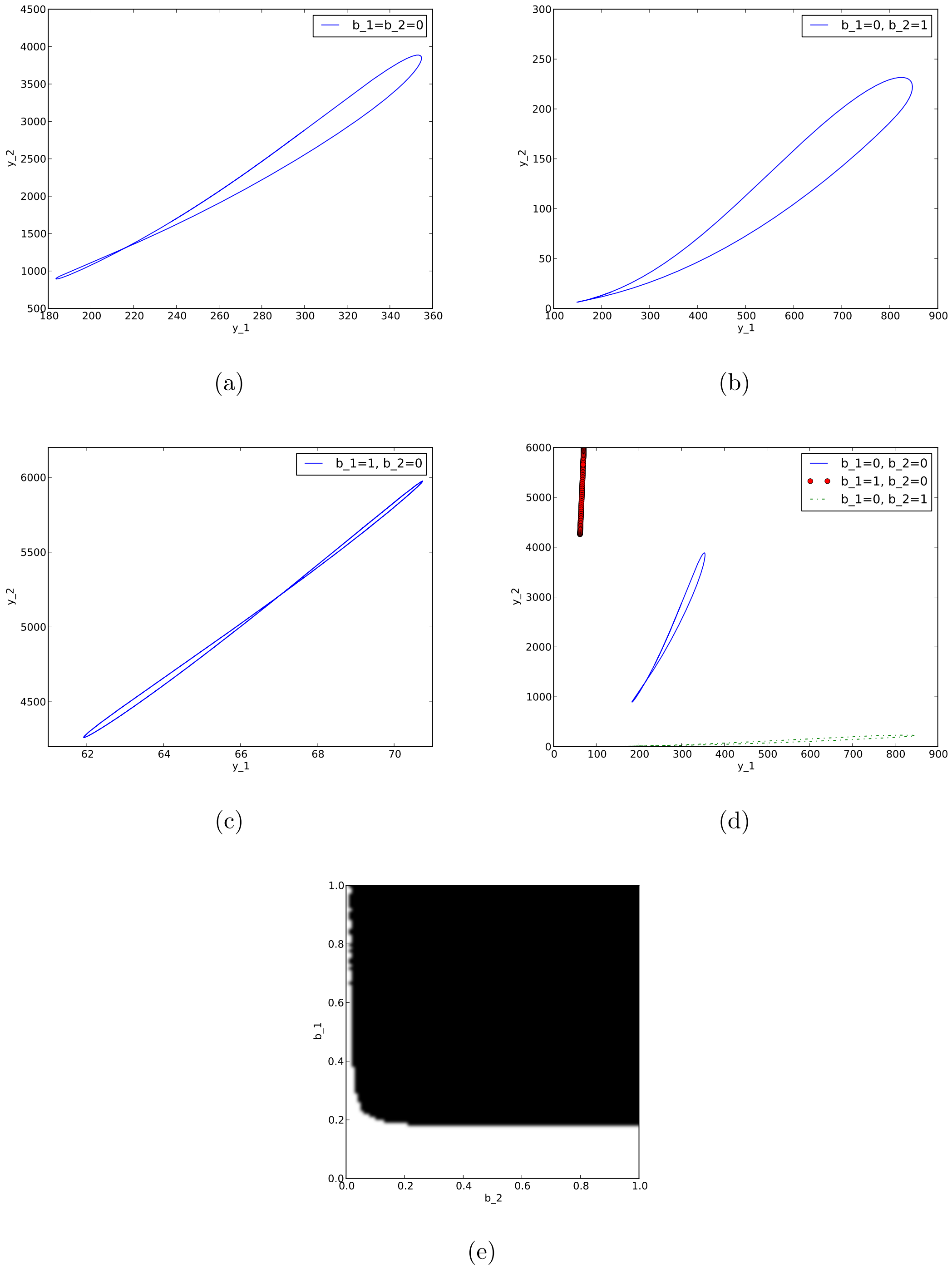

Figure III: The parameters are given in Table III. The graphs in Fig III (a), (b), (c) are the limit cycle solutions of system (1.1) projected in (y_1, y_2)-plane with $b_1 = b_2 = 0$ in Fig III(a), $b_1 = 0$, $b_2 = 1$ in Fig III (b), $b_1 = 1$, $b_2 = 0$ in Fig III (c). We put Fig III (a), (b), (c) in the same graph in Fig III (d). In Fig III (e), in the b_1-B_2 parameter region, $0 \leq b_1, b_2 \leq 1$, the white region represents that the numerical solutions are periodic and the black region represents that the numerical solutions are equilibrium solutions.