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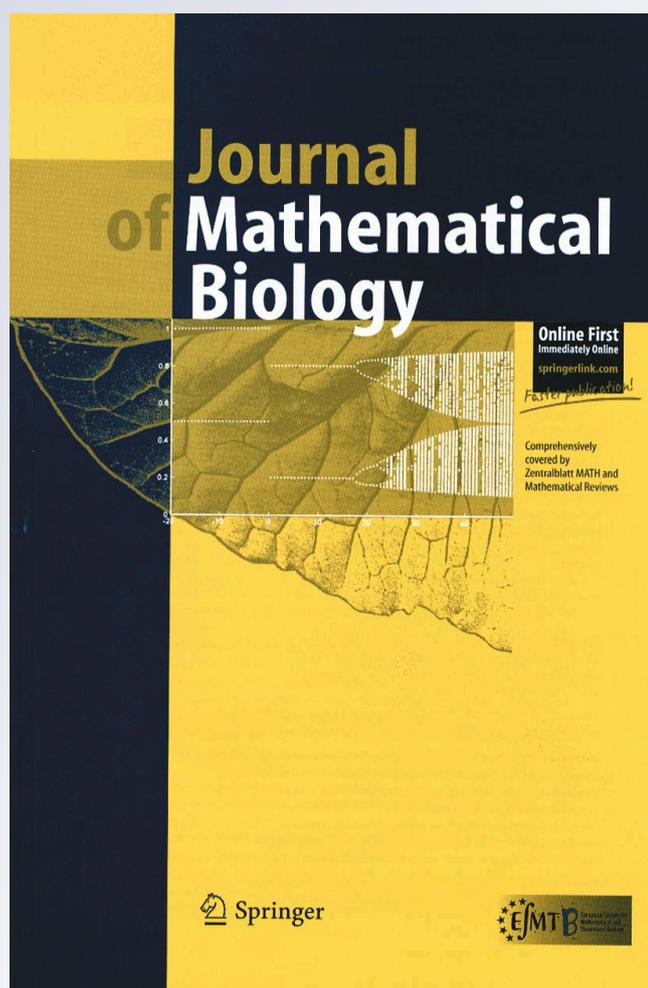
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Periodic orbits near heteroclinic cycles in a cyclic replicator system

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Abstract A species is semelparous if every individual reproduces only once in its life and dies immediately after the reproduction. While the reproduction opportunity is unique per year and the individual's period from birth to reproduction is just n years, the individuals that reproduce in the i th year (modulo n) are called the i th year class, $i = 1, 2, \dots, n$. The dynamics of the n year-class system can be described by a differential equation system of Lotka–Volterra type. For the case $n = 4$, there is a heteroclinic cycle on the boundary as shown in previous works. In this paper, we focus on the case $n = 4$ and show the existence, growth and disappearance of periodic orbits near the heteroclinic cycle, which is a part of the conjecture by Diekmann and van Gils (SIAM J Appl Dyn Syst 8:1160–1189, 2009). By analyzing the Poincaré map near the heteroclinic cycle and introducing a metric to measure the size of the periodic orbit, we show that (i) when the average competitive degree among subpopulations (year classes) in the system is weak, there exists an asymptotically stable periodic orbit near the heteroclinic cycle which is repelling; (ii) the periodic orbit grows in size when some competitive degree increases, and converges to the heteroclinic cycle when the average competitive degree tends to be strong; (iii) when the average competitive

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degree is strong, there is no periodic orbit near the heteroclinic cycle which becomes asymptotically stable. Our results provide explanations why periodic solutions expand and disappear and why all but one subpopulation go extinct.

Keywords Replicator equation · Periodic orbit · Heteroclinic cycle · Average competitive degree · Semelparous population

Mathematics Subject Classification (2000) 34C37 · 92D25 · 37N25

1 Introduction

There has been a growing literature on the theoretical study of semelparous population dynamics in recent years. Examples of semelparous species include annual and biennial plants, butterflies, cicadas, mayflies, Pacific salmon, etc (Behncke 2000). If there is a unique reproduction opportunity per year and the length of the life cycle is just n years, then the population can be classified into different year classes: the individuals that reproduce in the i th year (modulo n) are called the i th year class, $i = 1, 2, \dots, n$.

Various dynamical outcomes are likely in semelparous populations since interactions such as competition exist between different year classes as well as within the same year class, a specific year class may be driven to extinction. The species in which all year classes except one go extinct is called a periodical insect (Bulmer 1977). Interesting examples include the 13- and 17-year classes of some cicada species. Mathematically, the dynamics of semelparous populations can be described by a discrete-time nonlinear Leslie matrix model (Cushing 2006; Davydova 2004; Davydova et al. 2005; Diekmann and van Gils year; Drissche and Zeeman 1998; Kon 2005; Kon and Iwasa 2007; Mjølhus et al. 2005). The phenomenon of periodical insects can be explained by the invariance of coordinate axes and hyperplanes of the full life cycle map (Davydova et al. 2003) and the existence of heteroclinic cycles connecting different year cycles (Cushing 2009; Diekmann and van Gils 2009).

Diekmann and van Gils (2009) demonstrated that the n -dimensional discrete-time Leslie matrix model can be reduced to a cyclic replicator system on the $(n - 1)$ dimensional simplex and classified the repertoire of the dynamical behavior for $n = 2$ and 3. For $n = 4$, they derived almost all possible dynamical behaviors and identified some open problems about the dynamics near the heteroclinic cycles.

Consider the cyclic replicator system (Diekmann and van Gils 2009; Edalat A and Zeeman 1992)

$$\dot{u}_i = u_i \left(-(Bu)_i + \sum_{j=1}^n u_j (Bu)_j \right), \quad i = 1, 2, \dots, n, \tag{1.1}$$

where u is an n -dimensional vector in the simplex S_n which is defined by

$$S_n = \left\{ u \in R^n : \sum_{j=1}^n u_j = 1, u_j \geq 0, j = 1, 2, \dots, n \right\},$$

and $(Bu)_i$ denotes the i th component of the vector Bu . B is a circulant matrix defined by

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

where the rows of B are cyclic permutations of the first row. System (1.1) is derived from the cyclic competitive system

$$\dot{x}_i = x_i(1 - (Ax)_i), \quad x_i \geq 0, \quad i = 1, 2, \dots, n, \tag{1.2}$$

where x_i represents the population density of the i th year class of the semelparous species, and n represents the individuals' period from birth to reproduction while it is supposed that there is a unique reproduction opportunity per year (Cushing 2006, 2009; Kon and Iwasa 2007; Mjølhus et al. 2005). The individuals that reproduce in the i th year (modulo n) are called the i th year class. In system (1.2), all year classes have the same intrinsic growth rate and the interaction matrix A is circulant. These features are shown naturally in the interesting derivation in section A.2 of Diekmann and van Gils (2009).

The circulant matrix A in (1.2) is defined by

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

where $\frac{1}{a_1}$ represents the carrying capacity of every year class and $\frac{a_i}{a_1}$ ($i \neq 1$) represents the competitive degree from other year classes. As shown by Diekmann and van Gils (2009, p.1163), the derivation of (1.1) from (1.2) is mainly by the projection from R_+^n to S_n through $u_i = x_i / \sum_{j=1}^n x_j$ and

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

Since x_i denotes the population density of the i th year class, then u_i represents the fraction of the i th year class. As shown by Diekmann and van Gils (2009), the dynamical behavior of (1.1) with $n = 2, 3$ is completely understood and presented while that of the case $n = 4$ is given in an almost complete picture. Let $n = 4$, matrix B in (1.1) becomes

$$B = \begin{pmatrix} 0 & b_1 & b_2 & b_3 \\ b_3 & 0 & b_1 & b_2 \\ b_2 & b_3 & 0 & b_1 \\ b_1 & b_2 & b_3 & 0 \end{pmatrix}. \tag{1.3}$$

It is shown by [Diekmann and van Gils \(2009\)](#) that (i) when $b_1 + b_3 \neq 0$, Hopf bifurcations occur at $b_2 = 0$ and small periodic orbits emerge when b_2 is close to zero, and (ii) there exist heteroclinic cycles on the boundary of S_4 . Since the stability change of heteroclinic cycles will lead to large periodic orbits, an intriguing conjecture is put forward by [Diekmann and van Gils \(2009, p.1180\)](#): “*We conjecture that the small periodic orbits grow in size and finally disappear in the heteroclinic cycles*”.

In this paper, we consider the case $(b_1 + b_3)b_2 < 0$ and $b_1b_3 < 0$ while we focus on the case $b_1 + b_3 < 0$, $b_2 > 0$ and $b_1b_3 < 0$ because of the symmetry of system (1.1). Our aim is to establish the existence, uniqueness, growth and disappearance of periodic orbits near the heteroclinic cycle, which is part of the conjecture of [Diekmann and van Gils \(2009\)](#). By analyzing the Poincaré map near the heteroclinic cycle and introducing a metric to measure the size of periodic orbits, we show that (i) when $b_1 + b_2 + b_3$ is slightly less than zero, there exists a periodic orbit near the heteroclinic cycle and the periodic orbit is asymptotically stable while the heteroclinic cycle is repelling; (ii) the periodic orbit grows in size when b_2 increases and tends to the heteroclinic cycle when $b_1 + b_2 + b_3$ converges to zero; (iii) when $b_1 + b_2 + b_3$ is slightly larger than zero, there is no periodic orbit near the heteroclinic cycle which becomes asymptotically stable. While the expression $b_1 + b_2 + b_3$ corresponds to the average competitive degree among different year classes, our results provide explanations why periodic solutions expand and disappear, and why all but one year class go extinct: when the average competitive degree is weak, the year classes in the system coexist and exhibit periodic oscillations; the magnitude of the periodic oscillations grows in size when the competitive degree $\frac{a_3}{a_1}$ increases; when the average competitive degree is strong, the periodic oscillations disappear and all but one year class go extinct. Numerical simulations are also given to show the existence, growth and disappearance of periodic orbits.

The paper is organized as follows. In Sect. 2, we recall some results by [Diekmann and van Gils \(2009\)](#) on the cyclic replicator system. In Sect. 3, we establish the existence and uniqueness of periodic orbits. The growth and disappearance of periodic orbit is studied in Sect. 4. In Sect. 5, we give some ecological applications of our results and present some discussions.

2 The cyclic replicator system

In this section, some previous results about (1.1) for $n = 4$ are recalled. Since the dynamical behavior of (1.1) for the case $(b_1 + b_3)b_2 > 0$ is given by [Diekmann and van Gils \(2009\)](#), we analyze the case $(b_1 + b_3)b_2 < 0$ and $b_1b_3 < 0$ in this paper. While system (1.1) is invariant under $(B, t) \rightarrow (-B, -t)$, we focus on the case

$$b_1 + b_3 < 0, b_2 > 0, b_1b_3 < 0.$$

Results for the case $b_1 + b_3 > 0, b_2 < 0$ and $b_1b_3 < 0$ are similar: the directions of the orbits are just opposite to those in the case $b_1 + b_3 < 0, b_2 > 0$ and $b_1b_3 < 0$.

Without loss of generality, we suppose $b_3 < 0$. When both of the left and right sides of (1.1) are divided by $-b_3$ and a time rescaling $t \rightarrow t/(-b_3)$ is applied, matrix B

of (1.1) as shown in (1.3) becomes the following form while $b_1/(-b_3)$ and $b_2/(-b_3)$ are still denoted by b_1 and b_2 , respectively:

$$B = \begin{pmatrix} 0 & b_1 & b_2 & -1 \\ -1 & 0 & b_1 & b_2 \\ b_2 & -1 & 0 & b_1 \\ b_1 & b_2 & -1 & 0 \end{pmatrix}.$$

Then the case we focus on becomes

$$0 < b_1 < 1, \quad b_2 > 0, \quad b_3 = -1. \tag{2.1}$$

Let S be a circular matrix defined by

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

Lemma 2.1 (Diekmann and van Gils 2009) *The replicator system (1.1) is equivariant with respect to S , i.e., if u is a solution of (1.1), then Su is also a solution of (1.1).*

Let E_i denote the equilibrium with i coexisting species. When conditions in (2.1) hold, the equilibria of (1.1) (modulo cyclic permutation) are:

$$E_1 = (1, 0, 0, 0), \quad E_{2s} = \left(\frac{1}{2}, 0, \frac{1}{2}, 0\right), \quad E_4 = \left(\frac{1}{4}, \frac{1}{4}, \frac{1}{4}, \frac{1}{4}\right).$$

Lemma 2.2 (Diekmann and van Gils 2009)

- (i) *The equilibrium E_1 has eigenvalues $-b_1, 1, -b_2$ with corresponding eigenvectors $(1, 0, 0, -1), (-1, 1, 0, 0)$ and $(-1, 0, 1, 0)$, respectively;*
- (ii) *The equilibrium E_{2s} has eigenvalues $\frac{1}{2}b_2, \frac{1}{2}(b_2 - b_1 + 1), \frac{1}{2}(b_2 - b_1 + 1)$ with corresponding eigenvectors $(1, 0, -1, 0), (0, 1, \frac{1}{b_1}(-1 - b_1), \frac{1}{b_1})$ and $(1, 0, -\frac{1}{b_1}, \frac{1}{b_1}(1 - b_1))$, respectively;*
- (iii) *The equilibrium E_4 has eigenvalues $\frac{1}{4}(b_1 - 1 - b_2), \frac{1}{4}[b_2 \pm i(1 + b_1)]$ and the eigenvalue $\frac{1}{4}(b_1 - 1 - b_2)$ has an eigenvector $(-1, 1, -1, 1)$.*

Lemma 2.3 (Diekmann and van Gils 2009) *Let (2.1) hold.*

- (i) *A supercritical Hopf bifurcation occurs at $b_2 = 0$, i.e., there exist small stable periodic orbits near E_4 when b_2 is slightly larger than zero;*
- (ii) *There exists a heteroclinic cycle Γ , which connects the four equilibria E_1 (i.e., $E_1, SE_1, S^2E_1, S^3E_1$) in cyclic order. When $b_1 + b_2 - 1 > 0$, Γ is asymptotically stable.*

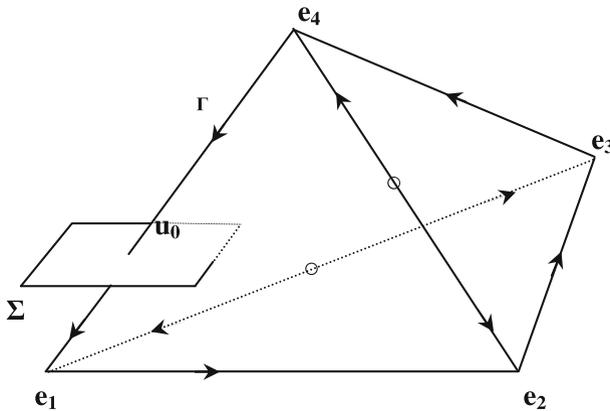


Fig. 1 The heteroclinic cycle Γ of (1.1) is the connection of e_i in the order of $e_1 \rightarrow e_2 \rightarrow e_3 \rightarrow e_4 \rightarrow e_1$. u_0 is a trivial point on Γ and Σ is a hyperplane perpendicular to Γ at u_0 . The empty circles denote the unstable equilibria (E_{2s}) on the boundary

Remark 2.4 While system (1.1) comes from (1.2) where $a_i \geq 0$ for $1 \leq i \leq n$, the constraints on b_i , $1 \leq i \leq n - 1$ in (1.1) for $n = 4$ are

$$\begin{aligned}
 b_1 + b_3 &\leq 1 - b_2, \\
 3b_1 - b_3 &\geq b_2 - 1, \\
 3b_3 - b_1 &\geq b_2 - 1, \\
 3b_2 - b_1 &\geq b_3 - 1.
 \end{aligned}
 \tag{2.2}$$

Since the analysis in this paper is limited in a parameter region $|b_1 + b_2 + b_3| < \epsilon$ where ϵ is sufficiently small, the constraints in (2.2) are not specifically considered. However, parameters are given under the constraints in numerical simulations.

3 Existence and uniqueness of periodic orbits

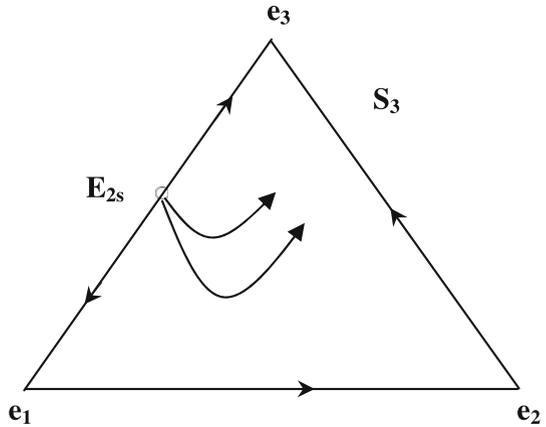
In this section, we establish the existence and uniqueness of a periodic orbit of (1.1) near the heteroclinic cycle Γ by analyzing the fixed point of the Poincaré map near Γ . In order to study how the dynamic behavior of (1.1) changes when the parameter b_2 varies, we fix the other parameters b_1 and b_3 .

Let $e_1 = (1, 0, 0, 0)^T$ and $e_i = S^{i-1}e_1$, $i = 2, 3, 4$. Then the heteroclinic cycle Γ is the connection of e_i in the order of $e_1 \rightarrow e_2 \rightarrow e_3 \rightarrow e_4 \rightarrow e_1$, which lies on the boundary of S_4 as shown in Fig. 1. The boundary of S_4 is denoted by $\text{bd}S_4$, and the following result shows the asymptotical stability of Γ on $\text{bd} S_4$.

Lemma 3.1 *Let (2.1) hold. The heteroclinic cycle Γ is asymptotically stable on $\text{bd}S_4$.*

Proof It follows from Lemma 2.1 that we only need to show Γ is asymptotically stable on the two-dimensional surface $S_3 = \{u \in S_4 : u_4 = 0 \text{ and } \sum_{i=1}^3 u_i = 1\}$. By Lemma 2.2, there are four equilibria of (1.1) on S_3 . Equilibrium e_1 has eigenvalues

Fig. 2 On S_3 , equilibria e_1 and e_2 are saddles, e_3 is a stable node and E_{2s} is an unstable node. Both equilibrium e_3 and the orbit $\overline{e_1 e_2} \cup \overline{e_2 e_3} \subset \Gamma$ are asymptotically stable on S_3



$-b_2$ and 1 with corresponding eigenvectors $(-1, 0, 1, 0)$ and $(-1, 1, 0, 0)$, respectively. It follows from $e_2 = Se_1$ and Lemma 2.2(i) that equilibrium e_2 has eigenvalues $-b_1$ and 1 with corresponding eigenvectors $(-1, 1, 0, 0)$ and $(0, -1, 1, 0)$, respectively. Then equilibria e_1 and e_2 are saddles on S_3 . Similarly, e_3 has eigenvalues $-b_1$ and $-b_2$ with corresponding eigenvectors $(0, -1, 1, 0)$ and $(1, 0, -1, 0)$, respectively. Then e_3 is a stable node. Since all the eigenvalues of E_{2s} are positive, E_{2s} is an unstable node on S_3 . While there is no interior equilibrium on the planar surface S_3 , we can draw the phase portraits of (1.1) on S_3 as shown in Fig. 2, where Γ is asymptotically stable on S_3 . \square

The Poincaré map near Γ can be approximated by the following projection (Hofbauer 1987; Hofbauer and Sigmund 1998, 15, p. 226, equation(17.20)):

$$L : z \rightarrow Pz + q, \tag{3.1}$$

where $z = (z_1, z_2)^T$. The heteroclinic cycle Γ corresponds to $z_1, z_2 \rightarrow +\infty$, and the periodic orbit of (1.1) near Γ corresponds to the fixed point $\hat{z} = (\hat{z}_1, \hat{z}_2)^T$ of L if \hat{z} is positive and large, i.e., $\hat{z} = (I - P)^{-1}q$ is positive and large when the matrix $I - P$ is invertible.

P and q in (3.1) are obtained as follows. At the equilibrium e_1 , eigenvalues $-b_1$ and 1 have eigenvectors on Γ , and eigenvalue $-b_2$ has an eigenvector $(-1, 0, 1, 0)$, which is transversal to Γ as shown in Fig. 1. By Lemma 2.1, similar discussions can be given for equilibria $e_i, i = 2, 3, 4$. That is, at e_i , eigenvalues $-b_1$ and 1 have eigenvectors on Γ , and eigenvalue $-b_2$ has an eigenvector which is transversal to $\Gamma, i = 2, 3, 4$. Hence, the matrix P comes from the combination of eight projections and can be expressed as the product of four matrices C (Hofbauer and Sigmund 1998, p. 226), i.e. $P = C^4$ and

$$C = \begin{pmatrix} b_2 & 1 \\ b_1 & 0 \end{pmatrix},$$

then

$$P = \begin{pmatrix} (b_1 + b_2^2)^2 + b_1 b_2^2 & b_2 (2b_1 + b_2^2) \\ b_1 b_2 (2b_1 + b_2^2) & b_1 (b_1 + b_2^2) \end{pmatrix}. \tag{3.2}$$

Similarly, the vector q comes from the combination of eight projections and can be expressed as the sum of four vectors as follows:

$$q = C^3 \alpha + C^2 \alpha + C \alpha + \alpha,$$

where $\alpha = (\alpha_1, \alpha_2)^T$ and

$$\alpha_1 = - \int_0^1 c_1(u_2) du_2, \quad \alpha_2 = - \int_0^1 c_2(u_2) du_2.$$

The function $c_1(u_2)$ is given by

$$\begin{aligned} c_1(u_2) &= \lim_{u_3, u_4 \rightarrow 0} \frac{\dot{u}_3}{u_3 \dot{u}_2} + b_2 \frac{1}{u_2} - \frac{1}{b_1} \frac{1}{1 - u_2} \\ &= \lim_{u_1 \rightarrow 1 - u_2} \frac{-b_2 u_1 + u_2 + (b_1 - 1) u_1 u_2}{u_1 u_2 (1 + (b_1 - 1) u_2)} + b_2 \frac{1}{u_2} - \frac{1}{b_1} \frac{1}{1 - u_2} \\ &= -b_2 \left(\frac{1}{u_2} + \frac{1 - b_1}{1 + (b_1 - 1) u_2} \right) + \left(\frac{1}{b_1} \frac{1}{1 - u_2} + \frac{b_1 - 1}{b_1} \frac{1}{1 + (b_1 - 1) u_2} \right) \\ &\quad + \frac{b_1 - 1}{1 + (b_1 - 1) u_2} + b_2 \frac{1}{u_2} - \frac{1}{b_1} \frac{1}{1 - u_2} \\ &= (b_1 - 1) \frac{1 + b_1 + b_1 b_2}{b_1 (1 + (b_1 - 1) u_2)}. \end{aligned}$$

Thus, we have

$$\alpha_1 = (1 + b_1 + b_1 b_2) \bar{b}_1, \quad \bar{b}_1 = \frac{-\log b_1}{b_1} > 0.$$

Similarly,

$$\begin{aligned} c_2(u_2) &= \lim_{u_3, u_4 \rightarrow 0} \frac{\dot{u}_4}{u_4 \dot{u}_2} + b_1 \frac{1}{u_2} + \frac{b_2}{b_1} \frac{1}{1 - u_2} \\ &= \lim_{u_1 \rightarrow 1 - u_2} \frac{-b_1 u_1 - b_2 u_2 + (b_1 - 1) u_1 u_2}{u_1 u_2 (1 + (b_1 - 1) u_2)} + b_1 \frac{1}{u_2} + \frac{b_2}{b_1} \frac{1}{1 - u_2} \\ &= -b_1 \left(\frac{1}{u_2} + \frac{1 - b_1}{1 + (b_1 - 1) u_2} \right) - b_2 \left(\frac{1}{b_1} \frac{1}{1 - u_2} + \frac{b_1 - 1}{b_1} \frac{1}{1 + (b_1 - 1) u_2} \right) \end{aligned}$$

$$\begin{aligned}
 & + \frac{b_1 - 1}{1 + (b_1 - 1)u_2} + b_1 \frac{1}{u_2} + \frac{b_2}{b_1} \frac{1}{1 - u_2} \\
 & = (b_1 - 1) \frac{b_1 + b_1^2 - b_2}{b_1(1 + (b_1 - 1)u_2)}.
 \end{aligned}$$

Therefore, we have

$$\alpha_2 = (b_1 + b_1^2 - b_2)\bar{b}_1.$$

Let

$$\mu = b_1 + b_2 - 1. \tag{3.3}$$

Then $P = P(\mu)$ and $q = q(\mu)$ are functions of μ since b_1 is fixed and $b_2 = 1 - b_1 + \mu$.

We now show that $I - P(\mu)$ is invertible. Since the matrix P in (3.2) is positive, it follows from Perron–Frobenius Theorem that there is a principal eigenvalue $\rho(\mu) > 0$ with corresponding left and right eigenvectors $v(\mu)$ and $w(\mu)$, which satisfy

$$\rho(\mu)^{-k} P^k z \rightarrow cw(\mu), \quad \forall z > 0, \quad k \rightarrow +\infty, \tag{3.4}$$

where $c = \sum_{i=1}^4 v_i z_i$ and $b_2 = 1 - b_1 + \mu$. A straightforward computation shows that $\rho(0) = 1$. Since the parameter b_1 in μ is fixed, all entries of matrix P in (3.2) are positive and strictly increasing functions of μ (i.e., b_2). Then $\rho(\mu)$ is a strictly increasing function of μ [21, p. 4]. Thus we have

$$\frac{d\rho}{d\mu} > 0.$$

Hence, if $\mu < 0$ then $\rho < 1$, and it follows from (3.4) that $P^k z \rightarrow 0+$, i.e., Γ is repelling. Similarly, if $\mu > 0$ then $\rho > 1$ and Γ is asymptotically stable.

Since $\frac{d\rho(\mu)}{d\mu} > 0$ and $\rho(0) = 1$, there is $\mu_1 > 0$ such that if $-\mu_1 < \mu < 0$, both eigenvalues of $P(\mu)$ are less than 1; if $0 < \mu < \mu_1$, only one of the eigenvalues is larger than 1. Thus, we have proved the following results.

Lemma 3.2 *There is $\mu_1 > 0$ such that when $|\mu| < \mu_1$ and $\mu \neq 0$,*

$$\det(I - P(\mu))\mu < 0.$$

Hence, $I - P(\mu)$ is invertible as $|\mu| < \mu_1$ and $\mu \neq 0$.

Next, we show that $(I - P(\mu))^{-1}q(\mu)$ is positive and large. When $|\mu| < \mu_1$ and $\mu \neq 0$, the projection L has a fixed point $\hat{z}(\mu)$:

$$\hat{z}(\mu) = (I - P(\mu))^{-1}q(\mu) = \frac{adj(I - P(\mu))q(\mu)}{\det(I - P(\mu))}. \tag{3.5}$$

Since

$$q(\mu) = (q_1(\mu), q_2(\mu))^T = \sum_{j=0}^3 C^j \alpha,$$

$$\sum_{j=0}^3 C^j = \begin{pmatrix} 1 + b_1 + b_2 + 2b_1b_2 + b_2^2 + b_2^3 & 1 + b_1 + b_2 + b_2^2 \\ b_1 + b_1b_2 + b_1^2 + b_1b_2^2 & 1 + b_1 + b_1b_2 \end{pmatrix},$$

where $b_2 = 1 - b_1 + \mu$, a long but straightforward computation shows that

$$q_1(\mu) = \left[1 + 13b_1 - 10b_1^2 + 6b_1^3 - 3b_1^4 + b_1^5 \right. \\ \left. + (20b_1 - 20b_1^2 + 12b_1^3 - 4b_1^4) \mu + O(\mu^2) \right] \bar{b}_1,$$

$$q_2(\mu) = \left[-1 + 3b_1 + 10b_1^2 - 6b_1^3 + 3b_1^4 - b_1^5 \right. \\ \left. + (-1 + 10b_1^2 - 8b_1^3 + 3b_1^4) \mu + O(\mu^2) \right] \bar{b}_1,$$

where $O(\mu^k)$ denotes that $\mu^k O(\mu^k)$ is a bounded function of μ as $\mu \rightarrow 0$ for $k \geq 1$.

Let $D = (d_{ij})_{2 \times 2}$ denote $\text{adj}(I - P(\mu))$. Then

$$D = \begin{pmatrix} 1 - b_1(b_1 + b_2^2) & b_2(2b_1 + b_2^2) \\ b_1b_2(2b_1 + b_2^2) & 1 - (b_1 + b_2^2)^2 - b_1b_2^2 \end{pmatrix}.$$

We have

$$(\text{adj}(I - P(\mu))q(\mu))_1 = d_{11}q_1 + d_{12}q_2 \\ = \left[16(b_1 - b_1^2 + b_1^3 - b_1^4) + 4(-1 + 8b_1 - 10b_1^2 \right. \\ \left. + 8b_1^3 - b_1^4) \mu + O(\mu^2) \right] \bar{b}_1,$$

$$(\text{adj}(I - P(\mu))q(\mu))_2 = d_{21}q_1 + d_{22}q_2 \\ = \left[16b_1^2(1 - b_1 + b_1^2 - b_1^3) + 4(1 - 4b_1 + 10b_1^2 \right. \\ \left. - 12b_1^3 + 9b_1^4) \mu + O(\mu^2) \right] \bar{b}_1. \tag{3.6}$$

Since

$$b_1 - b_1^2 + b_1^3 - b_1^4 > 0, \quad 1 - b_1 + b_1^2 - b_1^3 > 0,$$

it follows from (3.6) that there is $\mu_2 > 0$ ($\mu_2 < \mu_1$) such that when $|\mu| < \mu_2$, we have

$$(\text{adj}(I - P(\mu))q(\mu))_1 \geq 8(b_1 - b_1^2 + b_1^3 - b_1^4) \bar{b}_1 > 0, \\ (\text{adj}(I - P(\mu))q(\mu))_2 \geq 8b_1^2(1 - b_1 + b_1^2 - b_1^3) \bar{b}_1 > 0. \tag{3.7}$$

By Lemma 3.2, we have $\det(I - P(\mu)) > 0$ as $-\mu_2 < \mu < 0$ and $\det(I - P(0)) = 0$. Since

$$\hat{z}(\mu) = \frac{\text{adj}(I - P(\mu))q(\mu)}{\det(I - P(\mu))},$$

it follows from (3.7) and the continuity of $\det(I - P(\mu))$ that when $-\mu_2 < \mu < 0$, we have $\hat{z}(\mu) > 0$ and $\hat{z}(\mu) \rightarrow \infty$ as $\mu \rightarrow 0^-$. That is, there is a periodic orbit near Γ as μ is slightly less than zero, and the periodic orbit tends to Γ as μ converges to zero. We still denote the small interval by $-\mu_2 < \mu < 0$.

Finally, we show the periodic orbit of (1.1) is stable. By changing the variables $z = Z + \hat{z}(\mu)$ in the projection L , it becomes

$$L : Z \rightarrow PZ.$$

Since $\rho(\mu) < 1$ as $-\mu_2 < \mu < 0$, it follows from (3.4) that $P^k Z \rightarrow 0$ as $k \rightarrow +\infty$. That is, \hat{z} is asymptotically stable, which means that the periodic orbit is asymptotically stable. Then we have the following result on the stability of the periodic orbit.

Theorem 3.3 *Let (2.1) hold. There is $\mu_2 > 0$ ($\mu_2 < \mu_1$) such that when $-\mu_2 < \mu < 0$, there exists a periodic orbit near the heteroclinic cycle Γ . The periodic orbit is asymptotically stable and tends to Γ as $\mu \rightarrow 0$.*

We show the periodic orbit in Theorem 3.3 is unique in some region. On S_4 , let u_0 be a trivial point on Γ and Σ a hyperplane perpendicular to Γ at u_0 as shown in Fig. 1. While system (1.1) is defined on S_4 , we still denote $\Sigma \cap S_4$ by Σ . Let $O(u_0, \delta_\mu) = \{u : \|u - u_0\| < \delta_\mu\}$. It follows from Lemma 3.1 that for any μ with $|\mu| < \mu_2$, there is $\delta_\mu > 0$ such that the transversal section $O(u_0, \delta_\mu) \cap \Sigma$ satisfies that for any point $u \in O(u_0, \delta_\mu) \cap \Sigma$, the solution of (1.1) through u will cross Σ again at a point near u_0 . That is, the Poincaré map can be defined on $O(u_0, \delta_\mu) \cap \Sigma$.

Since δ_μ could be chosen such that it is a continuous function of μ , we have $\delta_0 = \min_{|\mu| \leq \mu_2/2} \delta_\mu > 0$. By Theorem 3.3, the periodic orbit tends to Γ as $\mu \rightarrow 0^-$. Then for $\delta_0 > 0$, there is $\mu_3 > 0$ ($\mu_3 < \mu_2/2$) such that for any μ with $-\mu_3 < \mu < 0$, there is a fixed point of (3.1) on $O(u_0, \delta_0) \cap \Sigma$. Since the matrix $I - P(\mu)$ is invertible as $-\mu_3 < \mu < 0$, the periodic orbit of (1.1) that crosses $O(u_0, \delta_0) \cap \Sigma$ is unique. Thus, we have just proved the following conclusion.

Theorem 3.4 *There are $\delta_0 > 0$ and $\mu_3 > 0$ ($\mu_3 < \mu_2/2$) such that as $-\mu_3 < \mu < 0$, the periodic orbit of (1.1) that crosses $O(u_0, \delta_0) \cap \Sigma$ is unique.*

4 Growth and disappearance of periodic orbits

In this section, we introduce a metric to measure the size of periodic orbits. Then we show that the periodic orbit, which is given in Theorems 3.3 and 3.4, grows in size as μ increases and disappears as μ is slightly larger than zero.

The size of the periodic orbit can be measured by $\|\hat{z}\| = |\hat{z}_1| + |\hat{z}_2|$. The reason is that while the heteroclinic cycle Γ corresponds to $z_1, z_2 \rightarrow +\infty$, then the larger the

$||\hat{z}||$ the closer the periodic orbit to Γ , which implies the larger the size of the periodic orbit. We show that the metric $||\hat{z}(\mu)||$ is a monotonously increasing function of μ . In fact, it follows from Lemma 3.2 that $\det(I - P(\mu)) > 0$ as $-\mu_3 < \mu < 0$. Then by (3.5), we need to show that (i) $\frac{d(\det(I - P(\mu)))}{d\mu} < 0$ and (ii) $\frac{d||adj(I - P(\mu))q(\mu)||}{d\mu} > 0$ when $-\mu_3 < \mu < 0$.

Since

$$\det(I - P) = \det \begin{pmatrix} 1 - (b_1 + b_2^2)^2 - b_1 b_2^2 & -b_2 (2b_1 + b_2^2) \\ -b_1 b_2 (2b_1 + b_2^2) & 1 - b_1 (b_1 + b_2^2) \end{pmatrix},$$

we have

$$\begin{aligned} \frac{d(\det(I - P(\mu)))}{d\mu} &= \frac{d(\det(I - P(\mu)))}{db_2} \\ &= 2b_2 \left(3b_1 (b_1 + b_2^2)^2 - 2(b_1 + b_2^2) + 2b_1^2 b_2^2 + b_1^3 - 2b_1 \right. \\ &\quad \left. - b_1 (2b_1 + b_2^2)^2 - 2b_1 b_2^2 (2b_1 + b_2^2) \right), \end{aligned}$$

where $b_2 = 1 - b_1 + \mu$. Let $\mu = 0$, i.e., $b_2 = 1 - b_1$, we have

$$\frac{d(\det(I - P(\mu)))}{d\mu} \Big|_{\mu=0} = -4(1 - b_1)(1 + b_1^2) < 0.$$

By the continuity of $\frac{d(\det(I - P(\mu)))}{d\mu}$, we have

Lemma 4.1 *There is $\mu_4 > 0$ ($\mu_4 < \mu_3$) such that when $-\mu_4 < \mu < 0$, $\frac{d(\det(I - P(\mu)))}{d\mu} < 0$.*

It follows from (3.7) that when $-\mu_4 < \mu < 0$, we have

$$(adj(I - P(\mu))q(\mu))_1 > 0, (adj(I - P(\mu))q(\mu))_2 > 0,$$

and

$$\begin{aligned} ||adj(I - P(\mu))q(\mu)|| &= (adj(I - P(\mu))q(\mu))_1 + (adj(I - P(\mu))q(\mu))_2 \\ &= [16(b_1 - b_1^2 + b_1^3 - b_1^4) + 16b_1^2(1 - b_1 + b_1^2 - b_1^3) \\ &\quad + 16(b_1 - b_1^3 + 2b_1^4)\mu + O(\mu^2)]\bar{b}_1, \end{aligned}$$

that is,

$$\frac{d||adj(I - P(\mu))q(\mu)||}{d\mu} \Big|_{\mu=0} = 16(b_1 - b_1^3 + 2b_1^4)\bar{b}_1 > 0.$$

It follows from the continuity of $\frac{d||adj(I - P(\mu))q(\mu)||}{d\mu}$ that there is $\mu_5 > 0$ ($\mu_5 < \mu_4$) such that when $-\mu_5 < \mu < 0$, $\frac{d||adj(I - P(\mu))q(\mu)||}{d\mu} > 0$. Hence, when $-\mu_5 < \mu < 0$

and μ increases, $\|\hat{z}\| = \frac{\|adj(I-P(\mu))q(\mu)\|}{det(I-P(\mu))}$ increases, which means that the periodic orbit in Theorems 3.3 and 3.4 increases in size. Then we have the following result.

Theorem 4.2 *Let (2.1) hold. There is $\mu_5 > 0$ ($\mu_5 < \mu_4$) such that as $-\mu_5 < \mu < 0$, the periodic orbit near the heteroclinic cycle Γ increases in size as μ increases.*

Finally, we will show that the large periodic orbit near Γ disappears when μ is slightly larger than zero. As discussed in the proof of Theorem 3.3, the fixed point of (3.1) as shown in (3.5) is positive when $-\mu_5 < \mu < 0$. However, when $0 < \mu < \mu_5$, it follows from Lemma 3.2 that $det(I - P(\mu)) < 0$. By (3.7), we have $adj(I - P(\mu))q(\mu) > 0$. Hence, $\hat{z}(\mu) = \frac{adj(I-P(\mu))q(\mu)}{det(I-P(\mu))}$ is negative. That is, there is no positive fixed point of (3.1) when $0 < \mu < \mu_5$. Then there is no periodic orbit of (1.1) which would cross through $O(u_0, \delta_0) \cap \Sigma$. Hence, the following conclusion holds.

Theorem 4.3 *Let (2.1) hold. When $0 < \mu < \mu_5$, there is no periodic orbit of (1.1) that would cross through $O(u_0, \delta_0) \cap \Sigma$.*

Therefore, it follows from Theorems 3.3, 3.4, 4.2 and 4.3 that the unique periodic orbit of (1.1), which crosses through $O(u_0, \delta_0) \cap \Sigma$ when $-\mu_5 < \mu < 0$, grows in size as b_2 increases, tends to Γ when $\mu \rightarrow 0-$, and disappears when $0 < \mu < \mu_5$.

Numerical simulations in Fig. 3 show that the periodic orbit of (1.1) grows in size when b_2 increases and disappears when $\mu > 0$. We select (u_1, u_2) in the solution $u = (u_1, u_2, u_3, u_4)$ as an example while similar principles can be shown for (u_3, u_4) . In the simulations, we fix $b_1 = 0.1$ and $b_3 = -0.2$. Then it follows from (2.2) that $0 < b_2 < 0.3$. Let $b_2 = 0.005, 0.01, 0.04, 0.11$, respectively, then $\mu = b_1 + b_2 + b_3 = -0.095, -0.09, -0.06, +0.01$, respectively. When $\mu = -0.095 < 0$, there is a small periodic orbit. The periodic orbit grows in size as b_2 increases from 0.005 to 0.01 to 0.04, and tends to Γ monotonously. When $\mu = 0.01 > 0$, the periodic orbit disappears and Γ is asymptotically stable. In Fig. 4, we select the first three components $(u_1(t), u_2(t), u_3(t))$ of solution $u(t)$ while $u_4(t) = 1 - u_1(t) - u_2(t) - u_3(t)$. Numerical simulations show that the periodic orbit of (1.1) is asymptotically stable in the three-dimensional space.

In Sect. 2, we changed the variables as follows: $\frac{b_1}{-b_3} \rightarrow b_1, \frac{b_2}{-b_3} \rightarrow b_2$ and $b_3 \rightarrow -1$. Now we take the reverse changes of variables and return to the original parameters b_1, b_2 and b_3 . Let $\hat{\mu} = -b_3\mu_5$. Then we can restate our results about (1.1) as follows.

Corollary 4.4 *Suppose $b_1 + b_3 < 0, b_2 > 0$ and $b_1b_3 < 0$. For $\hat{\mu} > 0$ and $\delta_0 > 0$, we have*

- (i) *When $-\hat{\mu} < b_1 + b_2 + b_3 < 0$, there is a unique periodic orbit of (1.1) that crosses through the transversal sector $O(u_0, \delta_0) \cap \Sigma$. The periodic orbit is asymptotically stable.*
- (ii) *The periodic orbit grows in size when b_2 increases in the interval $(-(b_1 + b_3) - \hat{\mu}, -(b_1 + b_3))$ and tends to the heteroclinic cycle Γ as $b_2 \rightarrow -(b_1 + b_3)$.*
- (iii) *There is no periodic orbit of (1.1) that would cross through $O(u_0, \delta_0) \cap \Sigma$ when $0 < b_1 + b_2 + b_3 < \hat{\mu}$.*
- (iv) *The heteroclinic cycle Γ is repelling as $b_1 + b_2 + b_3 < 0$ while it is asymptotically stable as $b_1 + b_2 + b_3 > 0$.*

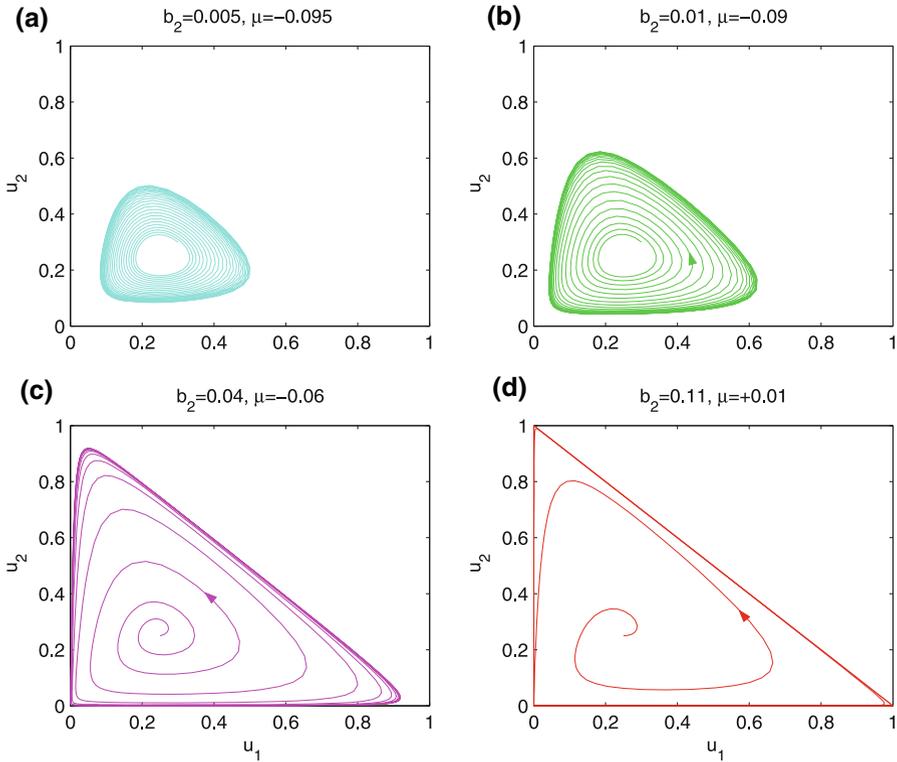


Fig. 3 In the computations, $b_1 = 0.1$ and $b_3 = -0.2$. Take $b_2 = 0.005, 0.01, 0.04, 0.11$, respectively, then $\mu = b_1 + b_2 + b_3 = -0.095, -0.09, -0.06, +0.01$, respectively. **a** When $\mu = -0.095 < 0$, there is a small periodic orbit. **b** The periodic orbit grows in size as b_2 increases from 0.005 to 0.01 to 0.04 and **c** tends to Γ monotonically. **d** When $\mu = 0.01 > 0$, the periodic orbit disappears and Γ is asymptotically stable

5 Applications and discussions

In this section, we apply our results to some ecological examples. As mentioned in Sect. 1, there are many semelparous species in natural environments. While different year classes of the species are identical except for their reproduction time, some of them go asymptotically extinct. The most interesting periodical species are the 13th and 17th year cicadas of eastern North America. What are the mechanisms that result in both the persistence of only one brood and the remaining of this brood? How could the year classes coexist?

The novel model (1.1) derived by Diekmann and van Gils (2009) provides a way to explore the mechanisms. Based on the model and basic results by Diekmann and van Gils (2009), our analysis gives some answers to the questions under conditions in Corollary 4.4. In fact, conditions in (2.1) have interesting ecological meanings. Consider the first equation of (1.2) for $n = 4$:

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

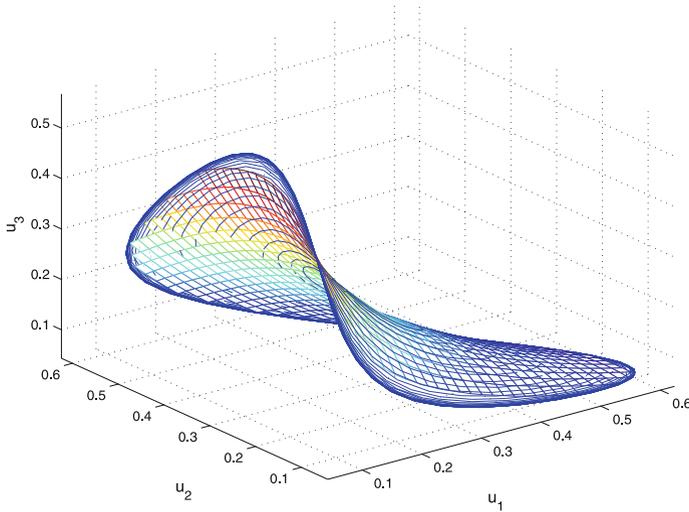


Fig. 4 In the computations, $b_1 = 0.1, b_2 = 0.01$ and $b_3 = -0.2$. The first three components $(u_1(t), u_2(t), u_3(t))$ of a solution $u(t)$ are selected while $u_4(t) = 1 - u_1(t) - u_2(t) - u_3(t)$. It is shown that the periodic orbit is asymptotically stable in the three-dimensional space

Then $\frac{a_i}{a_1}$ represents the competitive degree from the i th year class to the 1th year class, $i = 2, 3, 4$. As shown by [Adamic and Huberman \(2000\)](#) and [Lopez and Sanjuan \(2001\)](#), the competitive degree is called strong (weak) if $\frac{a_i}{a_1} > 1 (< 1)$. By (2.1), we have $b_1 > 0$ and $b_2 > 0$, i.e., $\frac{a_i}{a_1} > 1, i = 2, 3$. That is, the competition from the i th year class to the 1st year class is strong, $i = 2, 3$. By (2.1), we have $b_3 < 0$, i.e., $\frac{a_4}{a_1} < 1$. That is, the competition from the 4th year class to the 1st year class is weak. Since $b_1 = a_2 - a_1, b_2 = a_3 - a_1$ and $b_3 = a_4 - a_1$, condition $-(b_1 + b_3) - \hat{\mu} < b_2 < -(b_1 + b_3)$ in Corollary 4.4(i) can be rewritten as

$$1 - \frac{\hat{\mu}}{3a_1} < \frac{1}{3} \left(\frac{a_2}{a_1} + \frac{a_3}{a_1} + \frac{a_4}{a_1} \right) < 1.$$

That is, the average competitive degree $\frac{1}{3}(\frac{a_2}{a_1} + \frac{a_3}{a_1} + \frac{a_4}{a_1})$ from the other three year classes is slightly weak while two of them are strong. Corollary 4.4 shows that when the average competitive degree is slightly weak, the year classes coexist and present periodic oscillations. The oscillation magnitude grows monotonically as the parameter $\frac{a_3}{a_1}$ increases, where $\frac{a_3}{a_1}$ represents the competitive degree from the year class which is next to the next year class of the present one. In fact, as shown in Fig. 3a–c, orbits from the interior of the cone gradually converge to the periodic solution, which means the population densities of the broods change in a recurrent way and all of the broods are persistent as defined by [Hofbauer and Sigmund \(1998\)](#). Furthermore, the sizes of the periodic solutions in Fig. 3a–c increase monotonically as $\frac{a_3}{a_1}$ increases, which means the population densities of the broods vary in enlarged regions and the oscillations become more and more fierce. Here, the increase of $\frac{a_3}{a_1}$ is equivalent to the increase of b_2 since $b_2 = a_3 - a_1$ and a_1 is fixed in the simulations. Hence, the weak average

competitive degrees guarantee the coexistence of the broods, and the coexistence is in the form of periodic oscillations while the competitive degree $\frac{a_3}{a_1}$ plays an important role in the magnitude of the oscillations.

Corollary 4.4 also shows that when the average competitive degree becomes strong, i.e.,

$$1 < \frac{1}{3} \left(\frac{a_2}{a_1} + \frac{a_3}{a_1} + \frac{a_4}{a_1} \right) < 1 + \frac{\hat{\mu}}{3a_1},$$

the periodic solution disappears and Γ becomes asymptotically stable. Then the orbits near Γ converge to Γ gradually, which means the orbits spiral outward to the boundary of the cone in a recurrent and sequential movement near the equilibria e_i (with longer and longer time episodes). The ecological interpretation is as follows. When the orbits are not so close to Γ , the broods coexist and there is not a fixed brood that remains strong (dominant), i.e., the broods become the strong one in a cyclic way in the sense that one brood is growing when its predecessor declines while the dominant period of the broods becomes longer and longer. However, when the orbits gradually go close to e_i such that the quantities of other broods (i.e., not the i th brood) are less than one, all broods but the i th one go extinct. In fact, as shown in Fig. 3d, orbits initially converge to Γ in a recurrent way, which means that all the broods coexist while the strong brood is not the same one but changes in a cyclic way. When the orbits go close to e_i such that the quantities of all but the i th brood are less than one, only the i th brood could survive. Hence, it is the strong average competitive degree that results in the persistence of only one brood in the situation we considered.

The remaining of the particular year class can be discussed as follows. Since the orbit of (1.1) near Γ tends to Γ as $t \rightarrow \infty$, one of the year classes will go extinct as the first missing one when its number is less than one. Without loss of generality, let $x_4 = 0$. It follows from Lemma 3.1 that only the 3rd year classes can persist while other year classes will go extinct. Then by Lemma 2.1, if the i th year class is the first missing one, then the $(i - 1)$ th (modulo 4) year class will be the unique persistent class. Hence, the persistent year class is determined by the first missing class. The first missing class sensitively depends on the distribution of the initial population densities since the orbits of (1.1) tend to Γ in a cyclic way.

In a two-species competitive Lotka–Volterra system where the axial equilibria are locally stable, it is shown by Hofbauer and Sigmund (1988) and Murry (1993) that almost all the orbits converge to the axial equilibria without periodic oscillations and the strong subpopulation that has the largest initial density would persist. The result has been extended to higher dimensions (Drissche and Zeeman 1998; Wang 2003; Wang and Wu 2011; Xiao and Li 2000; Zeeman 1993; Zeeman and Zeeman 2002). It shows that in some ecological models where each of the competition degrees between subpopulations (not the average competitive degree) is strong, only the strongest one could persist while others go extinct. Our analysis shows a different result. In the situation we consider, there are both strong and weak competitions ($\frac{a_2}{a_1} > 1$, $\frac{a_3}{a_1} > 1$ but $\frac{a_4}{a_1} < 1$). While weak average competitive degrees imply coexistence with periodic oscillations, the strong average competitive degrees imply that there is only one persistent subpopulation, which is not necessarily the one that has the largest initial

density, but depends on the distribution of initial population densities in a sensitive way.

While the periodic orbits shown in this paper are close to the heteroclinic cycle on the boundary, the coexistence derived from their stability seems not so strong from the ecological viewpoint. However, our work demonstrates both the effect of the average competitive degrees on the coexistence and the effect of some particular factor on the increase of the magnitudes of the periodic oscillations, which is verified in large regions by numerical simulations. In fact, numerical simulations in Fig. 3 show that when the average competitive degree is weak as shown in Fig. 3a, there is a stable periodic orbit near the positive equilibrium (E_4) where the coexistence is strong. Furthermore, the increase of the particular factor ($\frac{a_3}{a_1}$) in large regions also leads to the increase of the magnitude of the periodic orbit as shown in Fig. 3a–c. While our result is restricted to a small region, it is possible that the result could be extended to large regions, which still remains a challenge in the conjecture by Diekmann and van Gils (2009).

References

- Adamic LA, Huberman BA (2000) Powerlaw distribution of the world wide web. *Science* 287:2115
- Behncke H (2000) Periodical cicadas. *J Math Biol* 40:413–431
- Bulmer MG (1977) Periodic insects. *Am Nat* 111:1099–1117
- Cushing JM (2006) Nonlinear semelparous Leslie models. *Math Biosci Eng* 3:17–36
- Cushing JM (2009) Three stage semelparous Leslie models. *J Math Biol* 59:75–104
- Davydova NV (2004) Old and young. Can they coexist? thesis, University of Utrecht. <http://igitur-archive.library.uu.nl/dissertations/2004-0115-092805/UUindex.html>
- Davydova NV, Diekmann O, van Gils SA (2003) Year class competition or competitive exclusion for strict biennials? *J Math Biol* 46:95–131
- Davydova NV, Diekmann O, van Gils SA (2005) On circulant populations. I. The algebra of semelparity *Linear Algebra Appl* 398:185–243
- Diekmann O, van Gils SA (2003) Invariance and symmetry in a year-class model, in bifurcations, symmetry and patterns (Porto, 2000). pp 141–150. Birkhäuser, Basel
- Diekmann O, van Gils SA (2009) On the cyclic replicator equation and the dynamics of semelparous populations *SIAM J Appl Dyn Syst* 8:1160–1189
- Edalat A, Zeeman EC (1992) The stable classes of the codimension-one bifurcations of the planar replicator system *Nonlinearity* 5:921–939
- Hofbauer J (1987) Heteroclinic cycles on the simplex. Farkas M, Kertész V, Stépán G (eds) *Proc Int Conf Nonlinear Oscillations*. Janos Bolyai Mathematical Society, Budapest
- Hofbauer J, Sigmund K (1988) *The theory of evolution and dynamical system: mathematical aspects of selection*. London Mathematical Society Student Texts, vol 7. Cambridge University Press, Cambridge
- Hofbauer J, Sigmund K (1998) *Evolutionary games and population dynamics*. Cambridge University Press, Cambridge
- Kon R (2005) Nonexistence of synchronous orbits and class coexistence in matrix population models *SIAM J Appl Math* 66:616–626
- Kon R, Iwasa Y (2007) Single-class orbits in nonlinear Leslie matrix models for semelparous populations *J Math Biol* 55:781–802
- Lopez L, Sanjuan MAF (2001) Defining strategies to win in the Internet market *Physica A* 301:512–534
- Mjølhus E, Wikan A, Solberg T (2005) On synchronization in semelparous populations *J Math Biol* 50: 1–21
- Murry JD (1993) *Mathematical biology*. Springer, New York
- van den Drissche P, Zeeman ML (1998) Three-dimensional competitive Lotka–Volterra systems with no periodic orbits *SIAM J Appl Math* 58:227–234

- Wang Y (2003) Necessary and sufficient conditions for the existence of periodic orbits in a Lotka–Volterra system *J Math Anal Appl* 284:236–249
- Wang Y, Wu H (2011) A mutualism-competition model characterizing competitors with mutualism at low density *Math Comput Model* 53:1654–1663
- Xiao D, Li W (2000) Limit cycles for the competitive three dimensional Lotka–Volterra system *J Differ Equ* 164:1–15
- Zeeman ML (1993) Hopf bifurcation in competitive three-dimensional Lotka–Volterra systems *Dyn Stab Syst* 8:189–217
- Zeeman EC, Zeeman ML (2002) From local to global behavior in competitive Lotka–Volterra systems *Trans Am Math Soc* 355:713–734