DISCRETE AND CONTINUOUS
DYNAMICAL SYSTEMS SERIES B
Volume **18**, Number **1**, January **2013**

doi:10.3934/dcdsb.2013.18.259

pp. **259–271**

# GLOBAL DYNAMICS AND BIFURCATIONS IN A FOUR-DIMENSIONAL REPLICATOR SYSTEM

Yuanshi Wang and Hong Wu

School of Mathematics and Computational Science
Sun Yat-sen University, Guangzhou 510275, China

Shigui Ruan

Department of Mathematics
University of Miami, Coral Gables, FL 33124-4250, USA

(Communicated by Yuan Lou)

Abstract. In this paper, the four-dimensional cyclic replicator system $\dot{u}_i = u_i[-(Bu)_i + \sum_{j=1}^{4} u_j(Bu)_j], 1 \leq i \leq 4$, with $b_1 = b_3$ is considered, in which the first row of the matrix $B$ is $(0\ b_1\ b_2\ b_3)$ and the other rows of $B$ are cyclic permutations of the first row. Our aim is to study the global dynamics and bifurcations in the system, and to show how and when all but one species go to extinction. By reducing the four-dimensional system to a three-dimensional one, we show that there is no periodic orbit in the system. For the case $b_1 b_2 < 0$, we give complete analysis on the global dynamics. For the case $b_1 b_2 \geq 0$, we extend some results obtained by Diekmann and van Gils (2009). By combining our work with that in Diekmann and van Gils (2009), we present the dynamics and bifurcations of the system on the whole $(b_1, b_2)$-plane. The analysis leads to explanations for the phenomena that in some semelparous species, all but one brood go extinct.

## 1. **Introduction.**

Consider the replicator system [9, 11]

$$\dot{u}_i = u_i[-(Bu)_i + \sum_{j=1}^{n} u_j(Bu)_j],\ i = 1, 2, ..., n, \tag{1}$$

in which $u$ is an $n$-dimensional vector in the simplex

$$\Sigma_n = \{u \in R^n : \sum_{j=1}^{n} u_j = 1, u_j \geq 0, j = 1, 2, ..., n\}.$$

In (1), $(Bu)_i$ is the $i$th component of the vector $Bu$, while $B$ is a circulant matrix

$$B = \begin{pmatrix} 0 & b_1 & \cdots & b_{n-1} \\ b_{n-1} & 0 & \cdots & b_{n-2} \\ \vdots & \vdots & \ddots & \vdots \\ b_1 & b_2 & \cdots & 0 \end{pmatrix}.$$

2010 *Mathematics Subject Classification.* 34C23, 92D25, 37N25.

*Key words and phrases.* Lotka-Volterra model, replicator system, periodic orbit, competition, semelparous population.

Y. Wang acknowledges support from NSF of Guangdong Province S2012010010320. S. Ruan acknowledges partial support from NSF grant DMS-1022728.

Thus the rows of $B$ are cyclic permutations of the first row. The system (1) is derived by Diekmann and van Gils [9] from the cyclic competition system

$$\dot{x}_i = x_i(1-(Ax)_i),\ x_i \geq 0,\ i=1,2,...,n, \tag{2}$$

in which $x_i$ denotes the population density of the $i$th year class of semelparous species. A species is called semelparous if each individual reproduces only once in its life and dies immediately after the reproduction. While the reproduction opportunity is unique per year and the length of the life cycle is just $n$ years, the individuals that reproduce in the $i$th year (modulo $n$) are the so-called $i$th year class, $i = 1, 2, ..., n$ [9]. In nature, there are various semelparous species such as cicadas, Pacific salmon and many other insects [3, 6, 7, 8, 13, 14, 15]. While different year classes of the species are identical except for their reproduction time, some of them are extinct during the evolution. If all but one year class are extinct in a species, the species is called periodical [2]. The most interesting periodical species is the 13th and 17th year cicadas of eastern North America. Applying to the population dynamics of semelparous species, a series of interesting questions have been put forward such as: what are the mechanisms that result in both the existence of only one brood and the selection of this brood; how these year classes could coexist, etc. [1, 4, 5, 16, 17].

In [9], Diekmann and van Gils obtained some interesting features of (2). For example, all year classes have the same intrinsic growth rate, and the interaction matrix $A$ is circulant

$$A = \begin{pmatrix} a_1 & a_2 & \cdots & a_n \\ a_n & a_1 & \cdots & a_{n-1} \\ \vdots & \vdots & \ddots & \vdots \\ a_2 & a_3 & \cdots & a_1 \end{pmatrix},\ a_i \geq 0,\ i=1,2,...,n,$$

in which $\frac{1}{a_1}$ denotes the carrying capacity of every year class and $\frac{a_i}{a_1}(i \neq 1)$ are the competitive degrees from other year classes.

System (1) is derived from (2) mainly by the projection $u_i = x_i/\sum_{j=1}^{n} x_j$ with (see [9], p.1163)

$$b_i = a_{i+1} - a_1,\ i=1,2,...,n-1. \tag{3}$$

While $x_i$ is the population density of the $i$th year class, $u_i$ denotes the fraction of the $i$th year class in the whole population. When $n = 2, 3$, the dynamics and bifurcations of (1) are completely determined by Diekmann and van Gils [9]. When $n = 4$, the dynamics and bifurcations of (1) are given in an almost complete picture in [9], where a series of novel Lyapunov functions are constructed. For the case $n = 4$, Wang et al. [18] showed the existence, growth and disappearance of periodic orbits near heteroclinic cycles when the parameters $b_1$, $b_2$ and $b_3$ vary in some critical areas.

In this paper, we focus on the global dynamics and bifurcations in system (1) when $n = 4$ and $b_1 = b_3$. Through a radial projection, we reduce the four-dimensional system to a three-dimensional one. Then we demonstrate that the $\omega$-limit sets of the system are contained in the $\omega$-limit sets of several two-dimensional systems, which are either Lotka-Volterra competitive systems or Lotka-Volterra cooperative systems. Through the dynamical behavior of the Lotka-Volterra systems, we present complete analysis on the global dynamics of the four-dimensional system: (i) there is no periodic orbit of the system; (ii) for the case $b_1b_2 < 0$, thorough analysis on the global dynamics is given; (iii) for the case $b_1b_2 \geq 0$, some results given by Diekmann and van Gils [9] are extended; (iv) global bifurcations of the system on the $(b_1, b_2)$-plane are shown. The analysis leads to the mechanisms how and when all but one species in the system go extinct and how this species is selected.

2. **The four-dimensional replicator system.** In this section, we describe the replicator system (1) when $n = 4$ and $b_1 = b_3$, and recall some previous results.

While $b_1 = b_3$, the matrix $B$ becomes

$$B = \begin{pmatrix} 0 & b_1 & b_2 & b_1 \\ b_1 & 0 & b_1 & b_2 \\ b_2 & b_1 & 0 & b_1 \\ b_1 & b_2 & b_1 & 0 \end{pmatrix}.$$

Then system (1) becomes

$$\dot{u}_i = u_i[-(Bu)_i + \sum_{j=1}^{4} u_j(Bu)_j], \; i = 1, 2, 3, 4, \tag{4}$$

where

$$(Bu)_1 = b_1(u_2 + u_4) + b_2u_3, \; (Bu)_2 = b_1(u_1 + u_3) + b_2u_4,$$
$$(Bu)_3 = b_1(u_2 + u_4) + b_2u_1, \; (Bu)_4 = b_1(u_1 + u_3) + b_2u_2.$$

Let $S$ be a circular matrix defined by

$$S = \begin{pmatrix} 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \end{pmatrix}.$$

**Theorem 2.1.** ([9]) *The replicator system (4) is equivariant with respect to $S$, i.e., if $u$ is a solution of (4), then $Su$ is also a solution of (4).*

Let $E_i$ be the equilibrium where only the $i$-th species persists. Let $E_{ij}$ be the equilibrium where only the $i$-th and $j$-th species persist. Let $E_{ijk}$ be the equilibrium where only the $i$-th, $j$-th and $k$-th species persist. Let $E_{1234}$ be the equilibrium where the four species coexist. Thus the equilibria of (4) (modulo cyclic permutation) are:

$$E_1 = (1, 0, 0, 0), \; E_{12} = (\frac{1}{2}, \frac{1}{2}, 0, 0), \; E_{13} = (\frac{1}{2}, 0, \frac{1}{2}, 0),$$
$$E_{123} = (\frac{b_1}{4b_1 - b_2}, \frac{2b_1 - b_2}{4b_1 - b_2}, \frac{b_1}{4b_1 - b_2}, 0), \; E_{1234} = (\frac{1}{4}, \frac{1}{4}, \frac{1}{4}, \frac{1}{4}).$$

Let (see Fig.1)

$$L = \{u \in \Sigma_4 : u_1 = u_3, \; u_2 = u_4\},$$
$$\Pi = \{u \in \Sigma_4 : u_1 + u_3 = u_2 + u_4\}.$$

**Theorem 2.2.** ([9])

*(i) The equilibrium $E_1$ has eigenvalues $-b_1, -b_1$ and $-b_2$ with corresponding eigenvectors $(1, 0, 0, -1)$,$(-1, 1, 0, 0)$ and $(-1, 0, 1, 0)$, respectively.*

*(ii) The equilibrium $E_{12}$ has eigenvalues $\frac{1}{2}, -\frac{1}{2}b_2, -\frac{1}{2}b_2$, and the eigenvalue $\frac{1}{2}$ has an eigenvector $(1, -1, 0, 0)$.*

*(iii) The equilibrium $E_{13}$ has eigenvalues $\frac{1}{2}b_2, \frac{1}{2}(b_2 - 2b_1)$ and $\frac{1}{2}(b_2 - 2b_1)$ with corresponding eigenvectors $(1, 0, -1, 0)$,$(0, 1, 0, -1)$ and $(\frac{1}{2}, 0, \frac{1}{2}, -1)$, respectively.*

*(iv) The equilibrium $E_{1234}$ has eigenvalues $\frac{1}{4}(2b_1 - b_2), \frac{1}{4}b_2$ and the eigenvalue $\frac{1}{4}(2b_1 - b_2)$ has an eigenvector $(-1, 1, -1, 1)$.*

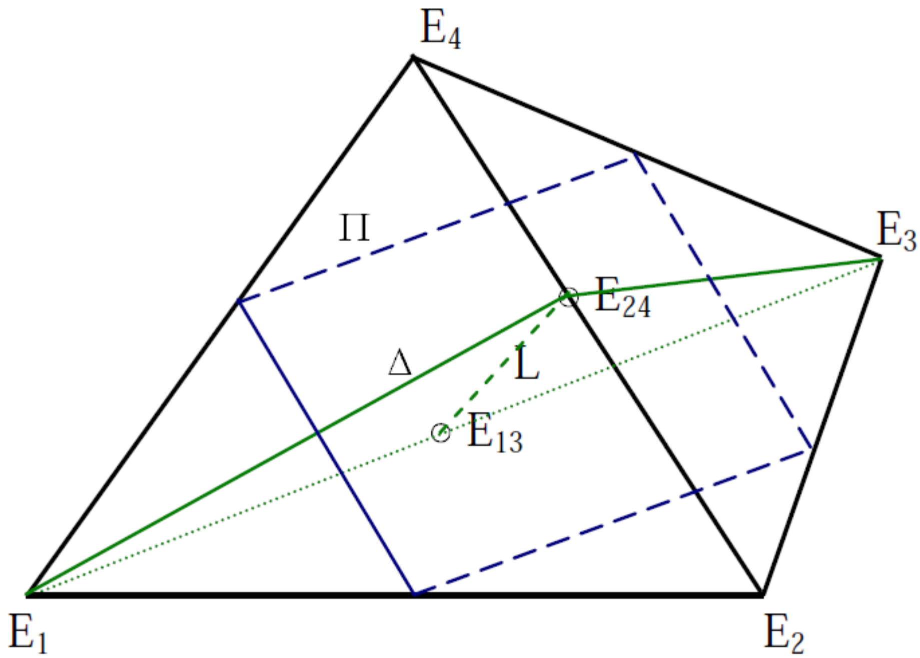


FIGURE 1. In the simplex $\Sigma_4$, the plane $\Pi$ is in blue lines, while the line $L$ connecting $E_{13}$ and $E_{24}$ is in green. The plane $\Delta$ is denoted by the triangle in green lines with vertexes $E_1, E_3$ and $E_{24}$. The region above $\Delta$ is the so-called $\Delta^+$, while the region below $\Delta$ is $\Delta^-$.

**Theorem 2.3.** ([9]) *Let $b_1 = 0$ and $b_2$ be positive (negative). Almost all orbits (i.e., except for a set of initial conditions of measure zero) that start in the interior of the simplex converge forward (backward) in time to a point on line segments $\overline{E_iE_{i+1}}$, i=1,2,3,4 (in particular all points on the segments are stationary) and backward (forward) in time either to $E_{13}$ or to $E_{24}$.*

**Theorem 2.4.** ([9])

*(i) If $b_1 = b_2 = 0$, then all orbits of (4) are equilibria.*
*(ii) If $b_1 < 0$ and $b_2 = 0$, then any orbit that starts in the interior of the simplex has its $\omega$-limit set contained in the plane $\Pi$, which consists of equilibria.*
*(iii) If $2b_1 < b_2 < 0$, then any orbit that does not start at the boundary of the simplex has $E_{1234}$ as its $\omega$-limit set.*
*(iv) If $2b_1 = b_2 < 0$, then any orbit that does not start at the boundary of the simplex has its $\omega$-limit set contained in the equilibrium line segment $L$.*

**Remark 1.** While the system (1) comes from (2) where $a_i \geq 0$ for $1 \leq i \leq n$, the constraints on $b_i$ in (4) are

$$\begin{aligned} 2b_1 &\leq 1 - b_2, \\ 2b_1 &\geq b_2 - 1, \\ 3b_2 &\geq 2b_1 - 1. \end{aligned} \tag{5}$$

3. **Global dynamics.** In this section, we first show the nonexistence of periodic orbits in system (4). Then we study the global dynamics of the system when $b_1b_2 < 0$.

For the vector field of (4) in the region $\{u \in \Sigma_4 : u_4 > 0\}$, we make the following projection

$$y_i = \frac{u_i}{u_4},\ i = 1, 2, 3, 4. \tag{6}$$

With a substitution on time $t$ (i.e., $u_4dt \to dt$), we have

$$\begin{aligned} \dot{y}_1 &= -y_1[b_1 - b_1y_1 + (b_1 - b_2)y_2 + (b_2 - b_1)y_3], \\ \dot{y}_2 &= -b_2y_2(1 - y_2), \\ \dot{y}_3 &= -y_3[b_1 + (b_2 - b_1)y_1 + (b_1 - b_2)y_2 - b_1y_3]. \end{aligned} \tag{7}$$

Thus the vector field of (4) is radically projected onto that of (7) on the super-plane $\{y = (y_1, y_2, y_3, y_4) \in R^4_+ : y_4 = 1\}$.

It follows from the second equation of (7) that the plane $y_2 = 1$ is invariant. When $b_2 \neq 0$, any orbit of (7) satisfies either $y_2 \to 0$, or $y_2 \to 1$, or $y_2 \to \infty$ as $t \to \infty$. Since $y_2 = \frac{u_2}{u_4}$, then $y_2 \to 0$ means $u_2 \to 0$, while $y_2 \to \infty$ means $u_4 \to 0$. It follows from the symmetry of $u_2$ and $u_4$ in (4) that the dynamics of (4) on the plane $u_4 = 0$ are same as those on the plane $u_2 = 0$. Thus we focus on the dynamics of (7) on the plane $y_2 = 1$ and $y_2 = 0$.

Let $b_1 \neq 0$. On the plane $y_2 = 1$, system (7) becomes

$$\begin{aligned} \dot{y}_1 &= -y_1[2b_1 - b_2 - b_1y_1 + (b_2 - b_1)y_3], \\ \dot{y}_3 &= -y_3[2b_1 - b_2 + (b_2 - b_1)y_1 - b_1y_3]. \end{aligned} \tag{8}$$

The system is a Lotka-Volterra model, which has four equilibria: $O(0, 0)$, $O_1(\frac{b_2-2b_1}{-b_1}, 0)$, $O_2(0, \frac{b_2-2b_1}{-b_1})$, and $P(1, 1)$ (see Fig. 2a). Since the Jacobian matrix $J$ of (8) at $P$ satisfies $trace(J) = 2b_1 \neq 0$, $P$ cannot be a center.

On the plane $y_2 = 0$, system (7) becomes

$$\begin{aligned} \dot{y}_1 &= -y_1[b_1 - b_1y_1 + (b_2 - b_1)y_3], \\ \dot{y}_3 &= -y_3[b_1 + (b_2 - b_1)y_1 - b_1y_3]. \end{aligned} \tag{9}$$

The system (9) is also a Lotka-Volterra model. It has four equilibria: $O(0, 0)$, $Q_1(1, 0)$, $Q_2(0, 1)$ and $Q(\frac{-b_1}{b_2-2b_1}, \frac{-b_1}{b_2-2b_1})$ (see Fig. 3a).

By Theorem 7.8.1 in [12], we obtain the following result.

**Lemma 3.1.** ([12]) *Solutions of system (4) converge to equilibria.*

Let

$$\Delta = \{u \in \Sigma_4 : u_2 - u_4 = 0\}.$$

While $y_2 = \frac{u_2}{u_4}$ and $y_2 = 1$ are invariant for (7), the plane $\Delta$ (see Fig. 1) is invariant for (4).

Next, we consider the dynamics of (4) in the case $b_1b_2 < 0$.

**Theorem 3.2.** *Let $b_1 < 0$ and $b_2 > 0$.*

*(i) On the plane $\Delta$, any orbit starting in intL (i.e., the interior of L) has $E_{1234}$ as its $\omega$-limit set, while any other orbit starting in int$\Delta$ (i.e., the interior of $\Delta$) has $E_{234}$ or $E_{412}$ as its $\omega$-limit set (Fig. 2b).*

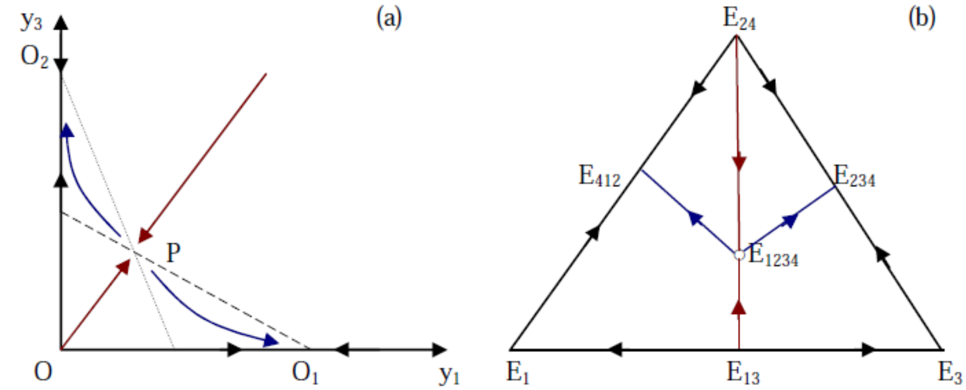


FIGURE 2. In (a), the equilibrium $P$ is a saddle with a stable manifold $y_1 = y_3$ (the deep-red line). Other orbits in $\text{int}R_2^+$ converge either to $O_1$ or to $O_2$, depending on their initial conditions. In (b), the equilibrium $E_{1234}$ has a stable manifold (the deep-red line). Other orbits in $\text{int}\Delta$ converge either to $E_{234}$ or to $E_{412}$, depending on their initial conditions.

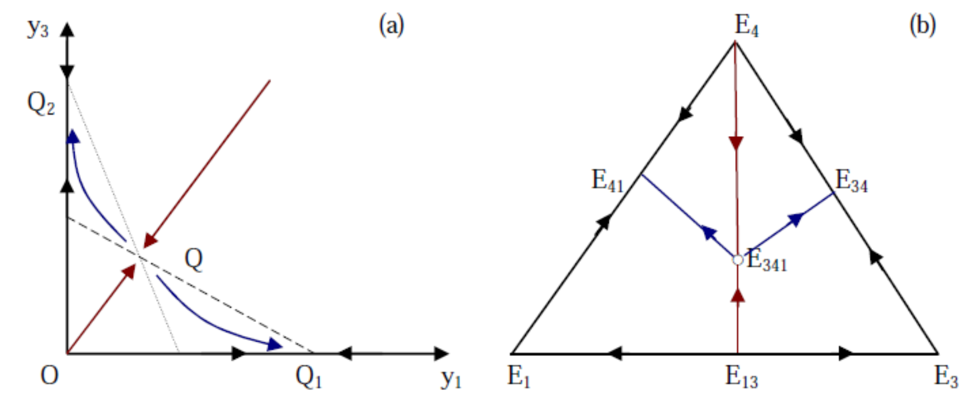


FIGURE 3. In (a), the equilibrium $Q$ is a saddle with a stable manifold $y_1 = y_3$ (the deep-red line). Other orbits in $\text{int}R_2^+$ converge either to $Q_1$ or to $Q_2$, depending on their initial conditions. In (b), the equilibrium $E_{341}$ has a stable manifold (the deep-red line) on the plane $u_2 = 0$. Other orbits in the interior of the plane converge either to $E_{34}$ or to $E_{41}$, depending on their initial conditions.

*(ii) Above the plane $\Delta$ (see Fig. 1), i.e., in the region*

$$\Delta^+ = \{u \in \Sigma_4 : u_2 - u_4 < 0\},$$

*the equilibrium $E_{341}$ has a two-dimensional stable manifold in $\text{int}\Delta^+$, while any other orbit starting in $\text{int}\Delta^+$ has $E_{34}$ or $E_{41}$ as its $\omega$-limit set (Fig. 3b).*

*(iii) Below the plane $\Delta$ (see Fig. 1), i.e., in the region*

$$\Delta^- = \{u \in \Sigma_4 : u_2 - u_4 > 0\},$$

*the equilibrium $E_{123}$ has a two-dimensional stable manifold in int$\Delta^-$, while any other orbit starting in int$\Delta^-$ has $E_{12}$ or $E_{23}$ as its $\omega$-limit set.*

*Proof.* (i) Since $b_1 < 0$ and $b_2 > 0$, system (8) is a Lotka-Volterra competitive model. The equilibrium $O$ is an unstable node, $O_1$ and $O_2$ are stable nodes, and $P$ is a saddle (Fig. 2a). While $P$ has a one-dimensional stable manifold (i.e. the line $y_1 = y_3$), other orbits in int$R^2_+$ either converge to $O_1$ or converge to $O_2$, depending upon their initial conditions. It follows from (6) that the result in (i) is proven.

(ii) In the region $\Delta^+$, we have $y_2 < 1$. It follows from the second equation of (7) that any orbit $y(t)$ with $y_2(0) < 1$ satisfies $y_2(t) \to 0$ as $t \to \infty$. On the plane $y_2 = 0$, system (9) is a Lotka-Volterra competitive model. The equilibrium $O$ is an unstable node, $Q_1$ and $Q_2$ are stable nodes, and $Q$ is a saddle (Fig. 3a). While $Q$ has a one-dimensional stable manifold (i.e. the line $y_1 = y_3$), other orbits in int$R^2_+$ either converge to $Q_1$ or converge to $Q_2$, depending upon their initial conditions. It follows from (6) that the result in (ii) is proven.

(iii) In the region $\Delta^-$, we have $y_2 > 1$. It follows from the second equation of (7) that any orbit $y(t)$ with $y_2(0) > 1$ satisfies $y_2(t) \to \infty$ as $t \to \infty$. By (6), we have $u_4 \to 0$ as $t \to \infty$. It follows from the symmetry of $u_2$ and $u_4$ in (4) and the result in (ii) that the result in (iii) is proven. □

The case $b_1 > 0$ and $b_2 < 0$ is considered as follows. By $b_2 < 0$ and the second equation of (7), any orbit $y(t)$ of (7) satisfies $y_2(t) \to 1$ as $t \to \infty$. On the plane $y_2 = 1$, system (7) becomes (8). It follows from the proof of Theorem 3.2(i) with time substitution $t \to -t$ that, the equilibria $E_{234}$, $E_{412}$ and $E_{1234}$ have two-dimensional stable manifolds respectively, while other orbits of (4) in int$\Sigma_4$ converge either to $E_{13}$ or to $E_{24}$, depending upon their initial conditions. Thus we obtain the following results.

**Theorem 3.3.** *Let $b_1 > 0$ and $b_2 < 0$. The equilibrium $E_{1234}$ has a two-dimensional stable manifold in the interior of the simplex (i.e. int$\Sigma_4$), while any other orbit starting in int$\Sigma_4$ has $E_{13}$ or $E_{24}$ as its $\omega$-limit set.*

## 4. Global bifurcation.

In this section, we study the bifurcations in system (4) when parameters $b_1$ and $b_2$ vary. First, we extend some results given by Diekmann and van Gils [9]. Then we draw the global bifurcation diagram.

Under conditions in the following Theorems 4.2 and 4.1, Diekmann and van Gils [9] showed that almost all orbits of (4) converge to bd$\Sigma_4$. Their proof is based on Lyapunov functions. We extend their results through qualitative analysis.

**Theorem 4.1.** *(i) If $b_1 > 0$ and $b_2 > 0$, then almost all orbits starting in the interior of the simplex have their $\omega$-limit sets in the set of $E_i, i = 1, 2, 3, 4$.*

*(ii) If $b_2 < 2b_1 < 0$, then almost all orbits starting in the interior of the simplex have their $\omega$-limit sets in the set of $E_{13}$ and $E_{24}$.*

*Proof.* (i) Based on systems (8) and (9), we need to consider three cases: (i1) $2b_1 > b_2 > 0$; (i2) $2b_1 = b_2 > 0$; (i3) $b_2 > 2b_1 > 0$.

For the case (i1), we need to consider three situations: (i11) $b_1 < b_2$; (i12) $b_1 = b_2$; (i13) $b_1 > b_2$. We focus on situation (i11), while similar discussion can be given for (i12) and (i13).

When $2b_1 > b_2 > 0$ and $b_1 < b_2$, it follows from the second equation of (7) that the plane $y_2 = 1$ is invariant. On this plane, system (8) is a Lotka-Volterra competitive model. The equilibrium $O$ is a stable node, $O_1$ and $O_2$ are saddles, and $P$ is an unstable node (Fig. 4a). Thus $O_1$ and $O_2$ have a one-dimensional stable manifold, respectively, other orbits either converge to $O$ or converge to $\infty$, depending upon their initial conditions. Therefore, on the plane $\Delta$, the equilibria $E_{13}$, $E_{234}$ and $E_{412}$ of (4) have a one-dimensional stable manifold, respectively. Other orbits (except $E_{1234}$) in the interior of the plane have their $\omega$-limit sets in the set of $E_1$, $E_3$ and $E_{24}$ (Fig. 4b).

By the second equation of (7), orbits with $y_2(0) < 1$ satisfy $y_2(t) \to 0$ as $t \to \infty$. On the plane $y_2 = 0$, system (9) is a Lotka-Volterra competitive model. The equilibrium $O$ is a stable node, $Q_1$ and $Q_2$ are saddles, and $Q$ is an unstable node. Therefore, on the plane $u_2 = 0$, the equilibria $E_{13}$, $E_{34}$ and $E_{41}$ of (4) have a one-dimensional stable manifold, respectively. Any other orbit (except $E_{341}$) in the interior of the plane has $E_1$, $E_3$ or $E_4$ as its $\omega$-limit set.

For any orbit of (7) with $y_2(0) > 1$, it satisfies $y_2(t) \to \infty$ as $t \to \infty$, i.e. $u_4 \to 0$ in the corresponding solution of (4). By the symmetry of $u_2$ and $u_4$ in (7), on the plane $u_4 = 0$, the equilibria $E_{12}$, $E_{13}$ and $E_{23}$ of (4) have a one-dimensional stable manifold, respectively. Any other orbit (except $E_{123}$) in the interior of the plane has $E_1$, $E_2$ or $E_3$ as its $\omega$-limit sets.

Therefore, in the case (i11), almost all orbits have their $\omega$-limit sets in the set of $E_i, i = 1, 2, 3, 4$.

For the case (i2) with $2b_1 = b_2 > 0$, the proof is similar to that for $2b_1 > b_2 > 0$. On the plane $\Delta$, system (4) is integrable. $L$ consists of equilibria, while other orbits have their $\omega$-limit sets in the set of $E_1$ and $E_3$. On the plane $u_2 = 0$ which corresponds to $y_2 = 0$, $E_{13}$ is an unstable node, $E_{34}$ and $E_{41}$ are saddles, and $E_i$ is a stable node, i=1,3,4. Thus almost all orbits have their $\omega$-limit sets in the set of $E_i$, i=1,3,4. By the symmetry of $u_2$ and $u_4$, almost all orbits of (4) have their $\omega$-limit sets in the set of $E_i$, i=1,2,3 on the plane $u_4 = 0$. Therefore, almost all orbits of (4) have their $\omega$-limit sets in the set of $E_i$, i=1,2,3,4.

For the case (i3) with $b_2 > 2b_1 > 0$, the proof is similar to that for $2b_1 > b_2 > 0$. On the plane $\Delta$, $E_{24}$ is an unstable node, $E_{13}$ and $E_{1234}$ are saddles, and $E_1$ and $E_3$ are stable nodes. Thus almost all orbits have their $\omega$-limit sets in the set of $E_1$ and $E_3$. On the plane $u_2 = 0$, $E_{13}$ is an unstable node, $E_{34}$ and $E_{41}$ are saddles, and $E_i$ is a stable node, i=1,3,4. By the symmetry of $u_2$ and $u_4$, almost all orbits of (4) have their $\omega$-limit sets in the set of $E_i$, i=1,2,3 on the plane $u_4 = 0$. Therefore, almost all orbits of (4) have their $\omega$-limit sets in the set of $E_i$, i=1,2,3,4.

(ii) For the situation $b_2 < 2b_1 < 0$, the proof is the same as that for $2b_1 > b_2 > 0$ when we replace $t$ with $-t$. □

**Theorem 4.2.** *If $b_1 > 0$ and $b_2 = 0$, then the plane $\Pi$ consists of equilibria, and any other orbit starting in the interior of the simplex has its $\omega$-limit set in line segments $\overline{E_1E_3}$ and $\overline{E_2E_4}$, which consist of equilibria (Fig. 5).*

*Proof.* Since $b_2 = 0$, it follows from the second equation of (7) that every plane $y_2 = c$ is invariant, where $c \geq 0$. Let $y_2 = c$ in (7), then (7) becomes

$$\begin{aligned} \dot{y}_1 &= -b_1 y_1(1 + c - y_1 - y_3), \\ \dot{y}_3 &= -b_1 y_3(1 + c - y_1 - y_3). \end{aligned} \tag{10}$$

Thus the line $y_1 + y_3 = 1 + c$ consists of equilibria of (10). Since $V = y_3/y_1$ is a constant of motion of (7), any orbit that does not start at an equilibrium converges either to O, or to $\infty$. Hence, for system (4), the plane $\{\Delta_c : u_2 = cu_4\}$ is invariant, which is a planar region surrounded by a triangle with vertexes $E_1, E_3$

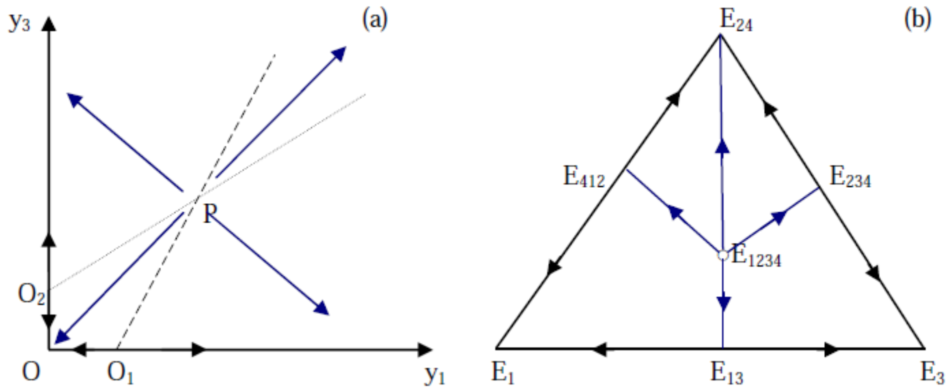


FIGURE 4. In (a), the equilibrium $P$ is an unstable node and $O_1$ and $O_2$ are saddles. All orbits except $P$ converge either to 0, or to $\infty$. In (b), the equilibrium $E_{1234}$ is an unstable node. All orbits (except $E_{1234}$) in the interior of $\Delta$ converge either to $E_1$, or to $E_3$, or to $E_{24}$, depending on their initial conditions.

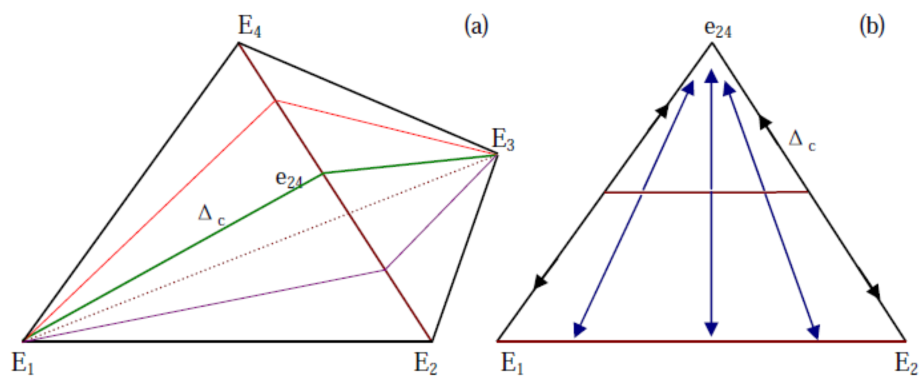


FIGURE 5. In (a), the plane $\Delta_c$ is the region surrounded by the triangle with vertexes $E_1$, $E_3$ and $e_{24}$, while $e_{24}$ is any point on the line segment $\overline{E_2E_4}$. The line segments $\overline{E_1E_3}$ and $\overline{E_2E_4}$ (in deep-red color) consist of equilibria. In (b), the two line segments in deep-red color consist of equilibria, while any other orbit on $\Delta_c$ has its $\omega$-limit set in the set of $e_{24}$ and the line segments.

and $e_{24}(0, \frac{c}{1+c}, 0, \frac{1}{1+c})$ (Fig. 5a). Here $e_{24}$ is any point on the line segment $\overline{E_2E_4}$. On the plane $\Delta_c$, the line $u_1 + u_3 = u_2 + u_4$ consists of equilibria, while any other orbit on $\Delta_c$ converges either to $e_{24}$ or to a point on the line segment $\overline{E_1E_3}$ (Fig. 5b).

Therefore, the plane $\Pi$ consists of equilibria, while any other orbit starting in the interior of the simplex has its $\omega$-limit set in the line segments $\overline{E_1E_3}$ and $\overline{E_2E_4}$, which consist of equilibria. □

| Conditions | ω-limits of almost all orbits |
|---|---|
| $b_1 = 0$, $b_2 = 0$ | All orbits are equilibria. |
| $b_1 > 0$, $b_2 = 0$ | $\overline{E_1E_3}, \overline{E_2E_4}$ |
| $b_1 > 0$, $b_2 > 0$ | $E_1, E_2, E_3, E_4$ |
| $b_1 = 0$, $b_2 > 0$ | $\overline{E_1E_2}, \overline{E_2E_3}, \overline{E_3E_4}, \overline{E_4E_1}$ |
| $b_1 < 0$, $b_2 > 0$ | $E_{12}, E_{23}, E_{34}, E_{41}$ |
| $b_1 < 0$, $b_2 = 0$ | $\Pi$ |
| $b_1 < 0$, $b_2 < 0$, $b_2 > 2b_1$ | $E_{1234}$ |
| $b_1 < 0$, $b_2 < 0$, $b_2 = 2b_1$ | $L$ |
| $b_1 < 0$, $b_2 < 0$, $b_2 < 2b_1$ | $E_{13}, E_{24}$ |
| $b_1 \geqslant 0$, $b_2 < 0$ | $E_{13}, E_{24}$ |

Based on Theorems 2.3-2.4, Theorems 3.2-3.3 and Theorems 4.1-4.2, we show the global bifurcations of (4) in the following table, from which we draw the bifurcation diagram in Fig. 6.

5. **Applications and discussion.** In this paper, we considered a four-dimensional cyclic replicator system. By applying a radial projection on the vector field, we reduced the four-dimensional system to a three-dimensional one and showed the nonexistence of periodic orbits. Then we presented the global dynamics for the case $b_1b_2 < 0$ and extended some results for the case $b_1b_2 \geq 0$ in [9]. By combining our results with those in [9], we provided a complete description on both the global dynamics and bifurcations in the system.

The results in this paper provide explanations on how and when all but one semelparous brood go to extinction. As shown in Fig. 6, all but one species go extinct if and only if $b_1(= b_3) > 0$ and $b_2 > 0$. By (3), we have

$$\frac{a_2}{a_1} > 1, \ \frac{a_3}{a_1} > 1, \ \frac{a_4}{a_1} > 1. \tag{11}$$

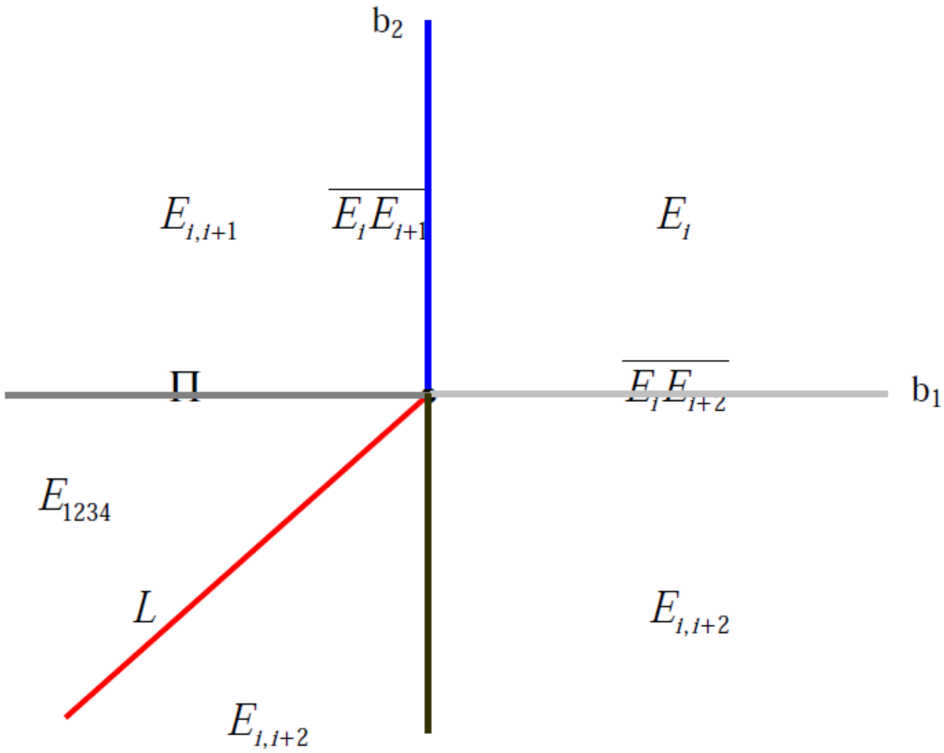


FIGURE 6. The $\omega$-limit sets of almost all orbits of (4). In each region, we have i=1,2,3,4. For example, in the region of $b_1 > 0$ and $b_2 > 0$, the $\omega$-limit sets $E_i$ means that the set of $E_1$, $E_2$, $E_3$ and $E_4$ forms the $\omega$-limit sets of almost all orbits of (4) when $b_1 > 0$ and $b_2 > 0$.

The ecological meaning of $\frac{a_i}{a_1}$ is as follows. The first equation of (2) for $n = 4$ is

$$\dot{x}_1 = x_1(1 - a_1x_1 - a_2x_2 - a_3x_3 - a_4x_4).$$

Then $\frac{a_i}{a_1}$ is the competitive degree from the $i$th year class to the 1st year class, $i = 2, 3, 4$. As shown in [17-21], the competitive degree is called strong (weak) if $\frac{a_i}{a_1} > 1$ $(< 1)$. By (11), the underlying reason for the persistence of only one brood is that the competition between each pair of broods is fierce, while the selection of the brood depends on both initial conditions and the degrees of competition. While van der Drissche and Zeeman [10] put forward an intriguing conjecture that all but one competitor would go to extinction in strongly competitive Lotka-Volterra systems, we confirmed the conjecture in a specific model.

The analysis in this work also shows that when the competition between each pair of species in (2) is weak (i.e., $\frac{a_i}{a_1} < 1$), then the species coexistence is not guaranteed. As shown in Fig. 6, the four species can coexist if and only if $b_1(= b_3) < 0$, $b_2 < 0$ and $b_2 \geq 2b_1$. The reason of coexistence is as follows. Since $b_2 < 0$, then any orbit of (7) with $y_2(0) > 0$ satisfies $y_2(t) \to 1$ as $t \to \infty$. On the plane $y_2 = 1$, system (7) is either a Lotka-Volterra system with weak competition (if $b_2 \geq b_1$), or a Lotka-Volterra system with weak cooperation (if $b_2 < b_1$). Thus the species can coexist. However, when $b_2 < 2b_1$, system (7) becomes a Lotka-Volterra system with strong competition. Thus the three species $y_i = \frac{u_i}{u_4}$ in system (7) cannot coexist, which corresponds to the non-coexistence of the four species $u_i = \frac{x_i}{\Sigma_{j=1}^4 x_j}$, i.e., the non-coexistence of the four species $x_i$, i=1,2,3,4.

When interactions among the four species consist of both strong and weak competitions, our analysis shows the way how some of the species coexist. As shown in Fig. 6, two non-consecutive species could coexist if $b_1(= b_3) > 0$ and $b_2 < 0$, which corresponds to $\frac{a_2}{a_1} > 1$, $\frac{a_3}{a_1} < 1$ and $\frac{a_4}{a_1} > 1$. Thus the 2nd and 4th species are in strong competition with the 1st species, while the 3rd species is in weak competition with it. Since $b_2 < 0$, any orbit of (7) with $y_2(0) > 0$ satisfies $y_2(t) \to 1$ as $t \to \infty$. On the plane $y_2 = 1$, system (7) is a Lotka-Volterra system with strong cooperation, while the intrinsic growth rates of both species are negative. Thus the species $y_1$ and $y_3$ converge either to 0 or to infinity, which corresponds to the extinction of species $u_1$ and $u_3$ (and the coexistence of $u_2$ and $u_4$) or to the extinction of species $u_2$ and $u_4$ (and the coexistence of $u_1$ and $u_3$). Similar discussion can be given for the situation $b_2 < 2b_1 \leq 0$.

As shown in Fig. 6, two consecutive species could coexist if $b_1(= b_3) < 0$ and $b_2 > 0$, which corresponds to $\frac{a_2}{a_1} < 1$, $\frac{a_3}{a_1} > 1$ and $\frac{a_4}{a_1} < 1$. Thus the 2nd and 4th species are in weak competition with the 1st species, while the 3rd species is in strong competition with it. As shown in the proof of Theorem 3.2, system (9) is a Lotka-Volterra system with strong competition. Thus two consecutive species $u_i$ and $u_{i+1}$ go extinct while the other two species $u_{i+2}$ and $u_{i+3}$ coexist, i=1,2,3,4. Similar discussion can be given for the situation $b_1 = 0$ and $b_2 > 0$.

In this work, we assumed $b_1 = b_3$. Since different year classes of semelparous species are identical except for their reproduction time, their competitive ability may be equal (i.e. $a_2 = a_4$). Thus the assumption $b_1 = b_3$ is possible in real environment. Despite the simplicity of the system, our work is helpful in both analyzing replicator equations and understanding ecological complexity in competitive systems.

## REFERENCES

[1] H. Behncke, *Periodical cicadas*, J. Math. Biol., **40** (2000), 413–431.
[2] M. G. Bulmer, *Periodic insects*, Am. Nat., **111** (1977), 1099–1117.
[3] J. M. Cushing, *Nonlinear semelparous Leslie models*, Math. Biosci. Eng., **3** (2006), 17–36.
[4] J. M. Cushing, *Three stage semelparous Leslie models*, J. Math. Biol., **59** (2009), 75–104.
[5] N. V. Davydova, O. Diekmann and S. A. van Gils, *Year class competition or competitive exclusion for strict biennials*, J. Math. Biol., **46** (2003), 95–131.
[6] N. V. Davydova, "Old and Young. Can They Coexist," Thesis, University of Utrecht, 2004, `http://igitur-archive.library.uu.nl/dissertations/2004-0115-092805/UUindex.html`.
[7] N. V. Davydova, O. Diekmann and S. A. van Gils, *On circulant populations. I. The algebra of semelparity*, Linear Algebra Apl., **398** (2005), 185–243.
[8] O. Diekmann and S. A. van Gils, *Invariance and symmetry in a year-class model*, in "Bifurcations, Symmetry and Patterns", (Porto, 2000), Birkhäuser, Basel, (2003), 141–150.
[9] O. Diekmann and S. A. van Gils, *On the cyclic replicator equation and the dynamics of semelparous populations*, SIAM J. Applied Dynamical Systems, **8** (2009), 1160–1189.
[10] P. van den Drissche and M. L. Zeeman, *Three-dimensional competitive Lotka-Volterra systems with no periodic orbits*, SIAM J. Appl. Math., **58** (1998), 227–234.
[11] A. Edalat and E. C. Zeeman, *The stable classes of the codimension-one bifurcations of the planar replicator system*, Nonlinearity, **5** (1992), 921–939.
[12] J. Hofbauer and K. Sigmund, "Evolutionary Games and Population Dynamics," Cambridge University Press, Cambridge, UK, 1998.
[13] R. Kon, *Nonexistence of synchronous orbits and class coexistence in matrix population models*, SIAM J. Appl. Math., **66** (2005), 616–626.

[14] R. Kon and Y. Iwasa, *Single-class orbits in nonlinear Leslie matrix models for semelparous populations*, J. Math. Biol., **55** (2007), 781–802.

[15] E. Mjolhus, A. Wikan and T. Solberg, *On synchronization in semelparous populations*, J. Math. Biol., **50** (2005), 1–21.

[16] J. D. Murry, "Mathematical Biology," Springer-Verlag, New York, 2003.

[17] Y. Wang, *Necessary and sufficient conditions for the existence of periodic orbits in a Lotka-Volterra system*, J. Math. Anal. Appl., **284** (2003), 236–249.

[18] Y. Wang, H. Wu and S. Ruan, *Periodic orbits near heteroclinic cycles in a cyclic replicator system*, J. Math. Biol., **64** (2012), 855–872.

Received October 2011; revised April 2012.

*E-mail address*: mcswys@mail.sysu.edu.cn(Y. Wang)
*E-mail address*: wuhong@mail.sysu.edu.cn(H. Wu)
*E-mail address*: ruan@math.miami.edu(S. Ruan)