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ANALYSIS OF A MODEL OF TWO PARALLEL FOOD CHAINS

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Abstract. In this paper we study a mathematical model of two parallel food chains in a chemostat. Each food chain consists of a prey species x and a predator species y. Two food chains are symmetric in the sense that the prey species are identical and so are the specialized predator species. We assume that both of the prey species in the parallel food chains share the same nutrient R. In this paper we show that as the input concentration $R^{(0)}$ of the nutrient varies, there are several possible outcomes: (1) all species go extinct; (2) only the two prey species survive; (3) all species coexist at equilibrium; (4) all species coexist in the form of oscillations. We analyze cases (1)–(3) rigorously; for case (4) we do extensive numerical studies to present all possible phenomena, which include limit cycles, heteroclinic cycles, and chaos.

1. **Introduction and the model.**

Populations often vary in nature. While they are subject to external forcing, communities are also capable of generating sustained oscillations through interspecific interactions such as predator-prey [8, 15, 10, 13] and intransitive competition of three or more species [9, 7]. Key questions are: what other food web configurations are capable of producing internally-generated nonequilibrium dynamics, under what environmental conditions do we expect oscillations, and what are the characteristics of these oscillations?

Here we investigate the dynamics of another simple food web module, that of two parallel food chains coupled by a shared basal resource. In the following we describe a mathematical model of symmetrical food chains in a chemostat. Let $R(t)$ denote the concentration of nutrient (or resource) at time t. Let $x_1(t)$ and $x_2(t)$ be the population density of two identical prey at time t on the first and second food chain, respectively; $y_1(t)$ and $y_2(t)$ be the population density of two identical

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predators respectively. Let $R^{(0)}$ be the input concentration and D be the dilution rate. The governing equations are

$$
\begin{aligned}
R'(t) &= (R^{(0)} - R(t))D - \frac{1}{\gamma_x} f(R(t))(x_1(t) + x_2(t)),\\
x_1'(t) &= (f(R(t)) - D)x_1(t) - \frac{1}{\gamma_y} g(x_1(t))y_1(t),\\
x_2'(t) &= (f(R(t)) - D)x_2(t) - \frac{1}{\gamma_y} g(x_2(t))y_2(t),\\
y_1'(t) &= (g(x_1(t)) - D)y_1(t),\\
y_2'(t) &= (g(x_2(t)) - D)y_2(t),\\
f(R(t)) &= \frac{mR(t)}{a + R(t)},\ g(x_i(t)) = \frac{\mu x_i(t)}{K + x_i(t)}, i = 1, 2,\\
R(0) &\geq 0,\ x_1(0) > 0,\ x_2(0) > 0,\ y_1(0) > 0,\ y_2(0) > 0,
\end{aligned}
\tag{1}
$$

where $f(R)$ and $g(x)$ are the growth rate of prey species x and predator y, respectively. They take the forms of the Michaelis-Menten formulation. m is the maximum growth rate, a is the half-saturation constant for the prey species x. μ is the maximal growth rate and K is the half-saturation constant for the predator species y. γ_x and γ_y are the yield constants for the prey species x and the predator species y respectively. By rescaling x and y, we may assume $\gamma_x = \gamma_y = 1$.

Let $\Sigma = R^{(0)} - (R + x_1 + x_2 + y_1 + y_2)$. Adding the equations in (1) yields

$$\Sigma'(t) = -D\Sigma(t).$$

It follows that $\Sigma(t) = \Sigma(0)e^{-Dt} \to 0$ as $t \to \infty$. Since $\lim_{t\to\infty} (R(t) + x_1(t) + x_2(t) + y_1(t) + y_2(t)) = R^{(0)}$, we conclude that the omega limit set of the system (1) lies in the set

$$\Omega = \{(R, x_1, x_2, y_1, y_2) : R + x_1 + x_2 + y_1 + y_2 = R^{(0)}\}.$$

Consider the limiting system of (1) on Ω

$$
\begin{aligned}
x_1'(t) &= (f(R(t)) - D)x_1(t) - g(x_1(t))y_1(t),\\
x_2'(t) &= (f(R(t)) - D)x_2(t) - g(x_2(t))y_2(t),\\
y_1'(t) &= (g(x_1(t)) - D)y_1(t),\\
y_2'(t) &= (g(x_2(t)) - D)y_2(t),\\
R(t) &= R^{(0)} - (x_1(t) + x_2(t)) - (y_1(t) + y_2(t)),\\
x_i(0) &> 0,\ y_i(0) > 0,\ i = 1, 2,\\
0 &< x_1(0) + x_2(0) + y_1(0) + y_2(0) < R^{(0)}.
\end{aligned}
\tag{2}
$$

In the rest of section we shall consider the following model (3), which is a generalization of (2).

$$
\begin{aligned}
&x_1'(t) = (f(R(t)) - d_x)x_1(t) - g(x_1(t))y_1(t),\\
&x_2'(t) = (f(R(t)) - d_x)x_2(t) - g(x_2(t))y_2(t),\\
&y_1'(t) = (g(x_1(t)) - d_y)y_1(t),\\
&y_2'(t) = (g(x_2(t)) - d_y)y_2(t),\\
&R(t) = R^{(0)} - (x_1(t) + x_2(t)) - (y_1(t) + y_2(t)),\\
&x_i(0) > 0, y_i(0) > 0,\ i = 1, 2,\\
&0 < x_1(0) + x_2(0) + y_1(0) + y_2(0) < R^{(0)},
\end{aligned}
\tag{3}
$$

where d_x and d_y are the death rates of prey and predator, respectively.

For convenience, we denote the break-even resource concentration λ_x and λ_y for prey species x and predator species y, respectively,

$$
\begin{aligned}
\lambda_x &= f^{-1}(d_x) = \frac{a}{(\frac{m}{d_x}) - 1},\\
\lambda_y &= g^{-1}(d_y) = \frac{K}{(\frac{\mu}{d_y}) - 1}.
\end{aligned}
$$

If $m \le d_x$ then $x_i(t) \to 0$ as $t \to \infty$, $i = 1, 2$. Similarly if $\mu \le d_y$ then $y_i(t) \to 0$ as $t \to \infty$, $i = 1, 2$. Hence we assume $\lambda_x > 0,\ \lambda_y > 0$.

The rest of the paper is organized as follows. In section 2, we state some preliminary results about the single food chain model. In section 3, we consider the two parallel food chains with either no predators or with only one predator. In section 4, we analyze and classify all cases on two parallel food chains sharing one nutrient. In section 5, we present our numerical studies and discuss their biological meanings.

2. **Preliminary results for the single food chain.** In this section we review some preliminary results about the single food chain model. Using the same notations in previous section, we consider the following system of the single food chain:

$$
\begin{aligned}
&x'(t) = (f(R(t)) - d_x)x(t) - g(x(t))y(t),\\
&y'(t) = (g(x(t)) - d_y)y(t),\\
&R(t) = R^{(0)} - (x(t) + y(t)),\\
&x(0) > 0,\ y(0) > 0,\\
&0 < x(0) + y(0) < R^{(0)}.
\end{aligned}
\tag{4}
$$

Then from [12], we have the following results.

Theorem 2.1.
(a) If $0 < R^{(0)} < \lambda_x$ then $x(t) \to 0,\ y(t) \to 0$ as $t \to \infty$.
(b) If $\lambda_x < R^{(0)} < \lambda_x + \lambda_y$ then $x(t) \to x^* > 0,\ y(t) \to 0$ as $t \to \infty$ where $x^* = R^{(0)} - \lambda_x$.
(c) If $R^{(0)} > \lambda_x + \lambda_y$ then there exists a unique equilibrium $E_c = (x_c, y_c)$ of the system (4), where $x_c = \lambda_y$ and y_c satisfies the equation $f(R^{(0)} - x_c - y) - d_x = d_y \frac{y}{x_c}$. Furthermore (x_c, y_c) is locally stable if

$$
\frac{\mu}{(K + x_c)^2} y_c < \frac{ma}{(a + R^{(0)} - x_c - y_c)^2}. \tag{*}
$$

(d) $(*)$ is equivalent to $R^{(0)} < \hat{R}$ for some $\hat{R} > 0$.
(e) If $\lambda_x + \lambda_y < R^{(0)} < \hat{R}$ then $(x(t), y(t)) \to E_c$ as $t \to \infty$.
(f) If $R^{(0)} > \hat{R}$ then there exists a limit cycle Γ.

Remark 1. In (f), we conjecture that $(x(t), y(t))$ approaches a unique limit cycle Γ as $t \to \infty$ provided $(x(0), y(0)) \neq (x_c, y_c)$.

3. **Two parallel food chains with either no predators or with only one predator.** In this section we first consider two parallel food chains without predators.

$$\begin{aligned}
&x_1'(t) = (f(R(t)) - d_x)x_1(t),\\
&x_2'(t) = (f(R(t)) - d_x)x_2(t),\\
&R(t) = R^{(0)} - (x_1(t) + x_2(t)),\\
&x_1(0) > 0,\ x_2(0) > 0,\\
&0 < x_1(0) + x_2(0) < R^{(0)}.
\end{aligned} \tag{5}$$

Theorem 3.1. *If $R^{(0)} > \lambda_x$, then the solution $(x_1(t), x_2(t)) \to (x_1^*, x_2^*)$ as $t \to \infty$ where the limit (x_1^*, x_2^*), $x_1^* \geq 0$, $x_2^* \geq 0$ depends on the initial condition $(x_1(0), x_2(0))$ satisfying $x_1^* + x_2^* = R^{(0)} - \lambda_x$, $x_1^* = \frac{x_1(0)}{x_2(0)} x_2^*$.*

Proof. Adding the two differential equations in (5) yields

$$\begin{aligned}
(x_1 + x_2)'(t) &= (f(R(t)) - d_x)(x_1 + x_2)(t)\\
&= (f(R^{(0)} - (x_1 + x_2)(t)) - d_x)(x_1 + x_2)(t)\\
&\begin{cases} > 0 & \text{if } (x_1 + x_2)(t) < R^{(0)} - \lambda_x,\\ = 0 & \text{if } (x_1 + x_2)(t) = R^{(0)} - \lambda_x,\\ < 0 & \text{if } (x_1 + x_2)(t) > R^{(0)} - \lambda_x. \end{cases}
\end{aligned}$$

Then $x_1(t) + x_2(t) \to R^{(0)} - \lambda_x$ as $t \to \infty$.

From (5) $\frac{x_1'}{x_1} = \frac{x_2'}{x_2} = f(R(t)) - d_x$,$\left(\frac{x_1}{x_2}\right)' = \frac{x_1'}{x_2} - \frac{x_1}{x_2}\frac{x_2'}{x_2} = \frac{x_1'}{x_2} - \frac{x_1}{x_2}\frac{x_1'}{x_1} = 0$. Hence $\frac{x_1(t)}{x_2(t)} = c$, $t \geq 0$ where $c = \frac{x_1(0)}{x_2(0)}$. Let $x_1(t) = cx_2(t)$. From $x_1(t) + x_2(t) \to R^{(0)} - \lambda_x$ as $t \to \infty$, we get $(1 + c)x_2(t) \to R^{(0)} - \lambda_x$, and $x_2(t) \to \frac{R^{(0)} - \lambda_x}{1+c} = x_2^*$, $x_1(t) \to \frac{c(R^{(0)} - \lambda_x)}{1+c} = x_1^*$. Thus $(x_1(t), x_2(t)) \to (x_1^*, x_2^*)$ as $t \to \infty$. $\square$

Remark 2. Every point in the set $\{(x_1, x_2)) : x_1 + x_2 = R^{(0)} - \lambda_x\}$ is an equilibrium for the system (5). It is easy to verify that each of them is stable, but not asymptotically stable.

Consider two parallel food chains with only one predator. The equations take the following form:

$$\begin{aligned}
&x_1'(t) = (f(R(t)) - d_x)x_1(t) - g(x_1(t))y_1(t),\\
&x_2'(t) = (f(R(t)) - d_x)x_2(t),\\
&y_1'(t) = (g(x_1(t)) - d_y)y_1(t),\\
&R(t) = R^{(0)} - (x_1(t) + x_2(t) + y_1(t)),\\
&x_1(0) > 0, x_2(0) > 0, y_1(0) > 0,\\
&0 < x_1(0) + x_2(0) + y_1(0) < R^{(0)}.
\end{aligned} \tag{6}$$

In this case we obtain an interesting result that says that a single predator in the parallel food chains cannot survive. The following is a useful lemma in the proof of Theorem 3.3.

Lemma 3.2. ([1])
If $\lim_{t\to\infty} f(t)$ exists, and $|f''(t)|$ is bounded, then $\lim_{t\to\infty} f'(t) = 0$.

Theorem 3.3. *If $R^{(0)} > \lambda_x$, then the solution $(x_1(t), x_2(t), y_1(t))$ of (6) satisfies $y_1(t) \to 0$ as $t \to \infty$ and $(x_1(t), x_2(t), y_1(t)) \to (x_1^*, x_2^*, 0)$, for some $x_1^*, x_2^* \geq 0$ satisfying $x_1^* + x_2^* = R^{(0)} - \lambda_x$.*

Proof. First, we add the three differential equations in (6) and get

$$(x_1 + x_2 + y_1)'(t) = [f(R(t)) - d_x](x_1 + x_2)(t) - d_y y_1(t). \tag{7}$$

From (7), if $f(R(t)) - d_x \leq 0$ then the quantity $(x_1 + x_2 + y_1)$ is decreasing. It is noted that

$$\begin{aligned} f(R(t)) - d_x \leq 0 &\Leftrightarrow R \leq \lambda_x \\ &\Leftrightarrow R^{(0)} - (x_1 + x_2 + y_1) \leq \lambda_x \\ &\Leftrightarrow R^{(0)} - \lambda_x \leq (x_1 + x_2 + y_1). \end{aligned}$$

So we divide the positive octant of $\mathbb{R}^3$ into two regions. Let

$$\begin{aligned} P &= \{(x_1, x_2, y_1) \in \mathbb{R}^3_+ | x_1 + x_2 + y_1 = R^{(0)} - \lambda_x\}, \\ \Omega_1 &= \{(x_1, x_2, y_1) \in \mathbb{R}^3_+ | R^{(0)} > x_1 + x_2 + y_1 > R^{(0)} - \lambda_x\}, \\ \Omega_2 &= \{(x_1, x_2, y_1) \in \mathbb{R}^3_+ | x_1 + x_2 + y_1 < R^{(0)} - \lambda_x\}. \end{aligned}$$

Suppose the trajectory $(x_1(t), x_2(t), y_1(t))$ stays in the region Ω_1 for all $t \geq 0$, then $(x_1 + x_2 + y_1)(t)$ is strictly decreasing and converges to a constant. It is easy to verify that $|x_1''(t) + x_2''(t) + y_1''(t)|$ is bounded. Then from Lemma 3.2 we have $(x_1 + x_2 + y_1)'(t) \to 0$ as $t \to \infty$. Since $f(R) - d_x < 0$ in Ω_1, then from (7) we have that $f(R) - d_x \to 0$ and $y_1(t) \to 0$ as $t \to \infty$. Hence $x_1(t) + x_2(t)$ converges to the constant $R^{(0)} - \lambda_x$ as $t \to \infty$. If the trajectory $(x_1(t), x_2(t), y_1(t))$ passes the plane P, then from (7) it enters the region Ω_2 and stays there.

Now, consider the trajectory in the region Ω_2. Since $R = R^{(0)} - (x_1 + x_2 + y_1)$, from (6)

$$x_2'(t) = (f(R(t)) - d_x)x_2(t).$$

$x_2(t)$ is strictly increasing and bounded above by $R^{(0)} - \lambda_x$, then $x_2(t)$ converges, say $x_2(t) \to x_2^* > 0$ as $t \to \infty$. Since $x_2(t)$ converges and $|x_2''(t)|$ is bounded, from Lemma 3.2 we obtain that $x_2'(t)$ approaches zero as $t \to \infty$. From the second equation of the system (6), it follows that

$$\begin{aligned} &f(R) - d_x \to 0 \text{ as } t \to \infty, \\ \Leftrightarrow &R(t) \to \lambda_x \text{ as } t \to \infty, \\ \Leftrightarrow &R^{(0)} - (x_1 + x_2 + y_1)(t) \to \lambda_x \text{ as } t \to \infty, \\ \Leftrightarrow &(x_1 + y_1)(t) \to (R^{(0)} - \lambda_x - x_2^*) \text{ as } t \to \infty. \end{aligned}$$

Similarly $(x_1+y_1)''(t)$ is bounded, from Lemma 3.2 we have $(x_1+y_1)'(t) \to 0$ as $t \to \infty$. Since $f(R) - d_x \to 0$ as $t \to \infty$ and $x_1(t)$ is bounded, it follows that

$$\begin{aligned}(x_1+y_1)'(t) =& [f(R(t)) - d_x]x_1(t) - d_y y_1(t)\\ \to & - d_y y_1(\infty) \text{ as } t \to \infty.\end{aligned}$$

Thus $y_1(t) \to 0$ and we have $(x_1(t), x_2(t), y_1(t)) \to (x_1^*, x_2^*, 0)$ as $t \to \infty$ for some $x_1^*, x_2^* \geq 0$, $x_1^* + x_2^* = R^{(0)} - \lambda_x$. □

4. **Mathematical analysis of two parallel food chains system.** In this section we focus on the limiting system (3). This is a system of four differential equations, and we proceed in the standard way: identify the rest points, determine their local stability, and discuss its global behavior.

4.1. **Rest points and their local stability.** The system has the following seven types of rest points:

$$\begin{aligned}E_0 =& (0,0,0,0), E_{10} = (\widetilde{x_1}, 0, 0, 0), E_{20} = (0, \widetilde{x_2}, 0, 0), E_x = (x_1^*, x_2^*, 0, 0),\\ E_1 =& (\overline{x_1}, 0, \overline{y_1}, 0), E_2 = (0, \overline{x_2}, 0, \overline{y_2}), E_c = (x_{1c}, x_{2c}, y_{1c}, y_{2c}).\end{aligned}$$

The rest point E_0 always exists; E_{10} and E_{20} exist if $R^{(0)} > \lambda_x$ where $\widetilde{x_1} = \widetilde{x_2} = R^{(0)} - \lambda_x$. The E_x exists if $R^{(0)} > \lambda_x$ where $x_1^* + x_2^* = R^{(0)} - \lambda_x$. From (3), E_1 exists if $R^{(0)} > \lambda_x + \lambda_y$, where $\overline{x_1} = \lambda_y$ and $\overline{y_1}$ satisfies

$$f(R^{(0)} - \overline{x_1} - \overline{y_1}) - d_x = d_y \frac{\overline{y_1}}{\overline{x_1}}, \tag{8}$$

$\overline{y_1}$ is uniquely determined from (8). Similarly E_2 has the same properties as E_1, so we just consider one of them. From (3) E_c exists if and only if $R^{(0)} > \lambda_x + 2\lambda_y$. It is easy to verify that $x_{1c} = x_{2c} = \lambda_y$ and $y_{1c} = y_{2c}$. We denote $x_c = x_{1c} = x_{2c}$, $y_c = y_{1c} = y_{2c}$. Then y_c satisfies

$$f(R^{(0)} - 2x_c - 2y_c) - d_x = d_y \frac{y_c}{x_c}. \tag{9}$$

Note that (9) has a unique positive solution if and only if $R^{(0)} > \lambda_x + 2\lambda_y$.

Now we establish the asymptotic stability of the rest points by showing the real parts of the eigenvalues of the variational matrix around the equilibria are negative. The variational matrix J about equilibrium E_i, which takes the form

$$J = \begin{bmatrix} m_{11} & m_{12} & m_{13} & m_{14} \\ m_{21} & m_{22} & m_{23} & m_{24} \\ m_{31} & 0 & m_{33} & 0 \\ 0 & m_{42} & 0 & m_{44} \end{bmatrix}.$$

At E_0,

$$J(E_0) = \begin{bmatrix} f(R^{(0)}) - d_x & 0 & 0 & 0 \\ 0 & f(R^{(0)}) - d_x & 0 & 0 \\ 0 & 0 & -d_y & 0 \\ 0 & 0 & 0 & -d_y \end{bmatrix}.$$

The eigenvalues are the diagonals. Hence if $R^{(0)} < \lambda_x$ then E_0 is asymptotically stable. If $R^{(0)} > \lambda_x$ then E_0 is a saddle point with two dimensional stable manifold.

At E_{10},

$$J(E_{10}) = \begin{bmatrix} m_{11} & m_{12} & m_{13} & m_{14} \\ 0 & 0 & 0 & 0 \\ 0 & 0 & m_{33} & 0 \\ 0 & 0 & 0 & m_{44} \end{bmatrix},$$

where $m_{11} = -f'(\widetilde{R})\widetilde{x_1}$, $m_{12} = -f'(\widetilde{R})\widetilde{x_1}$, $m_{13} = -f'(\widetilde{R})\widetilde{x_1} - g(\widetilde{x_1})$, $m_{14} = -f'(\widetilde{R})\widetilde{x_1}$, $m_{33} = g(\widetilde{x_1}) - d_y$, $m_{44} = -d_y$, $\widetilde{R} = R^{(0)} - \widetilde{x_1} = \lambda_x$.

The eigenvalues are 0, m_{11}, m_{33}, m_{44} with $m_{11} < 0$ and $m_{44} < 0$. We note that

$$\begin{aligned} m_{33} < 0 \Leftrightarrow & g(\widetilde{x_1}) - d_y < 0 \\ \Leftrightarrow & g(R^{(0)} - \lambda_x) < d_y \\ \Leftrightarrow & R^{(0)} < \lambda_x + \lambda_y. \end{aligned}$$

If $R^{(0)} > \lambda_x + \lambda_y$, then E_{10} is a saddle. Similarly results hold for E_{20}: if $R^{(0)} < \lambda_x + \lambda_y$ then $J(E_{20})$ has three negative eigenvalues and one zero eigenvalue, and E_{20} is a saddle if $R^{(0)} > \lambda_x + \lambda_x$.

At E_x,

$$J(E_x) = \begin{bmatrix} m_{11} & m_{12} & m_{13} & m_{14} \\ m_{21} & m_{22} & m_{23} & m_{24} \\ 0 & 0 & m_{33} & 0 \\ 0 & 0 & 0 & m_{44} \end{bmatrix},$$

where $m_{11} = m_{12} = m_{14} = -f'(R^*)x_1^*$, $m_{13} = -f'(R^*)x_1^* - g(x_1^*)$, $m_{21} = m_{22} = m_{23} = -f'(R^*)x_2^*$, $m_{24} = -f'(R^*)x_2^* - g(x_2^*)$, $m_{33} = g(x_1^*) - d_y$, $m_{44} = g(x_2^*) - d_y$, $R^* = R^{(0)} - (x_1^* + x_2^*) = \lambda_x$.

It is easy to see that m_{33} and m_{44} are two eigenvalues. The remaining two eigenvalues are the eigenvalues of the matrix $\begin{bmatrix} m_{11} & m_{12} \\ m_{21} & m_{22} \end{bmatrix}$. The characteristic polynomial of $\begin{bmatrix} m_{11} & m_{12} \\ m_{21} & m_{22} \end{bmatrix}$ is computed as

$$\begin{aligned} & [\lambda + f'(\lambda_x)x_1^*][\lambda + f'(\lambda_x)x_2^*] - [f'(\lambda_x)]^2 x_1^* x_2^* = 0 \\ \Rightarrow & \lambda^2 + [f'(\lambda_x)(R^{(0)} - \lambda_x)]\lambda = 0. \end{aligned}$$

Clearly, the other two eigenvalues of $J(E_x)$ are 0 and $-f'(\lambda_x)(R^{(0)} - \lambda_x)$. We note that $m_{33} < 0$ iff $x_1^* < \lambda_y$ and $m_{44} < 0$ iff $x_2^* < \lambda_y$. When $R^{(0)} - \lambda_x < \lambda_y$ we get $x_1^* < \lambda_y$, $x_2^* < \lambda_y$.

Case 1: If $\lambda_x + \lambda_y < R^{(0)} < \lambda_x + 2\lambda_y$, then the line $x_1 + x_2 = R^{(0)} - \lambda_x$ is divided into three parts (See Fig. 1):

1. If $(x_1^*, x_2^*) \in \overline{AD}$, then $J(E_x)$ has one zero eigenvalue, two negative eigenvalues and one positive eigenvalue. The unstable manifold of E_x points into the positive y_1 direction.
2. If $(x_1^*, x_2^*) \in \overline{CD}$, then $J(E_x)$ has one zero eigenvalue, three negative eigenvalues.
3. If $(x_1^*, x_2^*) \in \overline{BC}$, then $J(E_x)$ has one zero eigenvalue, two negative eigenvalues and one positive eigenvalue. The unstable manifold of E_x points into the positive y_2 direction.

Case 2: If $R^{(0)} > \lambda_x + 2\lambda_y$, then the line $x_1 + x_2 = R^{(0)} - \lambda_x$ is divided into three parts (See Fig. 2):

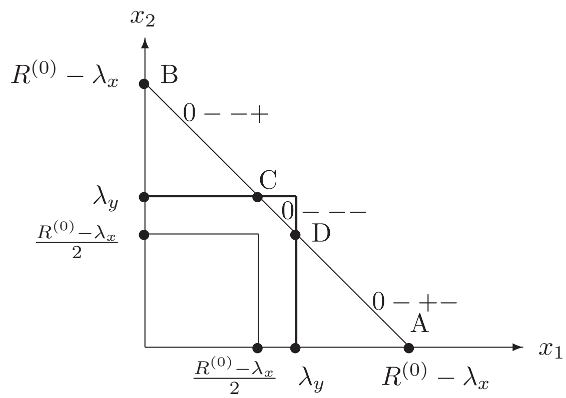

Figure 1: Case 1. $\lambda_x + \lambda_y < R^{(0)} < \lambda_x + 2\lambda_y$, $\overline{AB}$ is the line of equilibria (E_x). The plus and minus signs are the signs of the eigenvalues of $J(E_x)$.

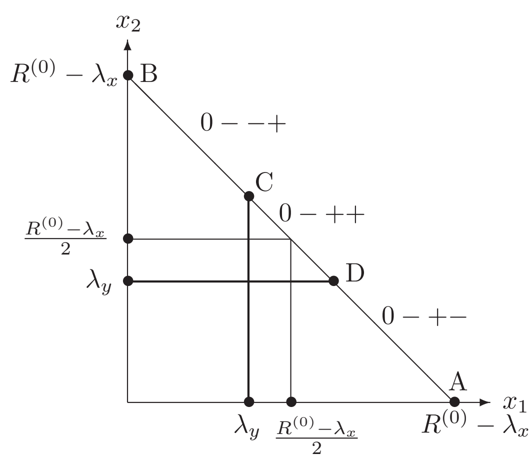

Figure 2: Case 2. $R^{(0)} > \lambda_x + 2\lambda_y$.

1. $(x_1^*, x_2^*) \in \overline{AD}$, the eigenvalues of $J(E_x)$ have same properties as in Case 1.
2. $(x_1^*, x_2^*) \in \overline{CD}$, then $J(E_x)$ has one zero eigenvalue, one negative eigenvalue, two positive eigenvalues.
3. $(x_1^*, x_2^*) \in \overline{BC}$, the eigenvalues of $J(E_x)$ have same properties as in Case 1.

Case 3: If $R^{(0)} = \lambda_x + 2\lambda_y$, then the line $x_1 + x_2 = R^{(0)} - \lambda_x$ is divided into two parts (See Fig. 3):

1. If $(x_1^*, x_2^*) \in \overline{AC}$, then $J(E_x)$ has one zero eigenvalue, two negative eigenvalues and one positive eigenvalue.
2. If $(x_1^*, x_2^*) \in \overline{BC}$, then $J(E_x)$ has one zero eigenvalue, two negative eigenvalues and one positive eigenvalue.

At E_1,

$$J(E_1) = \begin{bmatrix} m_{11} & m_{12} & m_{13} & m_{14} \\ 0 & m_{22} & 0 & 0 \\ m_{31} & 0 & 0 & 0 \\ 0 & 0 & 0 & m_{44} \end{bmatrix},$$

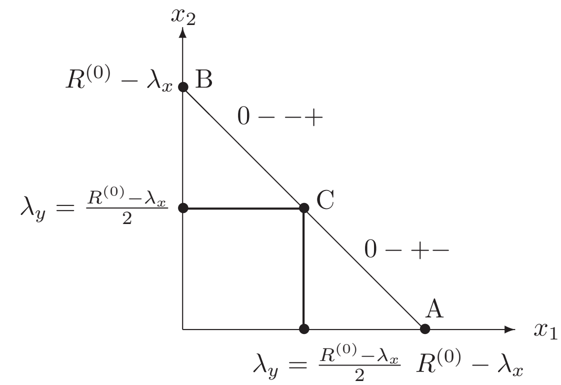

Figure 3: Case 3. $R^{(0)} = \lambda_x + 2\lambda_y$.

where $m_{11} = (f(\overline{R}) - d_x) - f'(\overline{R})\overline{x_1} - g'(\overline{x_1})\overline{y_1}$, $m_{12} = m_{14} = -f'(\overline{R})\overline{x_1}$, $m_{13} = -f'(\overline{R})\overline{x_1} - g(\overline{x_1})$, $m_{22} = f(\overline{R}) - d_x$, $m_{31} = g'(\overline{x_1})\overline{y_1}$, $m_{44} = -d_y$, $\overline{R} = R^{(0)} - (\overline{x_1} + \overline{y_1})$.

It is easy to see that one eigenvalue is $m_{44} = -d_y$. The rest of three eigenvalues are the eigenvalues of

$$\begin{bmatrix} m_{11} & m_{12} & m_{13} \\ 0 & m_{22} & 0 \\ m_{31} & 0 & 0 \end{bmatrix}.$$

The eigenvalues λ satisfy

$$\begin{aligned} &-\lambda(m_{11} - \lambda)(m_{22} - \lambda) - (m_{22} - \lambda)m_{13}m_{31} = 0 \\ \Rightarrow &(m_{22} - \lambda)(\lambda^2 - m_{11}\lambda - m_{13}m_{31}) = 0. \end{aligned}$$

One of eigenvalues is $m_{22} = f(R^{(0)} - \overline{x_1} - \overline{y_1}) - d_x = d_y \frac{\overline{y_1}}{\overline{x_1}} > 0$ by (8). The other two eigenvalues satisfy $\lambda^2 - m_{11}\lambda - m_{13}m_{31} = 0$. Since $m_{13}m_{31} < 0$, it follows that the real part of the other two eigenvalues is negative if and only if $m_{11} < 0$, i.e. $d_y \frac{\overline{y_1}}{\overline{x_1}} - f'(R^{(0)} - \overline{x_1} - \overline{y_1})\overline{x_1} - g'(\overline{x_1})\overline{y_1} < 0$. We conclude that if $m_{11} < 0$ then E_1 is a saddle point with three dimensional stable manifold, otherwise if $m_{11} > 0$ then E_1 is saddle with one dimensional stable manifold. Similarly for E_2, if $m_{22} < 0$ then E_2 is a saddle point with three dimensional stable manifold, otherwise if $m_{22} > 0$ then E_2 is saddle with one dimensional stable manifold.

At E_c,

$$J(E_c) = \begin{bmatrix} m_{11} & m_{12} & m_{13} & m_{14} \\ m_{21} & m_{22} & m_{23} & m_{24} \\ m_{31} & 0 & 0 & 0 \\ 0 & m_{42} & 0 & 0 \end{bmatrix} = \begin{bmatrix} p & q & s & q \\ q & p & q & s \\ r & 0 & 0 & 0 \\ 0 & r & 0 & 0 \end{bmatrix},$$

where

$$\begin{aligned} p =&(f(R_c) - d_x) - f'(R_c)x_c - g'(x_c)y_c, \\ q =&-f'(R_c)x_c < 0, \\ r =&g'(x_c)y_c > 0, \\ s =&-f'(R_c)x_c - g(x_c) < 0, \\ R_c =&R^{(0)} - 2(x_c + y_c). \end{aligned} \tag{10}$$

The stability analysis around E_c is presented in the following Lemma 4.1, whose proof is deferred to the appendix.

Lemma 4.1. *One of the following three cases holds:*
(a) E_c is a repeller (each eigenvalue of the variational matrix $J(E_c)$ has positive real part) or
(b) E_c is a saddle point with two dimensional stable manifold, or
(c) $J(E_c)$ has two eigenvalues that are purely imaginary, two eigenvalues with positive real part.

The local behavior of the rest points are summarized in Table 1.

Point	Existence	Stability
$E_0 = (0,0,0,0)$	Always	Asymptotically stable if $R^{(0)} < \lambda_x$. Saddle with 2-D stable manifold if $R^{(0)} > \lambda_x$.
$E_{10} = (\widetilde{x_1}, 0, 0, 0)$ $\widetilde{x_1} = R^{(0)} - \lambda_x$	$R^{(0)} > \lambda_x$	If $R^{(0)} < \lambda_x + \lambda_y$, then $J(E_{10})$ has three negative eigenvalues and one zero eigenvalue. Saddle if $R^{(0)} > \lambda_x + \lambda_y$.
$E_{20} = (0, \widetilde{x_2}, 0, 0)$ $\widetilde{x_2} = R^{(0)} - \lambda_x$	$R^{(0)} > \lambda_x$	If $R^{(0)} < \lambda_x + \lambda_y$, then $J(E_{20})$ has three negative eigenvalues and one zero eigenvalue. Saddle if $R^{(0)} > \lambda_x + \lambda_y$.
$E_x = (x_1^*, x_2^*, 0, 0)$ $x_1^* + x_2^* = R^{(0)} - \lambda_x$	$R^{(0)} > \lambda_x$	If $R^{(0)} < \lambda_x + \lambda_y$, then $J(E_x)$ has three negative eigenvalues and one zero eigenvalue. If $R^{(0)} > \lambda_x + \lambda_y$, there are Case 1, 2, 3 discsused above.
$E_1 = (\overline{x_1}, 0, \overline{y_1}, 0)$ $\overline{x_1} = \lambda_y$, $\overline{y_1}$ satisfies $f(R^{(0)} - \overline{x_1} - \overline{y_1}) - d_x = d_y \frac{\overline{y_1}}{\overline{x_1}}$	$R^{(0)} > \lambda_x + \lambda_y$	Saddle with 3-D stable manifold if $d_y \frac{\overline{y_1}}{\overline{x_1}} - f'(R^{(0)} - (\overline{x_1} + \overline{y_1})) - g'(\overline{x_1})\overline{y_1} < 0$. Saddle with 1-D stable manifold if $d_y \frac{\overline{y_1}}{\overline{x_1}} - f'(R^{(0)} - (\overline{x_1} + \overline{y_1})) - g'(\overline{x_1})\overline{y_1} > 0$.
$E_2 = (0, \overline{x_2}, 0, \overline{y_2})$ $\overline{x_2} = \lambda_y$, $\overline{y_2}$ satisfies $f(R^{(0)} - \overline{x_2} - \overline{y_2}) - d_x = d_y \frac{\overline{y_2}}{\overline{x_2}}$	$R^{(0)} > \lambda_x + \lambda_y$	Saddle with 3-D stable manifold if $d_y \frac{\overline{y_2}}{\overline{x_2}} - f'(R^{(0)} - (\overline{x_2} + \overline{y_2})) - g'(\overline{x_2})\overline{y_2} < 0$. Saddle with 1-D stable manifold if $d_y \frac{\overline{y_2}}{\overline{x_2}} - f'(R^{(0)} - (\overline{x_2} + \overline{y_2})) - g'(\overline{x_2})\overline{y_2} > 0$.
$E_c = (x_c, x_c, y_c, y_c)$ $x_c = \lambda_y$, y_c satisfies $f(R^{(0)} - 2x_c - 2y_c) - d_x = d_y \frac{y_c}{x_c}$	$R^{(0)} > \lambda_x + 2\lambda_y$	Saddle with 2-D stable manifold or a repeller or E_c satisfies (3) of Lemma 4.1.

Table 1:

4.2. **Global analysis of the two parallel food chains.** We have established the existence and local stability of the rest points. As the parameter $R^{(0)}$ varies, the system (3) has different behavior. In the following, we study the global asymptotic behavior of the solutions of (3).

Theorem 4.2.
(a) If $0 < R^{(0)} < \lambda_x$ then $(x_1(t), x_2(t), y_1(t), y_2(t)) \to E_0$ as $t \to \infty$.
(b) If $\lambda_x < R^{(0)} < \lambda_x + \lambda_y$ then $(x_1(t), x_2(t), y_1(t), y_2(t)) \to E_x = (x_1^*, x_2^*, 0, 0)$ for some $x_1^* > 0,\ x_2^* > 0,\ x_1^* + x_2^* = R^{(0)} - \lambda_x$ as $t \to \infty$.

Proof. (a) If $0 < R^{(0)} < \lambda_x$ then $f(R^{(0)}) - d_x < 0$. From (3) we have

$$\begin{aligned} x_i'(t) &\le (f(R(t)) - d_x)x_i(t),\\ &\le (f(R^{(0)}) - d_x)x_i(t),\\ &= -\delta x_i(t), i = 1, 2, \end{aligned}$$

where $\delta = d_x - f(R^{(0)}) > 0$. It follows that $\lim_{t\to\infty} x_i(t) = 0,\ i = 1, 2$. From (3) it is obvious that $x_i(t) \to 0\ t \to \infty$, implies $y_i(t) \to 0$ as $t \to \infty$.

(b) If $\lambda_x < R^{(0)} < \lambda_x + \lambda_y$ then $g(R^{(0)} - \lambda_x) < g(\lambda_y) = d_y$. From (3) we have

$$\begin{aligned} (x_1 + x_2)'(t) &\le (f(R(t)) - d_x)(x_1 + x_2)(t),\\ &\le (f(R^{(0)} - (x_1 + x_2)(t)) - d_x)(x_1 + x_2)(t). \end{aligned}$$

From the above differential inequality we get $(x_1 + x_2)(t) \le R^{(0)} - \lambda_x + \varepsilon$ for $\varepsilon > 0$ small such that $R^{(0)} - \lambda_x + \varepsilon < \lambda_y$, and t sufficiently large. From (3) it follows that

$$\begin{aligned} \frac{y_i'(t)}{y_i(t)} &= g(x_i(t)) - d_y\\ &\le g((x_1 + x_2)(t)) - d_y\\ &\le g(R^{(0)} - \lambda_x + \varepsilon) - d_y\\ &< 0, i = 1, 2 \text{ if } \varepsilon > 0 \text{ is small enough.} \end{aligned}$$

Hence $\lim_{t\to\infty} y_i(t) = 0,\ i = 1, 2$. Then we have

$$\begin{aligned} (x_1 + x_2)'(t) &= (f(R(t)) - d_x)(x_1 + x_2)(t) - g(x_1)y_1 - g(x_2)y_2\\ &= (f(R^{(0)} - (x_1 + x_2)(t)) - d_x)(x_1 + x_2)(t) + o(1) \text{ as } t \to \infty. \end{aligned}$$

Thus $(x_1 + x_2)(t) \to R^{(0)} - \lambda_x$ as $t \to \infty$. □

Further analysis of the system (3) with larger $R^{(0)}$ is very technical. Next we will prove the extinction of top predators. The method is similar to those in the papers of Hsu, Hwang, and Kuang [5, 6], and Hsu [4].

Theorem 4.3. *If $\lambda_x + \lambda_y < R^{(0)} < \lambda_x + 2\lambda_y$ then $\lim_{t\to\infty} y_1(t)y_2(t) = 0$.*

Proof. Without loss of generality we can assume that $y_1(0) > 0,\ y_2(0) > 0$. Let P be the hyperplane

$$P = \{(x_1, x_2, y_1, y_2) \in \mathbb{R}_+^4 | x_1 + x_2 + y_1 + y_2 = R^{(0)} - \lambda_x\},$$

and the regions Ω_1 and Ω_2 be

$$\begin{aligned} \Omega_1 &= \{(x_1, x_2, y_1, y_2) \in \mathbb{R}_+^4 | R^0 > x_1 + x_2 + y_1 + y_2 > R^{(0)} - \lambda_x\},\\ \Omega_2 &= \{(x_1, x_2, y_1, y_2) \in \mathbb{R}_+^4 | x_1 + x_2 + y_1 + y_2 < R^{(0)} - \lambda_x\}. \end{aligned}$$

Adding all differential equations in (3) yields

$$(x_1 + x_2 + y_1 + y_2)'(t) = [f(R(t)) - d_x](x_1 + x_2)(t) - d_y(y_1 + y_2)(t). \tag{11}$$

If the trajectory $(x_1(t), x_2(t), y_1(t), y_2(t))$ stays in Ω_1 for $t \geq T$ where T is large, then $(x_1 + x_2 + y_1 + y_2)(t)$ is decreasing, since

$$\begin{aligned}
&R^{(0)} > x_1 + x_2 + y_1 + y_2 > R^{(0)} - \lambda_x \\
\Rightarrow &R^{(0)} - (x_1 + x_2 + y_1 + y_2) < R^{(0)} - (R^{(0)} - \lambda_x) = \lambda_x \\
\Leftrightarrow &f(R) < d_x.
\end{aligned}$$

From (11) and Lemma 3.2, we get $(x_1 + x_2 + y_1 + y_2)' \to 0$ as $t \to \infty$, and it follows that $(y_1 + y_2)(t) \to 0$ as $t \to \infty$. If the trajectory $(x_1(t), x_2(t), y_1(t), y_2(t))$ passes through hyperplane P, then obviously it enters the region Ω_2 and stays there for rest of time.

Now we focus on the behavior of the trajectory in Ω_2. In this region we have

$$x_1 + x_2 + y_1 + y_2 < R^{(0)} - \lambda_x < (\lambda_x + 2\lambda_y) - \lambda_x = 2\lambda_y. \tag{12}$$

Note that

$$\begin{aligned}
\frac{y_1'}{y_1} + \frac{y_2'}{y_2} &= g(x_1) + g(x_2) - 2d_y \\
&= \frac{\mu x_1}{K + x_1} + \frac{\mu x_2}{K + x_2} - 2d_y \\
&= \frac{\mu x_1(K + x_2) + \mu x_2(K + x_1)}{(K + x_1)(K + x_2)} - 2d_y \\
&= \frac{P(x_1, x_2)}{(K + x_1)(K + x_2)}.
\end{aligned}$$

where

$$\begin{aligned}
P(x_1, x_2) =&\mu x_1(K + x_2) + \mu x_2(K + x_1) - 2d_y(K + x_1)(K + x_2) \\
=&\mu x_1(K + x_2) + \mu x_2(K + x_1) - 2\frac{\mu\lambda_y}{K + \lambda_y}(K^2 + (x_1 + x_2)K + x_1 x_2) \\
=&\frac{1}{K + \lambda_y}\left[\mu K\left((x_1 + x_2)(K - \lambda_y) + 2(x_1 x_2 - K\lambda_y)\right)\right].
\end{aligned}$$

Thus from (12)

$$\begin{aligned}
P(x_1, x_2) \leq&\frac{\mu K}{K + \lambda_y}\left[(x_1 + x_2)(K - \lambda_y) + \frac{(x_1 + x_2)^2}{2} - 2K\lambda_y\right] \\
<&\frac{\mu K}{K + \lambda_y}\left[(x_1 + x_2)(K - \lambda_y) + \lambda_y(x_1 + x_2) - 2K\lambda_y\right] \\
=&\frac{\mu K}{K + \lambda_y}\left[(x_1 + x_2)K - 2K\lambda_y\right] \\
<&\frac{\mu K}{K + \lambda_y}\left[2\lambda_y K - 2K\lambda_y\right] \\
=&0.
\end{aligned}$$

From above, we conclude that $\frac{y_1'(t)}{y_1(t)} + \frac{y_2'(t)}{y_2(t)} < -\delta_1 < 0$ for some $\delta_1 > 0$ for all $t \geq 0$. Then $y_1(t)y_2(t) \to 0$ exponentially as $t \to \infty$.

□

Conjecture 1. *If* $\lambda_x+\lambda_y < R^{(0)} < \lambda_x+2\lambda_y$*, the trajectory* $(x_1(t), x_2(t), y_1(t), y_2(t))$ *satisfies that* $\lim_{t\to\infty} y_i(t) = 0$ *for* $i = 1, 2$.

For the case $R^{(0)} > \lambda_x + 2\lambda_y$, the global asymptotic behavior of the solution of (3) is more complicated. In this case the interior equilibrium E_c exists and it is either a repeller or a saddle point with two dimensional stable manifold or it satisfies Lemma 4.1 (c). The following theorem describes what the stable manifold is.

Theorem 4.4. *Let* $R^{(0)} > \lambda_x+2\lambda_y$*. Assume* $x_1(0) = x_2(0) > 0$*,* $y_1(0) = y_2(0) > 0$*.*
(a) If $R^{(0)} < R^*$ *then* $(x_1(t), x_2(t), y_1(t), y_2(t)) \to E_c$ *as* $t \to \infty$*,*
(b) If $R^{(0)} > R^*$ *then there exists a limit cycle* Γ*,*
where R^* *is the unique root of the equation of* $R^{(0)}$*,*

$$\frac{\mu}{(K + x^*)^2} y^* = \frac{2ma}{(a + R^{(0)} - 2(x^* + y^*))^2},$$

where $x^* = \lambda_y$ *and* $y^* = y^*(R^{(0)})$ *satisfies* $f(R^{(0)} - 2x^* - 2y) - d_x = d_y \frac{y}{x^*}$.

Remark 3. We conjecture $(x_1(t), x_2(t), y_1(t), y_2(t))$ approaches the unique limit cycle Γ as $t \to \infty$.

Proof. Let $(x^*(t), y^*(t))$ be the solution of the initial value problem

$$\begin{aligned} x'(t) =& (f(R^{(0)} - 2(x + y)(t)) - d_x)x(t) - g(x(t))y(t),\\ y'(t) =& (g(x(t)) - d_y)y(t),\\ & x(0) = x_1(0) = x_2(0) > 0, y(0) = y_1(0) = y_2(0) > 0. \end{aligned}$$

Then $(x^*(t), x^*(t), y^*(t), y^*(t))$ satisfies (3). By uniqueness of the solution of an ordinary differential equation, it follows that $x_1(t) \equiv x_2(t) \equiv x^*(t)$, $y_1(t) \equiv y_2(t) \equiv y^*(t)$.

Note that

$$\begin{aligned} f(R^{(0)} - 2(x + y)) =& \frac{m(R^{(0)} - 2(x + y))}{a + (R^{(0)} - 2(x + y))}\\ =& \frac{2m\left(\frac{R^{(0)}}{2} - (x + y)\right)}{2\frac{a}{2} + 2\left(\frac{R^{(0)}}{2} - (x + y)\right)}. \end{aligned}$$

One makes the following changes:

$$\overline{R^{(0)}} \to \frac{R^{(0)}}{2},\ \bar{a} \to \frac{a}{2},\ \overline{\lambda_x} \to \frac{\lambda_x}{2}.$$

Substituting these into above differential equations and dropping the bars yields

$$\begin{aligned} x'(t) =& (f(R^{(0)} - (x + y)(t)) - d_x)x(t) - g(x(t))y(t),\\ y'(t) =& (g(x(t)) - d_y)y(t),\\ & x(0) > 0,\ y(0) > 0. \end{aligned}$$

It is the same as the system (4). Thus we complete the proof. □

Theorem 4.4 shows that when $R^{(0)} < R^*$ the two dimensional stable manifold of the saddle point E_c contains $\{(x_1, x_2, y_1, y_2) \in \mathbb{R}^4_+ : x_1 = x_2, y_1 = y_2\}$. In the following Theorem 4.5, we show that for the system (3) if the Hopf bifurcation occurs, it must occur at $R^{(0)} = R^*$. The proof is deferred to appendix 6.

Theorem 4.5. *For the system (3) Hopf bifurcation occurs only at $R^{(0)} = R^*$, where R^* is defined in Theorem 4.4.*

5. Discussion and numerical study.

Our analytic study on the mathematical model of the two parallel food chains (3) reveals some interesting outcomes as the input concentration of the nutrient $R^{(0)}$ varies. If $0 < R^{(0)} < \lambda_x$ then both of the prey species and both of the predator species go extinct (Theorem 4.2 (a)). If $\lambda_x < R^{(0)} < \lambda_x + \lambda_y$ then the prey species survive and the predator species go extinct with limiting value $E_x = (x_1^*, x_2^*, 0, 0)$ for some $x_1^*, x_2^* > 0$ satisfying $x_1^* + x_2^* = R^{(0)} - \lambda_x$ (Theorem 4.2 (b)). If $\lambda_x + \lambda_y < R^{(0)} < \lambda_x + 2\lambda_y$ then from Theorem 4.3 the predator species y_1 and y_2 satisfy $\lim_{t\to\infty} y_1(t)y_2(t) = 0$. For the case $R^{(0)} > \lambda_x + 2\lambda_y$, if the initial populations satisfy $x_1(0) = x_2(0) > 0$, $y_1(0) = y_2(0) > 0$ then the trajectory approaches $E_c = (x_c, x_c, y_c, y_c)$ as $t \to \infty$ provided $\lambda_x + 2\lambda_y < R^{(0)} < R^*$ (Theorem 4.4 (a)) or the trajectory approaches a unique limit cycle provided $R^{(0)} > R^*$ (Theorem 4.4 (b)).

In the case $\lambda_x + \lambda_y < R^{(0)} < \lambda_x + 2\lambda_y$, we know that y_1 and y_2 satisfy $\lim_{t\to\infty} y_1(t)y_2(t) = 0$. Furthermore, by extensive numerical simulations, we conjecture that y_1 and y_2 approach zero as time goes to infinity (See Fig 4).

For the case $R^* > R^{(0)} > \lambda_x + 2\lambda_y$, we present some numerical simulations with varying initial conditions (Fig 5). The interior equilibrium E_c is a saddle point with two-dimensional stable manifold. Each figure in (a)–(e) shows the same behavior for the solutions of the system (3). The prey populations $x_1(t)$ and $x_2(t)$ alternatively exchange between the maximum x_h and minimum x_l, $x_h + x_l = R^{(0)} - \lambda_x$. When the prey species $x_1(t)$ ($x_2(t)$) decreases rapidly from the maximum x_h to the minimum x_l, the prey species $x_2(t)$ ($x_1(t)$) increases rapidly from the minimum x_l to the maximum x_h and predator species $y_1(t)$ ($y_2(t)$) behaves like a pulse when $x_1(t)$ ($x_2(t)$) exchanges from x_h to x_l.

Moreover, the prey population $x_1(t)$, $x_2(t)$ stays at the maximum x_h and the minimum x_l longer and longer as time becomes large. We may explain this phenomena by Fig 6. From Fig 2, for each equilibrium P on the segment $\overline{AD}$ the one-dimensional unstable manifold $W^-(P)$ points into positive y_1 direction with zero y_2-component. $W^-(P)$ will approach the line $x_1 + x_2 = R^{(0)} - \lambda_x$ in x_1-x_2 plane (Theorem 3.3). Similarly for each equilibrium Q on the segment $\overline{BC}$, the one-dimensional unstable manifold $W^-(Q)$ points into positive y_2 direction with zero y_1-component. We conjecture that there exists a unique heteroclinic orbit Γ_1 from $P = (x_h, x_l, 0, 0)$ to $Q = (x_l, x_h, 0, 0)$ and a unique heteroclinic orbit Γ_2 from $Q = (x_l, x_h, 0, 0)$ to $P = (x_h, x_l, 0, 0)$ (See Fig 6 (a), (b)). Each time that the orbit $\gamma(t) = (x_1(t), x_2(t), y_1(t), y_2(t))$ approaches the equilibria $(x_h, x_l, 0, 0)$ and $(x_l, x_h, 0, 0)$, it stays there successively longer and longer. We note that in Fig 5 (f), the initial conditions satisfies $x_1(0) = x_2(0)$, $y_1(0) = y_2(0)$, i.e. $\gamma(0)$ lies on the stable manifold of the interior equilibrium E_c, the trajectory $\gamma(t)$ approaches E_c as $t \to \infty$.

In Figure 7 the input concentration $R^{(0)}$ satisfies $R^{(0)} > R^*$ and the interior equilibrium E_c is a repeller (i.e. each eigenvalue of the variational matrix $J(E_c)$ has positive real parts). In this case the behavior of the orbit $\gamma(t)$ is similar to above case except that $x_h \approx R^{(0)} - \lambda_x$ and $x_l \approx 0$. Figure 7 (a)–(e) show the prey population $x_1(t)$, $x_2(t)$ alternatively exchange between x_h and x_l and the predator population $y_1(t)$, $y_2(t)$ increase and decrease rapidly when prey population exchange their values. We note that Figure 7 (f) shows that $x(t) = x_1(t) = x_2(t)$ and $y(t) = y_1(t) = y_2(t)$ oscillate periodically when $x_1(0) = x_2(0)$, $y_1(0) = y_2(0)$.

In [9, 11, 2] the authors studied the competition of three species with same intrinsic growth rate

$$\begin{aligned}
x_1' &= x_1(1 - x_1 - \alpha_1 x_1 - \beta_1 x_3), \\
x_2' &= x_2(1 - \beta_2 x_1 - x_2 - \alpha_2 x_3), \\
x_3' &= x_3(1 - \alpha_3 x_1 - \beta_3 x_2 - x_3), \\
& x_1(0) > 0,\ x_2(0) > 0,\ x_3(0) > 0,
\end{aligned} \tag{13}$$

where the parameters $\alpha_i,\ \beta_i$, satisfy

$$0 < \alpha_i < 1 < \beta_i,\ i = 1,\ 2,\ 3. \tag{14}$$

The condition (14) implies that there exists a heteroclinic orbit O_3 on the x_1-x_2 plane from $e_2 = (0, 1, 0)$ to $e_1 = (1, 0, 0)$, a heteroclinic orbit O_2 on the x_1-x_3 plane from e_1 to $e_3 = (0, 0, 1)$ and a heteroclinic orbit O_1 on the x_2-x_3 plane from e_3 to e_2.

The system (13) is referred to as the asymmetric May-Leonard model or the rock-paper-scissors game. When $\alpha_1 = \alpha_2 = \alpha_3,\ \beta_1 = \beta_2 = \beta_3$, (13) is referred to as the symmetric May-Leonard model. Let $A_i = 1-\alpha_i,\ B_i = \beta_i - 1$. If $A_1A_2A_3 < B_1B_2B_3$ then it was shown [2, 11], the heteroclinic cycle $O = \bigcup_{i=1}^{3} O_i$ is an attractor.

The system (3) exhibits similar behavior as (13) for the case $R^{(0)} > \lambda_x + 2\lambda_y$ with some parameters ($m = 1.5$, $a = 0.3$, $\mu = 1.5$, $K = 0.5$, $d_x = d_y = 1$).

For the case $R^{(0)} > \lambda_x + 2\lambda_y$, if the initial populations for either prey or predator are not identical, then from our extensive numerical simulations there are many different kinds of behaviors for the trajectory of the system (3). The trajectory may approach a unique heteroclinic orbit in some parameter range as we discuss above (See Fig 5 and Fig 7). The trajectory may approach a limit cycle (See Fig 8) in some parameter range. It is possible that the trajectory is chaotic in some parameter range (See Fig 9). For fixed $R^{(0)}$ we denoted y_1^j as the j-th local maximum of $y_1(t)$ for $t \in [1000, 2000]$. In Fig 10, we plot the orbit diagram as $R^{(0)}$ varies.

We note that in [14] Vandermeer studied a two-prey and two-predator system with "switch" predation mechanism. The behavior of the system also exhibits periodic oscillation and chaotic behavior as our system (3) does.

There are still many open problems left for future investigation. We list as followings:

- **(Q1):** Under the assumption $\lambda_x + \lambda_y < R^{(0)} < \lambda_x + 2\lambda_y$, is it true that $y_1(t) \to 0$ and $y_2(t) \to 0$ as $t \to \infty$.
- **(Q2):** Existence and stability of hetroclinic orbit.
- **(Q3):** When does the period doubling routes to chaos occur?
- **(Q4):** How does the asymptotic behavior change when the two food chains are not perfectly symmetrical?

6. **Appendix.**

Proof of Lemma 4.1. By routine computation, the characteristic polynomial of $J(E_c)$ is

$$\lambda^4 + A_1\lambda^3 + A_2\lambda^2 + A_3\lambda + A_4 = 0, \tag{15}$$

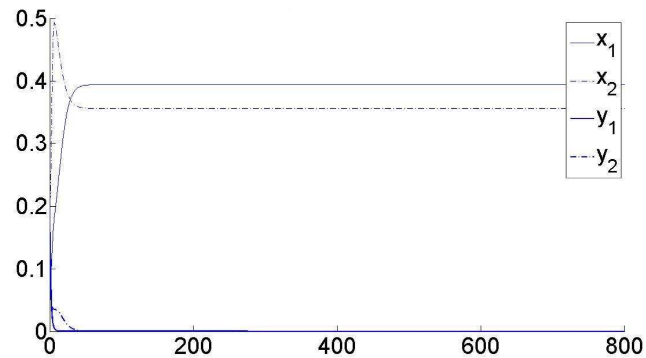

Figure 4: $R^{(0)} = 1$, $m = 2.2$, $a = 0.3$, $\mu = 1.8$, $K = 0.4$, $d_x = d_y = 1$, then $\lambda_x = 0.25$, $\lambda_y = 0.5$, $0.75 = \lambda_x + \lambda_y < 1 = R^{(0)} < \lambda_x + 2\lambda_y = 1.25$. The initial conditions are : $x_1(0) = 0.1$, $x_2(0) = 0.2$, $y_1(0) = 0.2$, $y_2(0) = 0.1$.

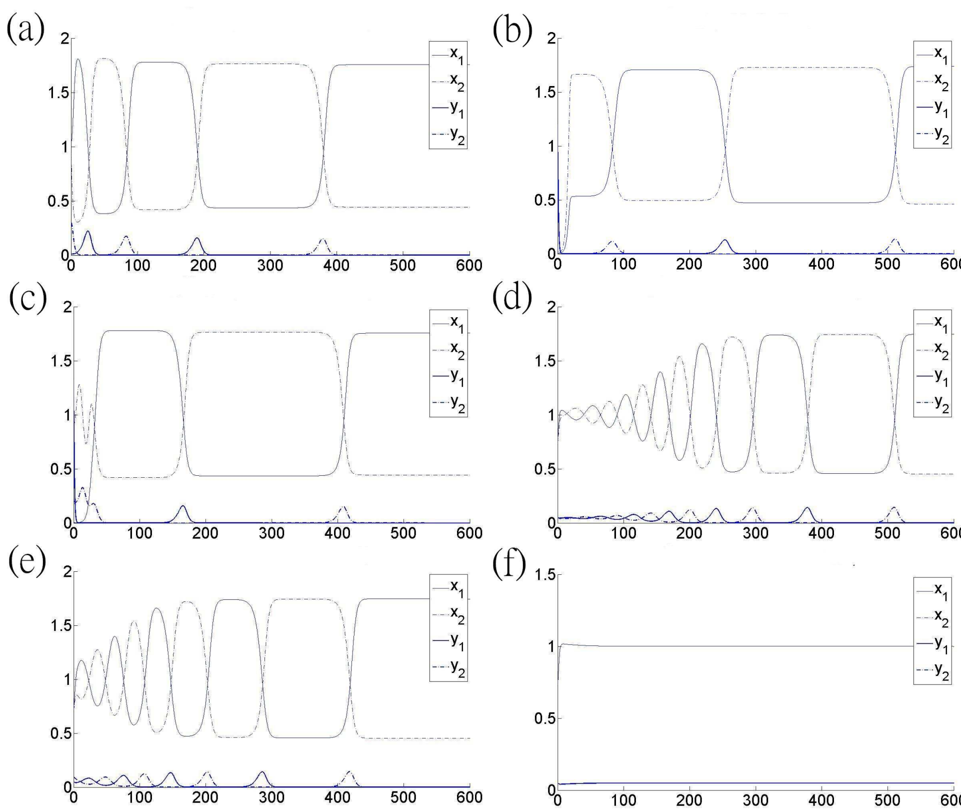

Figure 5: $R^{(0)} = 2.8$, $m = 1.5$, $a = 0.3$, $\mu = 1.5$, $K = 0.5$, $d_x = d_y = 1$. Then $\lambda_x = 0.6$, $\lambda_y = 1$, $R^* = 4.435 > R^{(0)} = 2.8 > \lambda_x + 2\lambda_y = 2.6$, $E_c = (1, 1, 0.05, 0.05)$. The initial conditions $(x_1(0), x_2(0), y_1(0), y_2(0))$ are (a) (1.1,1.05,0.01,0.3), (b) (0.06,0.12,1.2,1.03), (c) (0.05,1.1,1.32,0.2), (d) (0.75,0.7,0.05,0.05), (e)(0.7,0.7,0.05,0.1), (f) (0.7,0.7,0.05,0.05).

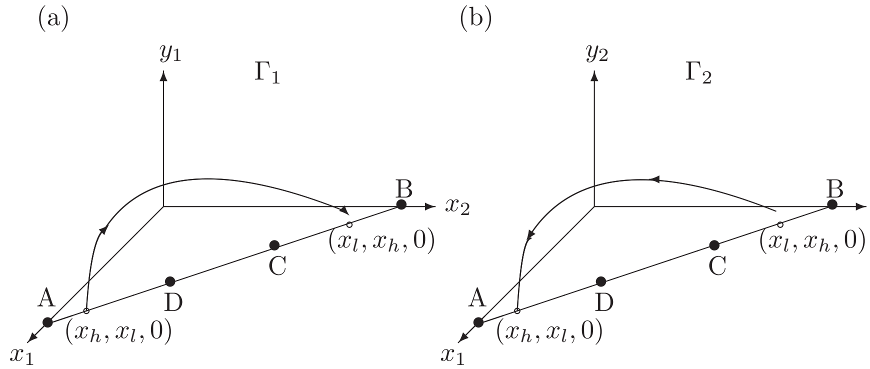

Figure 6

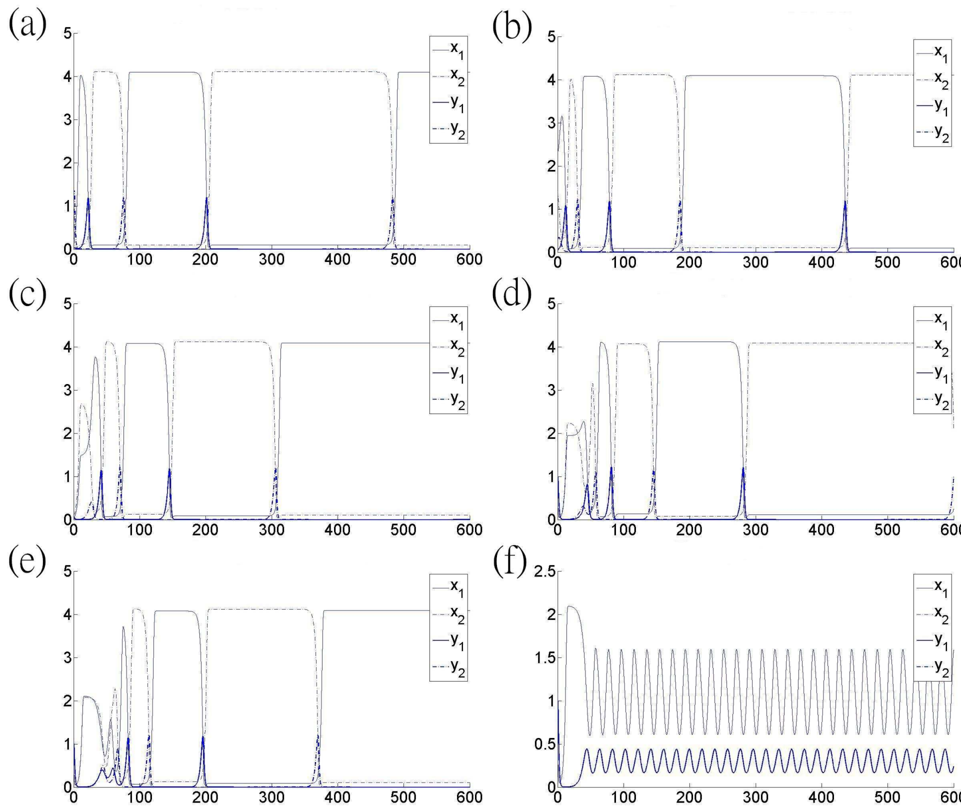

Figure 7: $R^{(0)} = 4.8$, $m = 1.5$, $a = 0.3$, $\mu = 1.5$, $K = 0.5$, $d_x = d_y = 1$, $E_c = (1, 1, 0.3175, 0.3175)$. The initial conditions $(x_1(0), x_2(0), y_1(0), y_2(0))$ are (a) (0.2,0.6,0.05,1.3), (b) (2.3,1.5,0.05,0.3), (c) (0.05,0.1,0.08,0.1), (d) (0.6,0.6,1.1,1.05), (e) (0.65,0.6,1.1,1.1), (f) (0.6,0.6,1.1,1.1).

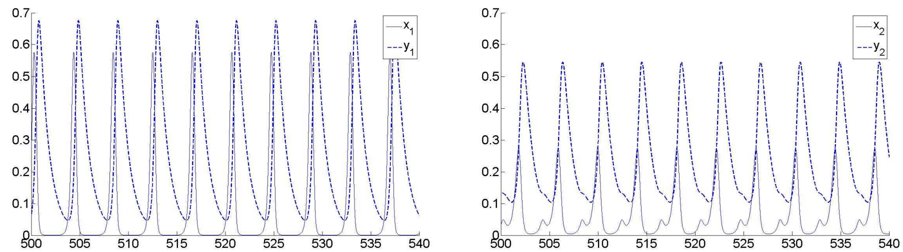

Figure 8: $R^{(0)} = 1.05$, $m = 10$, $a = 0.3$, $\mu = 10$, $K = 0.5$, $d_x = d_y = 1$, then $\lambda_x = 0.0333$, $\lambda_y = 0.0556$. The initial conditions $(x_1(0), x_2(0), y_1(0), y_2(0))$ are (0.1,0.2,0.2,0.1).

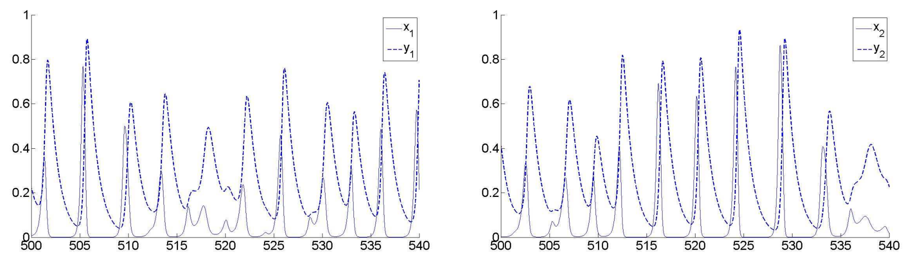

Figure 9: $R^{(0)} = 1.3$, $m = 10$, $a = 0.3$, $\mu = 10$, $K = 0.5$, $d_x = d_y = 1$, then $\lambda_x = 0.0333$, $\lambda_y = 0.0556$. The initial conditions $(x_1(0), x_2(0), y_1(0), y_2(0))$ are (0.1,0.2,0.2,0.1).

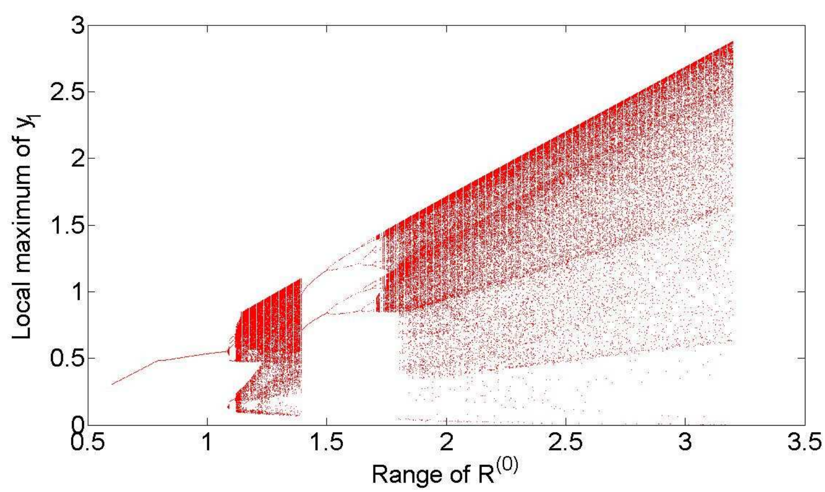

Figure 10: Fixed $m = 10$, $a = 0.3$, $\mu = 10$, $K = 0.5$, $d_x = d_y = 1$, then $\lambda_x = 0.0333, \lambda_y = 0.0556$. The range of $R^{(0)}$ is from 0.6 to 3.2.

where

$$\begin{aligned} A_1 =& -2p, \\ A_2 =& p^2 - q^2 - 2rs, \\ A_3 =& 2r(ps - q^2), \\ A_4 =& r^2(s^2 - q^2). \end{aligned} \tag{16}$$

The equation (15) can be rewritten as

$$(\lambda^2 + a_1\lambda + b_1)(\lambda^2 + a_2\lambda + b_2) = 0. \tag{17}$$

Then eigenvalues of $J(E_c)$ are the roots of

$$\lambda^2 + a_1\lambda + b_1 = 0,$$
$$\lambda^2 + a_2\lambda + b_2 = 0.$$

Let the roots of first and second equations be z_1, z_2 and z_3, z_4 respectively. Comparing (15) and (17) yields

$$\begin{aligned} A_1 =& a_1 + a_2 = -2p, \\ A_2 =& a_1a_2 + b_1 + b_2 = p^2 - q^2 - 2rs, \\ A_3 =& a_1b_2 + b_1a_2 = 2r(ps - q^2), \\ A_4 =& b_1b_2 = r^2(s^2 - q^2). \end{aligned} \tag{18}$$

From (11), it is easy to show that $b_1b_2 = r^2(s^2 - q^2) > 0$. Thus 0 is not an eigenvalue. If $Re(z_i) = 0$ for all $i = 1, 2, 3, 4$ then $p = 0$ and there are two pair of pure imaginary eigenvalues, therefore (17) becomes $(\lambda^2 + b_1)(\lambda^2 + b_2) = 0$ and $A_3 = 0$. However, $A_3 = -2rq^2 = -2g'(\lambda_y)y_c[f'(R_c)\lambda_y]^2 < 0$, a contradiction. From above observation, we know that there are at most one pair of pure imaginary eigenvalues.

On the other hand, $b_1b_2 > 0$ implies that both of b_1 and b_2 are either positive or negative. If $b_1 < 0,\ b_2 < 0$ then we have four real roots with two positive and two negative. Hence from now on, we only consider the case $b_1 > 0,\ b_2 > 0$.

The following lemma is useful to the proof of Lemma 4.1.

Lemma 6.1. *p as a function of $R^{(0)}$, $p(R^{(0)})$ is increasing in $R^{(0)}$ and there exists a $R^{**} \in (\lambda_x + 2\lambda_y, \infty)$ such that $p(R^{**}) = 0$.*

Proof. From (11) we let

$$\begin{aligned} p(R^{(0)}) =& f(R^{(0)} - 2\lambda_y - 2y_c(R^{(0)})) - d_x \\ & - f'(R^{(0)} - 2\lambda_y - 2y_c(R^{(0)}))\lambda_y - g'(\lambda_y)y_c(R^{(0)}). \end{aligned}$$

Differentiating $p(R^{(0)})$ with respect to $R^{(0)}$ yields

$$\begin{aligned} \frac{dp(R^{(0)})}{dR^{(0)}} =& f'(R^{(0)} - 2\lambda_y - 2y_c(R^{(0)})) \cdot (1 - 2y_c'(R^{(0)})) \\ & - f''(R^{(0)} - 2\lambda_y - 2y_c(R^{(0)}))\lambda_y \cdot (1 - 2y_c'(R^{(0)})) - g'(\lambda_y)y_c'(R^{(0)}). \end{aligned}$$

From (9) y_c satisfies

$$f(R^{(0)} - 2\lambda_y - 2y_c(R^{(0)})) - d_x = \frac{d_y}{\lambda_y} y_c(R^{(0)}). \tag{19}$$

Thus we have

$$f'(R^{(0)} - 2\lambda_y - 2y_c(R^{(0)})) \cdot (1 - 2y_c'(R^{(0)})) = \frac{d_y}{\lambda_y} y_c'(R^{(0)}), \tag{20}$$

$$y_c'(R^{(0)}) = \frac{f'(R^{(0)} - 2\lambda_y - 2y_x(R^{(0)}))}{\frac{d_y}{\lambda_y} + 2f'(R^{(0)} - 2\lambda_y - 2y_x(R^{(0)}))} > 0. \tag{21}$$

From (20) we have

$$\begin{aligned}
&f'(R^{(0)} - 2\lambda_y - 2y_c(R^{(0)})) \cdot (1 - 2y_c'(R^{(0)})) - g'(\lambda_y) y_c'(R^{(0)}) \\
=&\frac{d_y}{\lambda_y} y_c'(R^{(0)}) - g'(\lambda_y) y_c'(R^{(0)}) \\
=&y_c'(R^{(0)}) \left[\frac{g(\lambda_y)}{\lambda_y} - g'(\lambda_y) \right] \\
=&y_c'(R^{(0)}) \frac{\mu}{K + \lambda_y} \frac{\lambda_y}{K + \lambda_y} > 0.
\end{aligned}$$

From above and $f'' < 0$ we have $\frac{dp(R^{(0)})}{dR^{(0)}} > 0$ i.e. $p(R^{(0)})$ is strictly increasing in $R^{(0)}$. Next, we show that there is a unique root of $p(R^{(0)}) = 0$. When $R^{(0)} = \lambda_x + 2\lambda_y$, (19) implies $y_c(R^{(0)}) = 0$. Then $p(R^{(0)}) = -f'(\lambda_x)\lambda_y < 0$. Consider the case $R^{(0)} \to \infty$. From (19) and (21) it follows that $\frac{d_y}{\lambda_y} y_c(R^{(0)}) \le f(R^{(0)} - 2\lambda_y) - d_x < m - d_x$, and $\lim_{R^{(0)} \to \infty} y_c(R^{(0)}) = y_c(\infty) = \frac{\lambda_y}{d_y}(m - d_x)$. We note that

$$\begin{aligned}
p(R^{(0)}) =&f(R^{(0)} - 2\lambda_y - 2y_c(R^{(0)})) - d_x \\
&- f'(R^{(0)} - 2\lambda_y - 2y_c(R^{(0)}))\lambda_y - g'(\lambda_y) y_c(R^{(0)}) \\
=&\frac{m(R^{(0)} - 2\lambda_y - 2y_c(R^{(0)}))}{a + R^{(0)} - 2\lambda_y - 2y_c(R^{(0)})} - d_x \\
&- \frac{ma}{(a + R^{(0)} - 2\lambda_y - 2y_c(R^{(0)}))^2} \lambda_y - \frac{\mu K}{(K + \lambda_y)^2} y_c(R^{(0)}) \\
=&\frac{m(1 - \frac{2\lambda_y + 2y_c(R^{(0)})}{R^{(0)}})}{\frac{a}{R^{(0)}} + 1 - \frac{2\lambda_y + 2y_c(R^{(0)})}{R^{(0)}}} - d_x \\
&- \frac{\frac{ma}{(R^{(0)})^2}}{\left(\frac{a}{R^{(0)}} + 1 - \frac{2\lambda_y + 2y_c(R^{(0)})}{R^{(0)}} \right)^2} \lambda_y - \frac{\mu K}{(K + \lambda_y)^2} y_c(R^{(0)}) \\
\to& m - d_x - \frac{\mu K}{(K + \lambda_y)^2} y_c(\infty) \text{ as } R^{(0)} \to \infty.
\end{aligned}$$

Thus

$$\begin{aligned}
\lim_{R^{(0)} \to \infty} p(R^{(0)}) =&p(\infty) \\
=&\left[\frac{d_y}{\lambda_y} - \frac{\mu K}{(K + \lambda_y)^2} \right] y_c(\infty) \\
=&\frac{\mu \lambda_y}{(K + \lambda_y)^2} y_c(\infty) > 0.
\end{aligned}$$

Hence $p(\infty) = \frac{\mu}{(K + \lambda_y)^2} \lambda_y y_c(\infty) > 0$. Therefore there exists a unique root $R^{**} > \lambda_x + 2\lambda_y$ s.t. $p(R^{**}) = 0$. $\square$

In the following we discuss the properties of eigenvalues of $J(E_c)$ as p varies.

Case 1: If $p = 0$ then $\sum_{i=1}^{4} Re(z_i) = 0$. From above, we note that it is impossible that $Re(z_i) = 0$ for all $i = 1, 2, 3, 4$. If there exist $Re(z_i) = 0$ for some i, then there is exactly a pair of pure imaginary eigenvalues. Assume $z_i = \pm i\beta$ and $z_3,\ z_4$ are real. Then $z_3 + z_4 = 0$, $b_2 = z_3 z_4 < 0$, a contradiction to $b_2 > 0$. Thus $Re(z_i) \neq 0$ for all i. From $p = 0$ we have $a_1 = -a_2$ and two of real part of z_i are positive, two are negative.

Case 2: If $p > 0$, then

$$\begin{aligned}
&a_1 + a_2 = -2p < 0,\\
&a_1 b_2 + b_1 a_2 = 2r(ps - q^2) < 0.
\end{aligned}$$

W.L.O.G let $|a_1| \geq |a_2|$, there are three subcases. (i) $a_1 a_2 < 0 \Leftrightarrow a_1 < 0,\ a_2 > 0$. (ii) $a_1 a_2 > 0 \Leftrightarrow a_1 < 0,\ a_2 < 0$. (iii) $a_1 a_2 = 0 \Leftrightarrow a_1 < 0,\ a_2 = 0$.

For subcase (i) $a_1 < 0,\ a_2 > 0$, the eigenvalues $z_i,\ i = 1, 2, 3, 4$ satisfy

$$\begin{cases} z_1 z_2 = b_1 > 0,\\ z_1 + z_2 = -a_1 > 0.\end{cases}$$
$$\begin{cases} z_3 z_4 = b_2 > 0,\\ z_3 + z_4 = -a_2 < 0.\end{cases}$$

From above we have that $z_1,\ z_2$ have positive real parts and $z_3,\ z_4$ have negative real parts.

For subcase (ii) $a_1 < 0,\ a_2 < 0$, all 4 roots have positive real part.

For subcase (iii) $a_1 a_2 = 0 \Leftrightarrow a_1 < 0,\ a_2 = 0$, then there is a pair of pure imaginary eigenvalues $z_3,\ z_4$. Other eigenvalues $z_1,\ z_2$ have positive real parts.

Case 3: If $p < 0$, then $a_1 + a_2 = -2p > 0$. Similarly, let $|a_1| \geq |a_2|$ and consider the following subcases. (i) $a_1 a_2 < 0 \Leftrightarrow a_1 > 0,\ a_2 < 0$. (ii) $a_1 a_2 > 0 \Leftrightarrow a_1 > 0,\ a_2 > 0$. (iii) $a_1 a_2 = 0 \Leftrightarrow a_1 > 0,\ a_2 = 0$.

Similar to the discussion of Case 2, we have the following results. For the subcase (i) $a_1 > 0,\ a_2 < 0$, there are two roots with positive real parts and two with negative real parts. For subcase (ii) $a_1 > 0,\ a_2 > 0$ the real parts of all roots are negative. From Routh-Hurwitz criterion, we have $A_1 > 0,\ A_2 > 0,\ A_3 > 0$ and $A_4 > 0$ also $A_3(A_1 A_2 - A_3) > A_1^2 A_4$ ([3] p.55), or equivalently

$$\begin{aligned}
&-2p > 0,\\
&p^2 - q^2 - 2rs > 0,\\
&2r(ps - q^2) > 0,\\
&r^2(s^2 - q^2) > 0,\\
&(2r(ps - q^2))((-2p)(p^2 - q^2 - 2rs) - (2r(ps - q^2))) > (-2p)^2(r^2(s^2 - q^2)).
\end{aligned} \tag{22}$$

Assume (22) holds then from (11) and (18)

$$\begin{aligned}
&0 < a_1 + a_2 = -2p,\\
&0 < a_1 a_2 + b_1 + b_2 = p^2 - q^2 - 2rs \Rightarrow q^2 - p^2 < -2rs,\\
&0 < a_1 b_2 + b_1 a_2 = 2r(ps - q^2) \Rightarrow q^2 - ps < 0.
\end{aligned}$$

Note that

$$\begin{aligned}&(-2p)(p^2-q^2-2rs)-(2r(ps-q^2))\\=&2[p(q^2-p^2)+prs+q^2r]\\<&2[p(-2rs)+prs+q^2r]\\=&2[r(q^2-ps)]\\<&0.\end{aligned}$$

Thus

$$(2r(ps-q^2))((-2p)(p^2-q^2-2rs)-(2r(qs-q^2)))<0<(-2p)^2(r^2(s^2-q^2)),$$

which contradicts (22). Thus subcase (ii) cannot hold.

(iii) $a_1>0,\ a_2=0$, then $a_1b_2+b_1a_2=a_1b_2>0$. On the other hand $a_1b_2+b_1a_2=2r(ps-q^2)\le 0$, a contradiction.

From the above discussion, we complete the proof of Lemma 4.1. □

Proof of Theorem 4.5. From above discussion, Hopf bifurcation doesn't occur at $p\le 0$ i.e. $R^{(0)}\le R^{**}$.

If we reverse the time $t\to -t$ in the system (3), then the characteristic polynomial of $J(E_c)$ becomes

$$\lambda^4-A_1\lambda^3+A_2\lambda^2-A_3\lambda+A_4=0. \tag{23}$$

From (17) and Routh-Hurwitz criterion, $Re(\lambda)<0$ if and only if

$$\begin{aligned}B_1=&-A_1=2p>0,\\B_2=&A_2=p^2-q^2-2rs>0,\\B_3=&-A_3=-2r(ps-q^2)>0,\\B_4=&A_4=r^2(s^2-q^2)>0,\\\Delta=&B_3(B_1B_2-B_3)-B_1^2B_4\\=&[-2r(ps-q^2)][2p(p^2-q^2-2rs)+2r(ps-q^2)]-(2p)^2r^2(s^2-q^2)>0.\end{aligned}$$

$B_1>0,\ B_3>0$ and $B_4>0$ hold spontaneously. If $\Delta>0$, then $B_2>0$. Thus $\Delta>0$ if and only if all eigenvalues λ have strictly negative real parts. We claim that $\Delta=0$ if and only if there are two purely imaginary eigenvalues and two eigenvalues with negative real parts. Thus, if $\Delta<0$ then there are two eigenvalues with positive real parts and two eigenvalues with negative real parts. Therefore bifurcation occurs as $\Delta=0$.

To prove the claim, we use the similar discussion in the proof of Lemma 4.1, (23) can be rewritten as the form (17).

$$\begin{aligned}&\Delta=0\\\Leftrightarrow&B_3(B_1B_2-B_3)-B_1^2B_4=0\\\Leftrightarrow&(a_1b_2+a_2b_1)[(a_1+a_2)(a_1a_2+b_1+b_2)-(a_1b_2+a_2b_1)]-(a_1+a_2)^2(b_1b_2)=0\\\Leftrightarrow&a_1a_2[(b_1-b_2)^2+(a_1+a_2)(a_1b_2+a_2b_1)]=0.\end{aligned}$$

It is easy to get the sufficient direction. Conversely, we consider

$$\begin{aligned}\Delta=&[-2r(ps-q^2)][2p(p^2-q^2-2rs)+2r(ps-q^2)]-(2p)^2r^2(s^2-q^2)\\=&4r[(p-q)(p+q)(pq^2-sp^2+rq^2)].\end{aligned}$$

If $\Delta = 0$, then $p = -q$ and it implies $a_1b_2 + a_2b_1 = B_3 = 2rq(s+q) > 0$. Hence $[(b_1 - b_2)^2 + (a_1 + a_2)(a_1b_2 + a_2b_1)] > 0$ and $a_1a_2 = 0$. The claim holds.

From above $\Delta > 0$ if and only if $p + q > 0$, i.e. $(f(R_c) - d_x) - 2f'(R_c)\lambda_y - g'(\lambda_y)y_c > 0$.

$$\begin{aligned} &(f(R_c) - d_x) - 2f'(R_c)\lambda_y - g'(\lambda_y)y_c \\ =&\frac{1}{\lambda_y}d_y y_c - 2\frac{ma}{(a+R_c)^2}\lambda_y - \frac{\mu K}{(K+\lambda_y)^2}y_c \\ =&\lambda_y\left[\frac{\mu}{(K+\lambda_y)^2}y_c - 2\frac{ma}{(a+R_c)^2}\right]. \end{aligned}$$

Thus $(f(R_c)-d_x)-2f'(R_c)\lambda_y-g'(\lambda_y)y_c > 0$ if and only if $\frac{\mu}{(K+\lambda_y)^2}y_c - 2\frac{ma}{(a+R_c)^2} > 0$. The latter is the criterion in Theorem 4.4 such that $R^{(0)} > R^*$. Therefore $\Delta > 0$ if and only if $R^{(0)} > R^*$. Thus if Hopf bifurcation occurs, it must occur at $R^{(0)} = R^*$. □

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