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On the Cyclic Replicator Equation and the Dynamics of Semelparous Populations*

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Abstract. A semelparous organism reproduces only once in its life and dies thereafter. If there is only one opportunity for reproduction per year, and all individuals born in a certain year reproduce k years later, then the population can be divided into year classes according to the year of birth modulo k. The dynamics is described by a discrete-time nonlinear Leslie matrix model, where the nonlinearity enters through the density dependent fertility and mortality rates. When the reproduction ratio is close to one, the full-life-cycle-map can be approximated by the solution of a differential equation of Lotka–Volterra type, which inherits the cyclic symmetry that is present in the full-life-cycle-map. The Lotka–Volterra equation can next be reduced to the replicator equation on the $(k-1)$-dimensional simplex. In this paper we classify the repertoire of dynamical behavior for $k = 2, 3$ and derive an almost complete picture for $k = 4$, with some open problems identified. We pay special attention to the single year class (SYC) state (all but one year class are absent), multiple year class patterns (with several but not all year classes present), heteroclinic cycles, and periodic orbits.

Key words. replicator equation, semelparity, Lotka–Volterra

AMS subject classifications. 34C05, 34C23, 34C25, 34C37, 37G15

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1. Introduction.

In this paper we study the system of ordinary differential equations

$$\dot{u}_i = \left(-(Au)_i + \sum_j u_j (Au)_j \right) u_i, \quad i = 1, \dots, k, \tag{1.1}$$

where u is a k-vector that belongs to the $(k-1)$-dimensional simplex Σ, defined by

$$\Sigma = \left\{ u \in \mathbb{R}^k : \sum_{j=1}^{k} u_j = 1, \quad u_j \geq 0, \ j = 1, \dots, k \right\}, \tag{1.2}$$

and A is a circulant matrix, i.e.,

$$A = \begin{pmatrix} a_1 & a_2 & \dots & a_k \\ a_k & a_1 & \dots & a_{k-1} \\ \vdots & \vdots & & \vdots \\ a_2 & a_3 & \dots & a_1 \end{pmatrix} \tag{1.3}$$

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with

$$\sum_{1}^{k} a_i = 1, \tag{1.4}$$

or, in words, the rows of A are obtained from the first normalized row by cyclic permutation. Let S be the shift defined by

$$S = \begin{pmatrix} 0 & 0 & \dots & 0 & 1 \\ 1 & 0 & \dots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \dots & 1 & 0 \end{pmatrix}. \tag{1.5}$$

One easily verifies that $AS = SA$, that $u \cdot v = Su \cdot Sv$ (with $u \cdot v = \sum_{j=1}^{k} u_j v_j$), and that, as a consequence, $f(Su) = Sf(u)$, where $f : \mathbb{R}^k \to \mathbb{R}^k$ is componentwise defined by the right-hand side of (1.1). So S maps orbits of (1.1) onto orbits of (1.1), or, in more technical jargon, (1.1) is equivariant with the representation of the cyclic group generated by S. Accordingly we call (1.1) the cyclic replicator equation (see [12] for a motivated introduction to the replicator equation as well as a survey of the known results).

Our aim is to classify the repertoire of dynamical behavior that solutions to the replicator equation exhibit. We will succeed for $k = 2$ and $k = 3$ and almost succeed for $k = 4$. The study of higher values of k is left for the future (a Ph.D. student has just embarked on this subject). Our findings so far are summarized in the concluding section.

Of course the classification is greatly simplified by the restriction to cyclic symmetry. We refer the reader to [3, 6, 7, 8, 9, 10, 11] for classification under no or other restrictions.

In our way of thinking, the components of the vector u describe the relative magnitudes of k competing subpopulations. Indeed, one can deduce (1.1) from the cyclic logistic equation

$$\dot{y}_i = (1 - (Ay)_i)\, y_i, \quad i = 1, \dots, k, \tag{1.6}$$

by writing $y_i = u_i \sum_{j=1}^{k} y_j$ and next performing an implicit rescaling of the time to eliminate the scalar $\sum_{j=1}^{k} y_j$ from the equation for u. Equation (1.6) is nongeneric in two ways: all subpopulations have the *same* intrinsic growth rate, viz. 1, and the competitive interaction matrix A is a circulant. In section A.2 we show that both of these features occur naturally when we derive (1.6), by way of a limiting procedure, from a discrete-time model for a semelparous population.

A species is called *semelparous* if individuals reproduce only once in their lives (simply because reproduction has death as an inevitable consequence). Examples include annual and biennial plants, Pacific salmon, cicadas, and many other insects. If there is only one reproduction opportunity per year, the length of the life cycle is necessarily an integer number of years. In earlier work [14, 16, 17] with Natalia Davydova, we have extensively investigated a discrete-time model incorporating two key assumptions (see also [18, 19, 20]):

- The period between being born and reproducing is *exactly* k years.
- Interaction is by way of feedback to a *scalar* quantity describing the environmental condition.

The first of these guarantees that all individuals born in some year will, provided they survive, mate and reproduce k years later and hence are *reproductively isolated* from individuals born in other years. Let us call the subpopulation of individuals that reproduce in year j (modulo k) the jth *year class*. Then clearly year classes may be missing from the population. Bulmer [2] calls an insect *periodical* if all but one year class are missing. The most famous examples are certain cicada species in North America (see, e.g., [13] and the references therein).

Even though the year classes are reproductively isolated, they still interact by way of feedback to the environmental condition. How many year classes will coexist? How many are driven to extinction? How does the answer depend on the age-specific impact on the environmental condition and on the age-specific sensitivity to the environmental condition? And what kind of bifurcations mark the transition?

Note that year classes are *identical* except for the *timing* of birth. Yet, as implicated by the questions above, there can be winners and losers. The distinction is made by the phase in the life cycle at which certain environmental conditions are experienced (for instance, if food is plentiful when you need little, but scarce when you need a lot, you do have bad luck). If the environmental condition fluctuates periodically, the correspondence between the phase in the life cycle and the phase in the environmental cycle can have a decisive influence on the outcome of the competitive interaction!

The discrete-time dynamics is generated by a map which is the nonlinear analogue of a positive linear map which is irreducible but periodic, in the sense that the kth iterate is diagonal. The linearization at zero has eigenvalues $R_0 \cdot$ (roots of unity of order k) $= R_0 \exp^{i\frac{2\pi m}{k}}$ $(m = 0, 1, \ldots, k-1)$, where R_0 is the basic reproduction number, i.e., the expected number of offspring per newborn individual when density dependence is simply ignored. For $R_0 < 1$, all year classes become extinct; for $R_0 > 1$, every year class will persist if all the others are missing. From a mathematical point of view, the bifurcation at $R_0 = 1$ is highly degenerate. In particular, it is unclear what dynamics we should expect for R_0 slightly larger than one.

The derivation of (1.6) in section A.2 involves the following steps:

- consider the full-life-cycle-map, i.e., the kth iterate;
- assume $R_0 = 1 + \epsilon$ with ϵ positive but small; then the full-life-cycle-map is a near-identity map;
- zoom in on an ϵ-neighborhood of the origin in the state space;
- let ϵ tend to zero.

We therefore view (1.1) as a normal form description of the dynamics of a semelparous population with R_0 slightly bigger than one and a life cycle of precisely k years.

2. The cyclic replicator equation: Some general observations.

Before we start analyzing (1.1) in low dimensions, we first state some facts that hold in any dimension. That (1.1) is equivariant with respect to S is the content of the first lemma. Next we observe that we may reduce the number of parameters by one: only the differences $a_i - a_1$, $i = 2, \ldots, k$, matter for the dynamics of (1.1) on the simplex (1.2).

Lemma 2.1. *The replicator equation is equivariant with respect to S.*

Proof. Using the fact that A commutes with S, we find

$$\begin{aligned}\frac{d}{dt}(Su)_i = (S\dot{u})_i = \dot{u}_{i-1} &= (-(Au)_{i-1} + u \cdot Au)u_{i-1} \\ &= (-(SAu)_i + (Su \cdot SAu))(Su)_i \\ &= (-(ASu)_i + (Su \cdot ASu))(Su)_i,\end{aligned}$$

which shows that Su satisfies (1.1). ■

Adding a constant to a column of A does not change (1.1) on the simplex.

Lemma 2.2. *Let B be the matrix obtained from A by subtracting the constant c from every element of the jth column, i.e., $b_{il} = a_{il}$ for $l \neq j$ and $b_{ij} = a_{ij} - c$, $i = 1, \dots, k$. Let u be a function of t satisfying (1.2). Then u satisfies (1.1) iff u satisfies (1.1) with A replaced by B.*

Proof. We look at the ith equation,

$$\begin{aligned}\dot{u}_i &= u_i \left(-\sum_{l=1}^{k} a_{il}u_l + \sum_{m,l=1}^{k} u_m a_{ml} u_l \right) \\ &= u_i \left(-\sum_{l=1}^{k} b_{il}u_l - cu_j + \sum_{m,l=1}^{k} u_m b_{ml} u_l + \sum_{m=1}^{k} u_m c u_j \right) \\ &= u_i \left(-\sum_{l=1}^{k} b_{il}u_l + \sum_{m,l=1}^{k} u_m b_{ml} u_l \right),\end{aligned}$$

which proves the assertion. ■

Note that we did not use the normalization (1.4). So we may apply this lemma with $c = a_1$ successively to all columns. Thus we obtain the replicator equation with A replaced by B,

$$\dot{u}_i = \left(-(Bu)_i + \sum_j u_j (Bu)_j \right) u_i, \quad i = 1, \dots, k, \tag{2.1}$$

where

$$B = \begin{pmatrix} 0 & b_1 & \dots & b_{k-1} \\ b_{k-1} & 0 & \dots & b_{k-2} \\ \vdots & & & \vdots \\ b_1 & b_2 & \dots & 0 \end{pmatrix} \tag{2.2}$$

with

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

In conclusion, the dynamics generated by (1.1) on the simplex is exactly the same as the dynamics generated by (2.1).

Remark 2.3. Note that $\sum_{j=1}^{k-1} b_j = 1 - ka_1$. Hence the inverse parameter transformation is given by $a_1 = \frac{1}{k}\left(1 - \sum_{l=1}^{k-1} b_l\right)$, $a_j = b_{j-1} + a_1$ for $j \geq 2$, and the constraints on the parameters b_j are accordingly

$$\sum_{l=1}^{k-1} b_l \leq 1, \quad b_j + \tfrac{1}{k}\left(1 - \sum_{l=1}^{k-1} b_l\right) \geq 0, \ j = 1, \dots, k-1. \tag{2.3}$$

Remark 2.4. Note that (1.1) is invariant under $(A,t) \to (-A,-t)$. This *parameter symmetry* also holds when A is replaced by B. When drawing phase portraits, we can restrict our attention to half of the parameter space.

We will use the symbol $\mathbb{1}$ to denote the column vector with all ones. The dimension should be clear from the context.

Remark 2.5. If $\bar{u}$ is an *internal equilibrium* of (1.1), i.e., $\bar{u} \notin \partial\Sigma$, then

$$-B\bar{u} + \sum_{j=1}^{k} \bar{u}_j (B\bar{u})_j \, \mathbb{1} = 0.$$

If B is invertible, then $\bar{u} \in \operatorname{span}\{B^{-1}\mathbb{1}\}$. By inspection we see that $\bar{u} = \frac{1}{k}\mathbb{1}$ is an internal equilibrium. This equilibrium is unique, on the simplex, if B is invertible.

The linearized equation about this equilibrium is given by

$$\dot{z}_i = -\frac{1}{k}(Bz)_i + \frac{1}{k^2}\sum_{j=1}^{k}(Bz)_j \tag{2.4}$$

for vectors z satisfying $\sum_{j=1}^{k} z_j = 0$.

Remarkably, it turns out that one can determine the eigenvalues corresponding to the linear system (2.4) explicitly. The key observation is that B is a polynomial in S^{-1}:

$$B = \sum_{i=1}^{k-1} b_i S^{-i}.$$

Since

$$S\xi_n = \lambda_n \xi_n, \quad n = 0, 1, \ldots, k-1,$$

where

$$\lambda_n = e^{n\frac{2\pi i}{k}}$$

and

$$\xi_n = \begin{pmatrix} 1 \\ \lambda_n^{-1} \\ \vdots \\ \lambda_n^{-k+1} \end{pmatrix},$$

we obtain a precise determination of the eigenvalues of B as a direct corollary.

Lemma 2.6. *$B\phi = \mu\phi$ iff $\mu = p(\lambda_n^{-1})$ and $\phi = \xi_n$ for some $n \in \{0, 1, \ldots, k-1\}$. Here p is the polynomial*

$$p(z) = b_1 z + \cdots + b_{k-1} z^{k-1}.$$

Proof. $B\xi_n = p(\lambda_n^{-1})\xi_n$, so ξ_n is an eigenvector corresponding to eigenvalue $p(\lambda_n^{-1})$. As we find k independent eigenvectors in this manner, there are no other linearly independent eigenvectors. ■

The matrix associated with the right-hand side of (2.4) is C defined by

$$Cz = -\frac{1}{k}Bz + \frac{1}{k^2}\sum_{j=1}^{k}(Bz)_j \mathbb{1}.$$

Now observe that for $n \neq 0$

$$\sum_{j=1}^{k}\xi_{n,j} = \sum_{j=0}^{k-1}\lambda_n^{-j} = \frac{1-\lambda_n^{-k}}{1-\lambda_n^{-1}} = 0$$

and that consequently

$$\sum_{j=1}^{k}(B\xi_n)_j = p(\lambda_n^{-1})\sum_{j=1}^{k}\xi_{n,j} = 0.$$

In combination with Lemma 2.6, this observation leads to the characterization of the eigenvalues and eigenvectors of C.

Lemma 2.7. *For $n = 1, \ldots, k-1$ we have*

$$C\xi_n = -\frac{1}{k}p(\lambda_n^{-1})\xi_n.$$

These are the eigenvalues and eigenvectors associated with the invariant subspace $\{z : \sum_{j=1}^{k} z_j = 0\}$ of (2.4); for completeness we observe that $C\xi_0 = 0$, so ξ_0 spans an orthogonal invariant one-dimensional subspace corresponding to eigenvalue 0.

We finally observe that at a boundary equilibrium with $k-m$ components equal to 0 there are $k-m$ eigenvalues with corresponding eigenvectors that, after translation to the equilibrium, lie on the boundary of the simplex and m eigenvalues with corresponding eigenvectors that, after translation to the equilibrium, point into the simplex.

Lemma 2.8. *Let $\hat{u} = (\hat{u}_1, \ldots, \hat{u}_m, 0, \ldots, 0)^T$ be an equilibrium of (2.1). The linearization about this equilibrium takes the form*

$$\dot{\eta}_i = \begin{cases} \hat{u}_i(-(B\eta)_i + \eta \cdot B\hat{u} + \hat{u} \cdot B\eta), & i = 1, \ldots, m, \\ \eta_i(-(B\hat{u})_i + \hat{u} \cdot B\hat{u}), & i = m+1, \ldots, k. \end{cases} \tag{2.5}$$

Hence the following hold:

(i) *There are $k-m$ eigenvectors that have $k-m-1$ out of the last $k-m$ components equal to 0, and the corresponding eigenvalues are given by*

$$-(B\hat{u})_i + \hat{u} \cdot B\hat{u}, \ i = m+1, \ldots, k.$$

(ii) *$\hat{u} \cdot B\hat{u}$ is an eigenvalue with corresponding adjoint eigenvector given by $\mathbb{1}$.*

(iii) *The subspace*

$$Z := \left\{ \eta : \sum_{j=1}^{m}\eta_j = 0 \text{ and } \eta_i = 0 \text{ for } i = m+1, \ldots, k \right\}$$

is invariant. For $\eta \in Z$ we have $\eta \cdot B\hat{u} = 0$ and

$$\dot{\eta}_i = \hat{u}_i \left(-(M\eta)_i + \hat{u} \cdot M\eta\right),$$

where M denotes the m-truncation of B.

Proof. The statement (i) is a direct consequence of the block diagonal form of (2.5) and the fact that the lower right block is diagonal. To prove (ii), we first note that $\sum_{i=1}^{m} \hat{u}_i = 1$ and that $(B\hat{u})_i = \hat{u} \cdot B\hat{u}$ for $i = 1, \ldots, m$. By summation we deduce from (2.5) that

$$\begin{aligned}\sum_{i=1}^{k} \dot{\eta}_i = &-\sum_{i=1}^{m} \hat{u}_i (B\eta)_i + \eta \cdot B\hat{u} + \hat{u} \cdot B\eta \\ &- \sum_{i=m+1}^{k} \eta_i (B\hat{u})_i + \hat{u} \cdot B\hat{u} \sum_{i=m+1}^{k} \eta_i.\end{aligned}$$

The first and the third term on the right-hand side cancel. Hence

$$\begin{aligned}\sum_{i=1}^{k} \dot{\eta}_i &= \sum_{i=1}^{m} \eta_i (B\hat{u})_i + \hat{u} \cdot B\hat{u} \sum_{i=m+1}^{k} \eta_i \\ &= \hat{u} \cdot B\hat{u} \sum_{i=1}^{k} \eta_i.\end{aligned}$$

This establishes (ii) but also shows that the subspace

$$\left\{ \eta : \sum_{i=1}^{k} \eta_i = 0 \right\}$$

is invariant. Z is the intersection of this invariant subspace with another invariant subspace, viz.,

$$\{ \eta : \ \eta_i = 0 \text{ for } i = m+1, \ldots, k \}.$$

Since $(B\hat{u})_i$ is independent of i for $i = 1, \ldots, m$, we have that $\eta \cdot B\hat{u} = 0$ for $\eta \in Z$, and hence the last statement follows directly from (2.5). ■

Remark 2.9. The eigenvalues mentioned in (i) correspond to directions in which one new year class is introduced. They are called external eigenvalues in [12]. In our earlier discrete time work we called them transversal eigenvalues.

3. $k = 2$: Either coexistence or competitive exclusion.

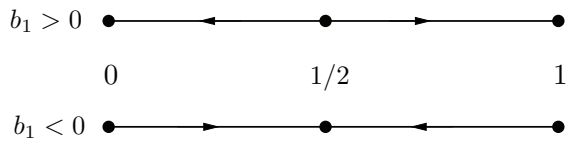
For $k = 2$ the system is completely described by the scalar equation

$$\dot{u}_1 = 2b_1 u_1 (u_1 - \tfrac{1}{2})(1 - u_1), \tag{3.1}$$

and so there are two generic situations:

(i) $b_1 > 0$. One of the two year classes outcompetes the other.

(ii) $b_1 < 0$. The two year classes coexist with equal population size.



The transition is by way of a vertical bifurcation: for $b_1 = 0$ the two year classes can coexist with any ratio between the two population sizes.

4. $k = 3$: A heteroclinic cycle as yet another possibility. If we reformulate the strict dichotomy that we found for $k = 2$ as "either coexistence in steady state or convergence to the boundary of the simplex," then we shall find the same dichotomy for $k = 3$. But now there are other candidate ω-limit sets at the boundary, in addition to the single year class (SYC) equilibria. Double year class equilibria may or may not exist, but, as it turns out, they are always unstable. For a substantial parameter region a heteroclinic cycle of stone-scissors-paper type attracts all interior orbits (apart from the coexistence steady state). Again the transition between the two generic possibilities is by way of a vertical bifurcation—this time a Hopf bifurcation. For the critical parameter values the vector field is Hamiltonian and a one-parameter family of periodic coexistence orbits "fills" the simplex.

When $k = 3$, the matrix B in (2.1) takes the form

$$B = \begin{pmatrix} 0 & b_1 & b_2 \\ b_2 & 0 & b_1 \\ b_1 & b_2 & 0 \end{pmatrix} \tag{4.1}$$

with eigenvalues $b_1 + b_2$ and $-\frac{1}{2}(b_1 + b_2) \pm \frac{1}{2}\sqrt{3}i(b_2 - b_1)$.

We adopt the convention that the symbol E_n denotes an equilibrium with n nonvanishing year classes.

The eigenvalues associated with the linearization about the internal equilibrium $E_3 = \frac{1}{3}\mathbb{1}$ are

$$\tfrac{1}{6}(b_1 + b_2) \pm i\tfrac{\sqrt{3}}{6}(b_2 - b_1),$$

and so the stability character of E_3 is determined by the sign of $b_1 + b_2$. In order to show that the sign of $b_1 + b_2$ has a strong impact on the global dynamics, we introduce the Lyapunov function

$$V(u) = u_1 u_2 u_3. \tag{4.2}$$

A straightforward but lengthy computation shows that on the invariant simplex, where $u_3 = 1 - u_1 - u_2$,

$$\begin{aligned} \dot{V}(u) &= -(b_1 + b_2)V(u)(1 - 3u_1 - 3u_2 + 3u_1^2 + 3u_1u_2 + 3u_2^2) \\ &= -(b_1 + b_2)V(u)\{(u_1 - \tfrac{1}{3})^2 + (u_1 - \tfrac{1}{3})(u_2 - \tfrac{1}{3}) + (u_2 - \tfrac{1}{3})^2\}. \end{aligned}$$

The function $u \mapsto (u_1 - \frac{1}{3})^2 + (u_1 - \frac{1}{3})(u_2 - \frac{1}{3}) + (u_2 - \frac{1}{3})^2$ takes its minimum zero at E_3 but is strictly positive everywhere else on the simplex.

Remark 4.1. The use of this Lyapunov function goes back to [4].

Theorem 4.2. (i) *If $b_1 + b_2 > 0$, the function V strictly decreases along every interior orbit that is not E_3. Consequently, the ω-limit set of any such orbit belongs to the boundary of the simplex.*

(ii) *If $b_1 + b_2 < 0$, the function V strictly increases along every interior orbit that is not E_3. Consequently, E_3 is globally asymptotically stable in the sense that it is the ω-limit set of any orbit starting in the interior of the simplex.*

(iii) *If $b_1 + b_2 = 0$, the system is Hamiltonian with*

$$H(u) = b_1 u_1 u_2 (1 - u_1 - u_2). \tag{4.3}$$

For $b_1 \neq 0$ the level sets of H are closed curves, and so the simplex is "filled" with (foliated by) a one-parameter family of periodic orbits with E_3 in the "middle" and a heteroclinic cycle at the boundary.

Proof. The statements (i) and (ii) follow directly from the formula for $\dot{V}(u)$ presented above, so we concentrate on (iii). If $b_1 + b_2 = 0$, then $u \cdot Bu = 0$ and

$$\dot{u}_1 = b_1 u_1 (1 - u_1 - 2u_2) = \frac{\partial H}{\partial u_2},$$
$$\dot{u}_2 = b_1 u_2 (-1 + 2u_1 + u_2) = -\frac{\partial H}{\partial u_1}.$$

The statement about the level curves follows directly from the fact that H has a maximum or a minimum at E_3, depending on the sign of b_1, while there are no other critical points in the interior of the simplex. Note that the boundary of the simplex is precisely the level set of H corresponding to the value zero. ■

Next we investigate the boundary dynamics. Because of the cyclic symmetry, we can restrict our attention to the invariant line segment

$$\{u : \ u_3 = 0, \, u_2 = 1 - u_1, \, 0 \leq u_1 \leq 1\},$$

on which the dynamics is generated by

$$\dot{u}_1 = u_1 (1 - u_1) \{(b_1 + b_2) u_1 - b_1\}. \tag{4.4}$$

The steady states $u_1 = 0$ and $u_1 = 1$ are both of the E_1 category. If b_1 and b_2 have the same sign, there is a steady state

$$u_1 = \frac{b_1}{b_1 + b_2}$$

with corresponding

$$u_2 = \frac{b_2}{b_1 + b_2},$$

which is of the E_2 category. In order for this steady state to be stable within the invariant line segment, we need that b_1 and b_2 are negative, and according to Theorem 4.2(ii), the E_2 equilibria are unstable in this case. We conclude that the E_2 equilibria cannot be stable.

We can now supplement Theorem 4.2(i) and characterize the ω-limit set of interior orbits more precisely:

- If both $b_1 > 0$ and $b_2 > 0$, the ω-limit set is one of the three E_1 equilibria. The domains of attraction of these three attractors are separated by the stable manifolds of the E_2 equilibria.
- If b_1 and b_2 are of different sign (or one is zero), but $b_1 + b_2 > 0$, the ω-limit set is a heteroclinic cycle connecting the three E_1 equilibria (in the direction $1 \to 2 \to 3$ if $b_1 \leq 0$ and the other way around if $b_1 > 0$).

Figure 1 summarizes the information derived above by showing how, for $k = 3$, the phase portrait depends on the parameters b_1 and b_2.

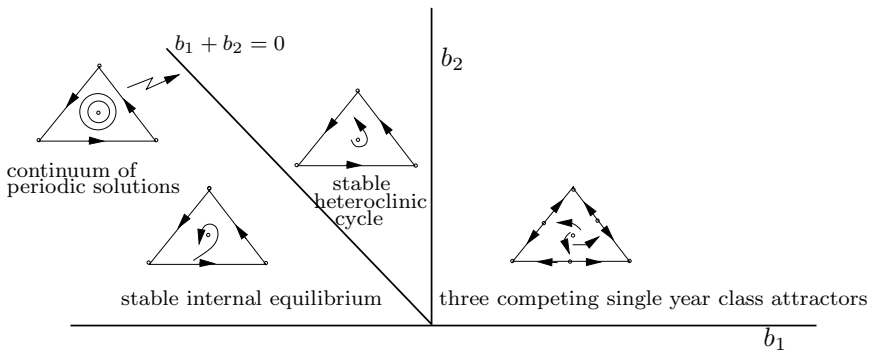


Figure 1. *The phase portrait in the (b_1, b_2)-plane. For opposite values $(-b_1, -b_2)$ of (b_1, b_2), the phase portraits are related by reversal of all arrows.*

5. The replicator equation in dimension four.

When $k = 4$ we lose the strict dichotomy. The attractors that occur in an open region in parameter space are E_1, the SYC solution, E_{2a}, the two-consecutive-year classes solution, E_{2s}, the two-nonconsecutive-year classes solution, E_4, the internal steady state with all year classes present, HCI, the heteroclinic cycle that connects the four single-year class solutions, HCII, the heteroclinic cycle that connects the four two-consecutive-year classes solutions, and finally periodic solutions.

Essential is a codimension two manifold in parameter space for which the whole state space is filled with periodic orbits, equilibria, and heteroclinic cycles. The precise unfolding of this codimension two bifurcation, even within the class of replicator equations considered here, is beyond the scope of this paper.

5.1. Global aspects.

When $k = 4$, the matrix B in (2.1) takes the form

$$B = \begin{pmatrix} 0 & b_1 & b_2 & b_3 \\ b_3 & 0 & b_1 & b_2 \\ b_2 & b_3 & 0 & b_1 \\ b_1 & b_2 & b_3 & 0 \end{pmatrix} \tag{5.1}$$

with the constraints

$$\begin{aligned} b_1 + b_3 &\leq 1 - b_2, \\ 3b_1 - b_3 &\geq b_2 - 1, \\ 3b_3 - b_1 &\geq b_2 - 1, \\ 3b_2 - b_1 &\geq b_3 - 1. \end{aligned} \tag{5.2}$$

There are two invariant subspaces

$$V_1 = \left\{ \begin{pmatrix} u_1 \\ u_1 \\ u_1 \\ u_1 \end{pmatrix} \;\middle|\; u_1 \in \mathbb{R} \right\}, \; V_2 = \left\{ \begin{pmatrix} u_1 \\ u_2 \\ u_1 \\ u_2 \end{pmatrix} \;\middle|\; u_1, u_2 \in \mathbb{R} \right\}. \tag{5.3}$$

The intersection of V_1 with the simplex is the fixed-point $E_4 = \frac{1}{4}\mathbb{1}$. The intersection of V_2 with the simplex is the line segment

$$\mathcal{L} = \left\{ u = \tfrac{1}{2} \begin{pmatrix} 0 \\ 1 \\ 0 \\ 1 \end{pmatrix} + u_1 \begin{pmatrix} 1 \\ -1 \\ 1 \\ -1 \end{pmatrix} \;\middle|\; 0 \le u_1 \le \tfrac{1}{2} \right\}, \tag{5.4}$$

and the dynamics on $\mathcal{L}$ is generated by the equation

$$\dot{u}_1 = \tfrac{1}{2}(b_2 - b_1 - b_3)u_1(2u_1 - 1)(4u_1 - 1). \tag{5.5}$$

As the analysis of the Lyapunov function was quite successful in the previous section, we introduce here

$$V(u) = u_1 u_2 u_3 u_4. \tag{5.6}$$

A long but straightforward computation shows that

$$\frac{d}{dt}V = 4V\{(b_2 - b_1 - b_3)(u_1 + u_3 - \tfrac{1}{2})^2 - b_2((u_1 + u_2 - \tfrac{1}{2})^2 + (u_2 + u_3 - \tfrac{1}{2})^2)\}. \tag{5.7}$$

From this identity we draw the following conclusions.

Theorem 5.1.

(i) *If $b_1 + b_3 < b_2 < 0$, then any orbit that does not start at the boundary of the simplex has E_4 as its limit for $t \to \infty$.*

(ii) *If $b_1 + b_3 > b_2 > 0$, then any orbit that does not start at E_4 has its ω-limit set contained in the boundary of the simplex.*

(iii) *If $b_2 = 0$, $b_1 + b_3 < 0$, and $b_1 \neq b_3$, then any orbit that starts in the interior converges to E_4 as $t \to \infty$.*

(iv) *If $b_2 = 0$, $b_1 + b_3 > 0$, and $b_1 \neq b_3$, then any orbit that does not start at E_4 has its ω-limit set contained in the boundary of the simplex.*

(v) *If $b_2 = 0$ and $b_1 = b_3 > 0$, then any orbit that does not start in the planar set*

$$\mathcal{P} = \{u \in \Sigma \mid u_1 + u_3 = u_2 + u_4\} \tag{5.8}$$

has its ω-limit set contained in $\partial\Sigma$. The set $\mathcal{P}$ consists of fixed points.

(vi) *If $b_2 = 0$ and $b_1 = b_3 < 0$, then any orbit that starts in the interior of the simplex has its ω-limit set contained in the plane $\mathcal{P}$, which consists of fixed points.*

(vii) *If $b_2 - b_1 - b_3 = 0$ and $b_2 < 0$, then any orbit that does not start at the boundary of the simplex has its ω-limit set contained in the fixed point line segment*

$$\mathcal{L} = \{u \in \Sigma \mid u_1 = u_3 \text{ and } u_2 = u_4\}.$$

(viii) *If $b_2 - b_1 - b_3 = 0$ and $b_2 > 0$, then the ω-limit set of any orbit that does not start on $\mathcal{L}$ is contained in $\partial\Sigma$.*

(ix) *If $b_2 = 0$ and $b_1 + b_3 = 0$, then V is a conserved quantity.*

Proof. The first two statements are a direct consequence of (5.7). If $b_2 = 0$, then the set defined by $\dot{V} = 0$ consists of the boundary of the simplex, where $V = 0$, and the set $\mathcal{P}$. For $b_2 = 0$ and $u \in \mathcal{P}$ we have

$$\begin{aligned}\dot{u}_1 &= u_1\{\tfrac{1}{4}(b_1 + b_3) - \tfrac{1}{2}b_3 - (b_1 - b_3)u_2\},\\ \dot{u}_2 &= u_2\{\tfrac{1}{4}(b_1 + b_3) - \tfrac{1}{2}b_1 + (b_1 - b_3)u_1\}.\end{aligned}$$

If we let $\xi = u_1 + u_3 - u_2 - u_4$, we compute that on $\mathcal{P}$

$$\dot{\xi} = -\tfrac{1}{4}(b_1 - b_3)(-1 + 4u_2)(-1 + 4u_1).$$

As $b_1 \neq b_3$, the largest invariant subset is contained in the set $\{u_1 = \frac{1}{4} \text{ or } u_2 = \frac{1}{4}\}$. When $u_1 = \frac{1}{4}$ and we are in the set $\mathcal{P}$, we find

$$\dot{u}_1 = -\tfrac{1}{16}(b_1 - b_3)(-1 + 4u_2),$$

and hence we conclude that the largest interior invariant set of $\mathcal{P}$ consists of the fixed point E_4. This proves (iii) and (iv). If $b_2 = 0$ and $b_1 = b_3$, one computes that the whole set $\mathcal{P}$ consists of fixed points. A straightforward computation yields that

$$\frac{d}{dt}(u_1 + u_3 - u_2 - u_4)^2 = 4b_1(u_1 + u_3 - u_2 - u_4)^2((u_2 + u_4)(u_1 + u_3)).$$

As the largest invariant set where $\dot{V} = 0$ consists of the union of the boundary of the simplex and the plane $\mathcal{P}$, this proves, in view of (5.7), (v) and (vi). The statements (vii) and (viii) follow from the observation that the line $\mathcal{L}$ consists entirely of fixed points when $b_2 - b_1 - b_3 = 0$; cf. (5.5). (See Figure 2.) The final statement is an immediate consequence of (5.7). ■

There is another function that acts as a Lyapunov function in part of the parameter space. The proof of the following result is given in section A.1.

Theorem 5.2. *If $b_2 > b_1 + b_3 > 0$ ($b_2 < b_1 + b_3 < 0$), then $r_1 = u_1u_3 + u_2u_4$ is a global Lyapunov function: $\frac{dr_1}{dt} < 0$ ($\frac{dr_1}{dt} > 0$) on the simplex, except at E_4, E_{2s}, and the line segments connecting consecutive E_1, where $\frac{dr_1}{dt} = 0$.*

The consequences of this result are formulated in Theorem 5.8 and in section 5.4.

5.2. Classification of equilibria.

5.2.1. All year classes present. We start by investigating the equilibria with all year classes present. If B is nonsingular, there is a unique steady state $E_4 = \frac{1}{4}\mathbb{1}$. The matrix

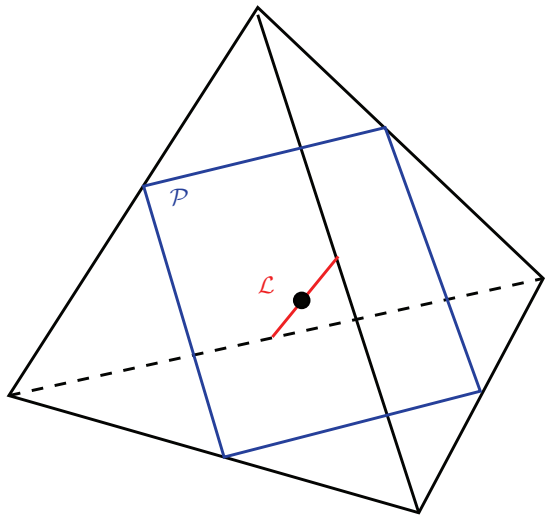


Figure 2. *The simplex with the line segment $\mathcal{L}$, which consists of fixed points when $b_2 - b_1 - b_3 = 0$, and the set $\mathcal{P}$, which consists of fixed points when $b_2 = 0$ and $b_1 = b_3$. $\mathcal{P}$ and $\mathcal{L}$ intersect in the always present internal fixed point $E_4 = \frac{1}{4}\mathbb{1}$.*

B has the eigenvalue $b_1 + b_2 + b_3$ with corresponding eigenvector $\xi_0 = \mathbb{1}$, the eigenvalue $b_2 - b_1 - b_3$ with eigenvector $\xi_2 = (1, -1, 1, -1)^T$, and the last two eigenvalues of B are given by $-b_2 \pm i(b_1 - b_3)$ with eigenvectors $\xi_{1,3} = (1, \mp i, -1, \pm i)^T$. Hence, the matrix B is singular iff

$$\begin{aligned} &\text{(i)} \quad b_1 + b_2 + b_3 = 0, \\ &\text{(ii)} \quad b_2 - b_1 - b_3 = 0, \text{ or} \\ &\text{(iii)} \quad b_2 = 0 \text{ and } b_1 = b_3. \end{aligned}$$

In case (i), the normalization $\sum_{j=1}^4 u_j = 1$ still guarantees the uniqueness of the internal steady state. In case (ii) we have fixed points on the line segment $\mathcal{L}$, and in case (iii) the set $\mathcal{P}$ consists of fixed points.

5.2.2. Three year classes present. Without loss of generality we restrict our attention to $u_4 = 0$. Indeed, all other cases are obtained by cyclic permutation. Let M denote the 3×3 matrix

$$M = \begin{pmatrix} 0 & b_1 & b_2 \\ b_3 & 0 & b_1 \\ b_2 & b_3 & 0 \end{pmatrix}$$

obtained by truncating B. We need to solve $Mu = Q\mathbb{1}$ where now (with a slight abuse of notation) $u = (u_1, u_2, u_3)^T$, $\mathbb{1} = (1, 1, 1)^T$, $\sum_{j=1}^3 u_j = 1$, and $Q = \sum_{j=1}^3 u_j (Mu)_j$. If M is nonsingular, then $u = QM^{-1}\mathbb{1}$. Hence

$$1 = \sum_{j=1}^3 u_j = Q \sum_{j=1}^3 (M^{-1}\mathbb{1})_j,$$

i.e., $Q = \left(\sum_{j=1}^{3} (M^{-1}\mathbb{1})_j\right)^{-1}$. So we do not need to solve any quadratic equation to find Q.

Since

$$M^{-1} = \frac{1}{b_2(b_1^2 + b_3^2)} \begin{pmatrix} -b_1 b_3 & b_2 b_3 & {b_1}^2 \\ b_1 b_2 & -{b_2}^2 & b_2 b_3 \\ {b_3}^2 & b_1 b_2 & -b_1 b_3 \end{pmatrix},$$

we thus find $Q = (\det M) R^{-1}$ and the steady state

$$E_3 = \frac{1}{R} \begin{pmatrix} b_1(b_1 - b_3) + b_2 b_3 \\ b_2(b_1 + b_3 - b_2) \\ b_3(b_3 - b_1) + b_1 b_2 \\ 0 \end{pmatrix} \stackrel{\text{def}}{=} \frac{1}{R} \begin{pmatrix} Q_1 \\ Q_2 \\ Q_3 \\ 0 \end{pmatrix} \tag{5.9}$$

with

$$R = (b_1 - b_3)^2 + 2b_2(b_1 + b_3 - \tfrac{1}{2} b_2) \tag{5.10}$$

provided all components are nonnegative (see Figure 3). M is singular iff either $b_2 = 0$ or $b_1 = b_3 = 0$. In case $b_2 = 0$, the vector $\mathbb{1}$ does not belong to $\mathcal{R}(M)$ unless $b_1 = b_3$, which is case (iii) above. The intersection of $\mathcal{P}$ with the boundary of the simplex consists of four line segments. In case $b_1 = b_3 = 0$, the vector $\mathbb{1}$ does not belong to $\mathcal{R}(M)$. The eigenvectors of M corresponding to the eigenvalue zero happen to have at least one zero component, so we will encounter those when we further reduce the number of year classes that are present.

5.2.3. Two year classes present. There are two essentially different cases.

Case 1. $u_3 = u_4 = 0$. Going through the same procedure as above, we find

$$\begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = \frac{1}{b_1 + b_3} \begin{pmatrix} b_1 \\ b_3 \end{pmatrix} \stackrel{\text{def}}{=} E_{2a}. \tag{5.11}$$

If either $b_1 = 0$, $b_3 \neq 0$ or $b_3 = 0$, $b_1 \neq 0$, there are no solutions. The condition for positivity is $\operatorname{sign} b_1 = \operatorname{sign} b_3$.

Case 2. $u_2 = u_4 = 0$. In this case we find an equilibrium that exists for all values of b. It is given by

$$\begin{pmatrix} u_1 \\ u_3 \end{pmatrix} = \tfrac{1}{2} \begin{pmatrix} 1 \\ 1 \end{pmatrix} \stackrel{\text{def}}{=} E_{2s}.$$

5.3. Stability of the equilibria.

5.3.1. Stability of E_4. Application of Lemma 2.7 yields that the eigenvalues about $E_4 = \frac{1}{4}\mathbb{1}$ are given by $\frac{1}{4}(b_1 + b_3 - b_2)$ and $\frac{1}{4}(b_2 \pm (b_1 - b_3)i)$. Hence, this equilibrium is locally stable when $b_2 < 0$ and $b_1 + b_3 - b_2 < 0$. This gives no new information, as we know already from the analysis of the Lyapunov function that we even have *global stability* in this case.

Theorem 5.3. *The internal equilibrium is globally stable if $b_2 < 0$ and $b_1 + b_3 - b_2 < 0$ and unstable if $b_2 > 0$ or $b_1 + b_3 > b_2$ or both.*

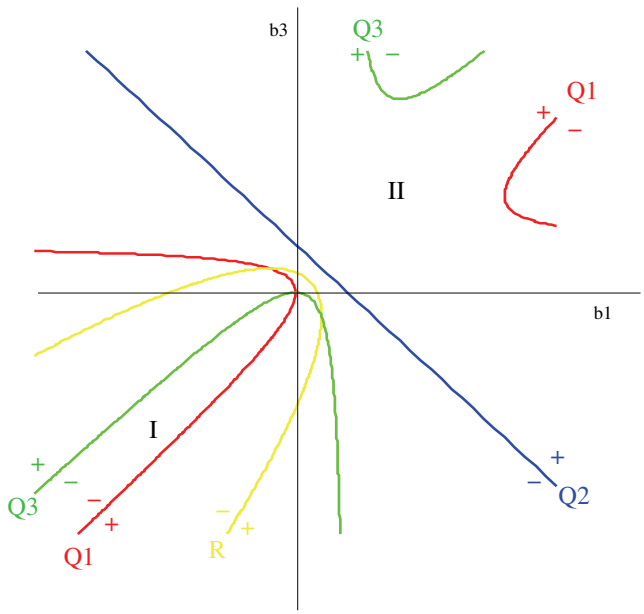


Figure 3. *The equilibrium E_3 exists in the regions* I–II. *In this picture* $b_2 = 0.4$.

For the statement concerning the (in)stability of, respectively, $\mathcal{L}$ and $\mathcal{P}$, see Theorem 5.1(v)–(viii).

5.3.2. Stability of E_3. When we linearize the replicator equation about an equilibrium E_3, the eigenvalues come in two categories corresponding to, respectively, the invasibility of the missing year class and perturbations of the year classes that are present; compare with Lemma 2.8.

The invasibility of the missing year class is governed by the sign of

$$\begin{aligned} \frac{\dot{u}_4}{u_4}\rfloor_{u=E_3} &= Q - \frac{1}{R}\left(b_1^2(b_1-b_3) + b_2^2(b_1+b_3-b_2) + b_3^2(b_3-b_1) + 2b_1b_2b_3\right) \\ &= \frac{1}{R}((b_2-b_1-b_3)((b_1-b_3)^2+b_2^2)) \end{aligned} \tag{5.12}$$

in the sense that there is invasibility iff this quantity is positive. The corresponding eigenvector "points into" the simplex. The "internally" linearized problem reads

$$\frac{dz_i}{dt} = \bar{u}_i\left\{\sum_j (\bar{u}_j(Mz)_j + (M\bar{u})_j z_j) - (Mz)_i\right\},$$

where we must restrict our attention to z satisfying $\sum z_i = 0$. Since $(M\bar{u})_j$ is independent of j, we can therefore simplify to

$$\frac{dz_i}{dt} = \bar{u}_i\left\{\sum_j \bar{u}_j(Mz)_j - (Mz)_i\right\}, \quad i = 1,2,3. \tag{5.13}$$

The proof of the first statement in the following lemma is tedious but straightforward. The last statement is a repetition of (5.12).

Lemma 5.4. *E_3 has two eigenvalues $\lambda_3^{(1)}$ and $\lambda_3^{(2)}$ corresponding to eigenvectors in the plane $u_4 = 0$. They are implicitly given by*

$$\lambda_3^{(1)} + \lambda_3^{(2)} = \frac{b_2\left({b_1}^2 + {b_3}^2\right)}{R},$$
$$\lambda_3^{(1)}\,\lambda_3^{(2)} = \frac{b_2\left(b_2\,b_1 - b_1\,b_3 + {b_3}^2\right)\left({b_1}^2 - b_1\,b_3 + b_2\,b_3\right)\left(-b_2 + b_1 + b_3\right)}{R^2}.$$

The third eigenvalue, which characterizes the invasibility, is given by

$$\lambda_3^{(3)} = -\frac{\left(-b_2 + b_1 + b_3\right)\left((b_1 - b_3)^2 + b_2^2\right)}{R}.$$

By combining the conditions for the stability of E_3 with the condition that the nonzero components are positive, we arrive at a remarkable conclusion.

Theorem 5.5. *E_3 is never a stable equilibrium.*

Proof. E_3 exists (on the simplex) iff

$$\frac{Q_i}{R} > 0, \quad i = 1, 2, 3,$$

while it is linearly stable iff $\lambda_3^{(1)} + \lambda_3^{(2)} < 0$, $\lambda_3^{(3)} < 0$, and $\lambda_3^{(1)}\lambda_3^{(2)} > 0$, which amounts to

$$\frac{b_2}{R} < 0, \; -\frac{Q_2}{b_2 R} < 0, \; \frac{Q_1 Q_2 Q_3}{R^2} > 0.$$

From the first two inequalities we conclude that $Q_2 < 0$. As both $\frac{Q_1}{R}$ and $\frac{Q_3}{R}$ are positive, the third inequality above leads to a contradiction. ■

5.3.3. Stability of E_{2a}. The equilibrium E_{2a} has two eigenvalues with corresponding eigenvectors that introduce a new year class. According to Lemma 2.8, these are given by

$$\lambda_{2a}^1 = \tfrac{b_1 b_3 - b_1 b_2 - b_3^2}{b_1 + b_3} = -\frac{Q_3}{b_1 + b_3},$$
$$\lambda_{2a}^2 = \tfrac{b_1 b_3 - b_2 b_3 - b_1^2}{b_1 + b_3} = -\frac{Q_1}{b_1 + b_3}. \tag{5.14}$$

Invasibility of the third year class corresponds to $\lambda_{2a}^1 > 0$, and invasibility of the fourth year class corresponds to $\lambda_{2a}^2 > 0$.

The internally linearized problem is given by

$$\frac{dz}{dt} = \frac{b_1 b_3}{(b_1 + b_3)^2}\begin{pmatrix} b_3 & -b_1 \\ -b_3 & b_1 \end{pmatrix} z.$$

The matrix at the right-hand side has the eigenvalue $b_1 + b_3$ when we restrict our attention to the subspace $\{z : \sum z_j = 0\}$. So the two year class equilibrium E_{2a} is internally linearly

stable iff $\frac{b_1 b_3}{b_1+b_3} < 0$ or, in view of the existence condition $\operatorname{sign} b_1 = \operatorname{sign} b_3$, iff both b_1 and b_3 are negative.

Theorem 5.6. *The equilibrium E_{2a} exists and is stable if $b_2 > 0$ and (recall (5.9)) $Q_1 < 0$ and $Q_3 < 0$. If at least one of the inequalities $b_2 < 0$, $Q_1 > 0$, $Q_3 > 0$ holds, then either E_{2a} does not exist or, if it exists, it is unstable.*

Proof. E_{2a} exists iff

$$\frac{b_1}{b_1+b_3} > 0, \quad \frac{b_3}{b_1+b_3} > 0,$$

while linearized stability is equivalent with

$$\frac{b_1 b_3}{b_1+b_3} < 0, \quad -\frac{Q_1}{b_1+b_3} < 0, \quad -\frac{Q_3}{b_1+b_3} < 0.$$

Combining the first inequality with the conditions for existence, we conclude that (b_1, b_3) should lie in the third quadrant. From the last two inequalities it follows that (b_1, b_3) should lie in the set where both Q_1 and Q_3 are negative. This set lies in the third quadrant iff $b_2 > 0$. ■

Remark 5.7. In Figure 3 the stability of E_{2a} occurs in region I.

When we repeat the analysis for the equilibrium E_{2s}, we find that both the second and the fourth year classes can invade iff $b_2 - b_1 - b_3 > 0$. The relevant eigenvalue for internal stability is $\frac{1}{2}b_2$. For $b_2 = 0$ the line segment $u_1 + u_3 = 1$, line $\mathcal{L}$ in Figure 2, consists entirely of steady states.

Theorem 5.8. *The steady state E_{2s} is linearly stable iff $b_2 < 0$ and $b_1 + b_3 > b_2$. When $b_2 < b_1 + b_3 < 0$, it is globally attracting in view of Theorem 5.2. All orbits converge to one of the two equilibria E_{2s} except for the orbits in the at most two-dimensional stable manifolds of the other equilibria.*

5.3.4. Stability of E_1. Finally, we note that the single year class (SYC) solution is linearly stable iff $b_i > 0$, $i = 1, 2, 3$. If $b_1 + b_3 > b_2 > 0$, then it is a consequence of (5.7) that all orbits converge to one of the equilibria E_1, except for the stable manifolds of the other boundary equilibria. These manifolds are at most two-dimensional. Here we use that the restriction of the equations to the part of the boundary of Σ with $u_i = 0$ is equivalent to a quadratic Lotka–Volterra system, which cannot have a limit cycle. This result is due to Bautin in 1954; see [1, p. 213, section 12, Example 7].

5.3.5. Confluence. When either $b_1 \to 0$ or $b_3 \to 0$, the *two-consecutive-year classes solution* E_{2a} runs into an *SYC solution*. When $b_2 - b_1 - b_3 \to 0$, the *three year classes* solution E_3 approaches the (always present) *two-nonconsecutive-year classes* solution E_{2s}. For $b_2 \to 0$, $E_3 \to \frac{1}{b_1 - b_3}\begin{pmatrix} b_1 \\ 0 \\ -b_3 \end{pmatrix}$, which is positive iff $\operatorname{sign} b_1 \neq \operatorname{sign} b_3$. If $b_1 \to \frac{b_3^2}{b_3 - b_2}$, then $u_3 \to 0$ and E_3 approaches the *two-consecutive-year classes* solution E_{2a}.

5.3.6. Summary. We collect the information that we have gathered so far about the equilibria and the corresponding eigenvalues in two lemmas.

Lemma 5.9. *The equilibria are, modulo cyclic permutation, given by*

$$
\begin{aligned}
E_1 &= (1,0,0,0),\\
E_{2s} &= (\tfrac{1}{2},0,\tfrac{1}{2},0),\\
E_{2a} &= \left(\frac{b_1}{b_1+b_3},\frac{b_3}{b_1+b_3},0,0\right),\ \textit{provided}\ \operatorname{sign} b_1 = \operatorname{sign} b_3,\\
E_3 &= \frac{1}{R}(Q_1,Q_2,Q_3,0),\ \textit{provided}\ \frac{Q_i}{R} > 0\ \textit{for}\ i=1,2,3\ \textit{(see Figure 3)},\\
E_4 &= (\tfrac{1}{4},\tfrac{1}{4},\tfrac{1}{4},\tfrac{1}{4}),
\end{aligned}
$$

where

$$
\begin{aligned}
R &= b_1^2 + 2b_2b_1 - 2b_1b_3 + 2b_2b_3 + b_3^2 - b_2^2,\\
Q_1 &= b_1^2 + b_3(b_2-b_1),\\
Q_2 &= b_2(b_1+b_3-b_2),\\
Q_3 &= b_3^2 + b_1(b_2-b_3).
\end{aligned}
$$

Lemma 5.10. *The equilibria E_1, E_{2s}, E_{2a}, and E_4 have eigenvalues with corresponding eigenvectors as given in the following table:*

Equilibrium	Eigenvalue	Eigenvector
E_1	$-b_1$	$(1,0,0,-1)$
	$-b_3$	$(-1,1,0,0)$
	$-b_2$	$(-1,0,1,0)$
E_{2s}	$\frac{b_2}{2}$	$(1,0,-1,0)$
	$\frac{b_2-b_1-b_3}{2}$	$\langle(0,1,\frac{b_3-b_1}{b_1},-\frac{b_3}{b_1}),\ (1,0,\frac{b_3}{b_1},-\frac{b_3+b_1}{b_1})\rangle$
E_{2a}	$\frac{b_1b_3}{b_3+b_1}$	$(1,-1,0,0)$
	$-\frac{Q_1}{b_3+b_1}$	$(1,\frac{b_3\left(b_2\,b_3-b_2\,b_1+b_1\,b_3+{b_1}^2\right)}{b_1\left({b_1}^2-{b_3}^2+2\,b_2\,b_3\right)},0,-\frac{(b_3+b_1)\left({b_1}^2+b_2\,b_3\right)}{b_1\left({b_1}^2-{b_3}^2+2\,b_2\,b_3\right)})$
	$-\frac{Q_3}{b_1+b_3}$	$(-\frac{b_1\left(b_1\,b_3+b_2\,b_1+{b_3}^2-b_2\,b_3\right)}{b_2\,{b_1}^2+b_1\,b_2\,b_3+b_1\,{b_3}^2+{b_3}^3},\frac{b_3\left({b_1}^2-2\,b_2\,b_1-{b_3}^2\right)}{b_2\,{b_1}^2+b_1\,b_2\,b_3+b_1\,{b_3}^2+{b_3}^3},1,0)$
E_4	$\frac{b_1+b_3-b_2}{4}$	$(-1,1,-1,1)$
	$\frac{1}{4}(b_2 \pm i(b_3-b_1))$	$*$

5.4. Heteroclinic cycles. There are two types of heteroclinic cycles that can occur. The first type, *HCI* (see Figure 4), connects the four single year class solutions in cyclic order. It exists if the two-consecutive-year classes solutions E_{2a} are absent, i.e., when $b_1b_3 \le 0$. It is stable when $b_1+b_2+b_3 > 0$; see [12, Chapter 17, pp. 225 and 226]. It is a consequence of Theorem 5.2 that HCI is a global (except for E_4) attractor if $b_2 > b_1+b_3 > 0$.

The second type, *HCII* (see Figure 5), connects the four steady states of two-consecutive-year classes solutions (see also [5, section 20.4]). It is a "planar" heteroclinic cycle in the sense introduced in [12, Chapter 17, p. 229]. A necessary condition for the existence of a heteroclinic cycle connecting the equilibria of type E_{2a} is that the two eigenvalues corresponding to the

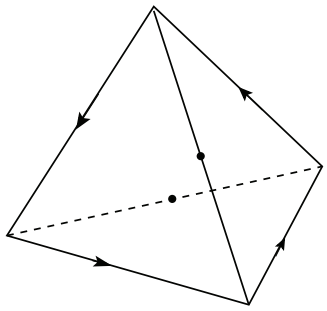


Figure 4. *This type of heteroclinic cycle occurs stably in the region in parameter space where* $\{b \mid b_1 + b_2 + b_3 > 0$ *and* $b_1 b_3 < 0\}$.

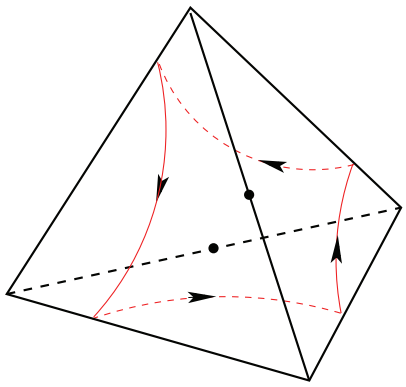


Figure 5. *This type of heteroclinic cycle occurs stably when* $b_2 > 0$ *and* $(b_1 - b_3)^2 + b_2(b_1 + b_3) < 0$.

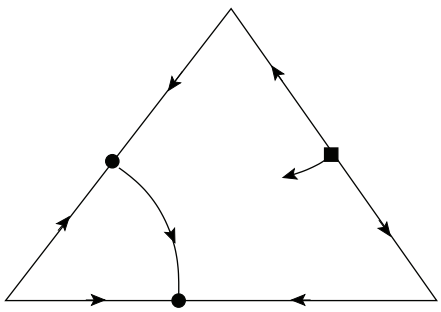


Figure 6. *A sketch of the phase portrait in the two-dimensional face.*

eigenvectors that point into the two-dimensional faces of the simplex have opposite sign. This requires that $\operatorname{sign}(Q_1) = -\operatorname{sign}(Q_3)$. Consequently, the equilibrium E_3 is not present. As E_{2a} is assumed to be on the simplex, we also need that $\operatorname{sign}(b_1) = \operatorname{sign}(b_3)$. We consider $b_2 > 0$, and so we must have $b_1 < 0$ and $b_3 < 0$, as otherwise $\operatorname{sign}(Q_1) = \operatorname{sign}(Q_3)$. We thus have that E_{2s} is a source, one of the E_{2a} equilibria is a saddle, and the other is a sink. In the two-dimensional face the two single year class solutions E_1 adjacent to E_{2s} are saddles and the third SYC solution is a source. We obtain the phase portrait depicted in Figure 6.

The heteroclinic cycle is stable when the sum of the two eigenvalues corresponding to the eigenvectors that point into the two-dimensional faces of the simplex is negative [12, Exercise 17.5.5, p. 231]. This is the case when

$$(b_1 - b_3)^2 + b_2(b_1 + b_3) < 0. \tag{5.15}$$

This condition holds for small negative values of b_1 and b_3. It becomes a condition on b_1 or b_3 when the curve $(b_1 - b_3)^2 + b_2(b_1 + b_3) = 0$ intersects the b_1- or b_3-axis, which is the case for $b_1 = -b_2$ and $b_3 = -b_2$. See Figure 7.

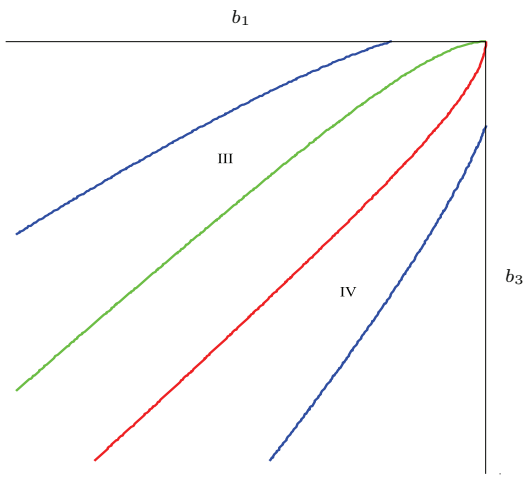


Figure 7. *In regions* III *and* IV*, a stable heteroclinic cycle of type* II *occurs. In this picture* $b_2 = 0.1$.

5.5. Periodic orbits. Small periodic orbits appear through a Hopf bifurcation, and the next theorem gives the details about the location in parameter space as well as the direction of bifurcation. Usually determining the direction of bifurcation requires quite a bit of work. We are here in the lucky situation that we can determine the stability of the fixed point at bifurcation by the use of a suitable Lyapunov function. Therefore, we do not need a normal form calculation to determine the first Lyapunov coefficient.

Theorem 5.11. *A Hopf bifurcation occurs at the surface* $b_2 = 0$ *whenever this surface is transversally crossed with* $b_1 - b_3 \neq 0$. *The bifurcation is subcritical for* $b_1 + b_3 > 0$ *and supercritical for* $b_1 + b_3 < 0$.

Proof. The linearization at the nontrivial equilibrium $\frac{1}{4}\mathbb{1}$ has eigenvalues $\frac{1}{4}(b_1 - b_2 + b_3)$ and $\frac{1}{4}b_2 \pm i\,(b_3 - b_1)$, so a Hopf bifurcation occurs at $b_2 = 0$. With $V = u_1u_2u_3u_4$ and $b_2 = 0$ we have (compare (5.7))

$$\dot{V} = -4V(b_1 + b_3)(u_1 + u_3 - \tfrac{1}{2})^2.$$

Therefore, V is decreasing when $b_1 + b_3$ is positive and increasing when $b_1 + b_3$ is negative, except on $\mathcal{P}$. From

$$\frac{d}{dt}u_1 + u_3\rfloor_{b_2=0,u_1+u_3=\frac{1}{2}} = 2(b_3 - b_1)(u_1 - \tfrac{1}{4})(u_2 - \tfrac{1}{4})$$

we see that, except for the subsets of $\mathcal{P}$ where either $u_1 = \frac{1}{4}$ or $u_2 = \frac{1}{4}$, the flow is transversal to $\mathcal{P}$ in points of $\mathcal{P}$. Another straightforward computation shows that these lines do not contain invariant subsets except for E_4:

$$\frac{d}{dt}u_1\big|_{b_2=0,u_1+u_3=\frac{1}{2},u_1=\frac{1}{4}} = \tfrac{1}{4}(b_3 - b_1)(u_2 - \tfrac{1}{4})$$

and

$$\frac{d}{dt}u_2\big|_{b_2=0,u_1+u_3=\frac{1}{2},u_2=\frac{1}{4}} = -\tfrac{1}{4}(b_3 - b_1)(u_1 - \tfrac{1}{4}).$$

Hence the internal fixed point $\frac{1}{4}\mathbb{1}$ is asymptotically stable if $b_1 + b_3 < 0$ and unstable if $b_1 + b_3 > 0$. ■

Remark 5.12.

- When $b_2 = 0$ and $b_1 = b_3$, E_4 is a degenerate Takens–Bogdanov point, and the plane $\mathcal{P}$ consists entirely of fixed points.
- If $b_2 = 0$ and $b_1+b_3 > 0$, then E_4 is unstable in the "third" direction and the bifurcating cycle will inherit this instability, so it will be a repellor for $b_2 < 0$ but small.

The previous theorem provides the local existence and stability of periodic orbits for b_2 close to zero. But clearly we lack information about the global fate of these bifurcating periodic orbits.

Global bifurcation of large periodic orbits occurs when the heteroclinic cycles lose their stability. We conjecture that the small periodic orbits grow in size and finally disappear in the heteroclinic cycles.

On the line $b_1 = -b_3$ the Hopf bifurcation is vertical and, in addition, the third eigenvalue corresponding to E_4 is zero. We already know that V is a conserved quantity (recall Theorem 5.1(ix)). In Theorem 5.14 below we shall find a two-parameter family of closed orbits. One may hope to obtain more detailed information about periodic solutions by a perturbation analysis, starting from points on this line.

5.6. Two special cases. There are two cases that deserve some more attention. The first is $b_2 \neq 0$, $b_1 = 0 = b_3$, a parameter combination for which the E_1 are Bogdanov–Takens points. The second is $b_2 = 0$, $b_1 + b_3 = 0$, a parameter combination for which E_4 is a Fold–Hopf point (see also [4]).

Theorem 5.13. *Let $b_1 = b_3 = 0$ and b_2 be positive (negative). Except for a set of initial conditions of measure 0, an orbit that starts in the interior of the simplex converges forward (backward) in time to a point on an edge connecting consecutive SYC points (in particular all points on such an edge are stationary) and backward (forward) in time to one of the two (always present) "two-nonconsecutive-year classes" solutions E_{2s}.*

Proof. One computes that

$$\frac{d}{dt}(u_1 - u_3) = 2b_2(u_1 - u_3)f,$$
$$\frac{d}{dt}(u_2 - u_4) = 2b_2(u_2 - u_4)f,$$

where

$$f = (u_1u_3 + u_2u_4).$$

Applying a time rescaling, we will achieve that $b_2 = 1$. The plane $u_1 = u_3$ is invariant, and so is the plane $u_2 = u_4$. These planes divide the simplex into four parts, which are mapped onto each other by the two reflection symmetries of exchanging u_1 and u_3, respectively, u_2 and u_4. Without loss of generality we focus our attention on $u_1 - u_3 > 0$ and $u_2 - u_4 > 0$. Since $f \geq 0$ the quantities $u_1 - u_3$ and $u_2 - u_4$ increase monotonically and so must have a limit which necessarily is finite. So f must tend to zero for $t \to \infty$. This in turn requires that both $u_1 u_3$ and $u_2 u_4$ tend to zero, which (given $u_1 > u_3$ and $u_2 > u_4$) requires that both u_3 and u_4 tend to zero for $t \to \infty$. So the orbit converges to the edge $u_1 + u_2 = 1$. Finally, note that the ratio of $u_1 - u_3$ and $u_2 - u_4$ is constant in time. So this ratio determines the exact point on the edge to which the orbit converges. Within the plane $u_1 = u_3$ all orbits with $u_2 - u_4 > 0$ converge to the SYC vertex with $u_2 = 1$, and a similar statement holds for the plane $u_2 = u_4$. On the line $\mathcal{L}$ (which is the intersection of the two invariant planes) the two nonconstant orbits have E_4 as the ω-limit set and E_{2s} as the α-limit set.

Again by monotonicity and boundedness we must have that $u_1 - u_3$ and $u_2 - u_4$ converge for $t \to -\infty$ as well. If f would tend to zero for $t \to -\infty$, then we would as above conclude that both u_3 and $u_4 \to 0$ while $u_1 \to \frac{c}{1+c}$ and $u_2 \to \frac{1}{1+c}$, where c is the (initial) ratio of $u_1 - u_3$ and $u_2 - u_4$. But then the derivatives of u_3 and u_4 would be approximately $-\frac{c}{1+c}u_3$, respectively, $-\frac{1}{1+c}u_4$, and so would have the wrong sign. We conclude that necessarily both $u_1 - u_3$ and $u_2 - u_4$ converge to zero for $t \to -\infty$. So the limit set belongs to the line $\mathcal{L}$. On $\mathcal{L}$ the backward flow is from E_4 toward the two E_{2s} points. So generically the α-limit set is one of the two E_{2s} points and the domains of backward attraction are separated by the two-dimensional unstable manifold of E_4. ■

Theorem 5.14. *If $b_2 = 0$, $b_1 \neq 0$, and $b_1 + b_3 = 0$, then the interior of the simplex is filled with periodic orbits and the line segment $\mathcal{L}$ that consists of equilibria.*

Proof. When $b_2 = 0$ and $b_3 = -b_1$, the system reduces to

$$\begin{aligned} \frac{du_1}{dt} &= -b_1(u_2 - u_4)u_1, \\ \frac{du_2}{dt} &= b_1(u_1 - u_3)u_2, \\ \frac{du_3}{dt} &= b_1(u_2 - u_4)u_3, \\ \frac{du_4}{dt} &= -b_1(u_1 - u_3)u_4. \end{aligned} \tag{5.16}$$

Scaling the time, we may achieve that $b_1 = 1$. There are two integrals:

$$I_1 = u_1 u_3, \quad I_2 = u_2 u_4. \tag{5.17}$$

For fixed values of h_1 and h_2, with $\sqrt{h_1} + \sqrt{h_2} < \frac{1}{2}$, the closed orbits are

$$\begin{aligned} u_1 + \frac{h_1}{u_1} + u_2 + \frac{h_2}{u_2} &= 1, \\ u_3 = \frac{h_1}{u_1}, \ u_4 &= \frac{h_2}{u_2}. \end{aligned} \tag{5.18}$$

The line segment $\mathcal{L}$ corresponds to $\sqrt{h_1} + \sqrt{h_2} = \frac{1}{2}$. ■

5.7. Permanence. The content of this subsection boils down to solving Exercise 2 in section 20.1 of [5]; also see [4, Chapter 14]. An inspection of the results so far reveals that we have identified an attractor at the boundary in much of the parameter space (see Figures 8 and 9 below). The only open regions for which this is not the case are $\{b : b_1 + b_3 < b_2 < 0\}$ and

$$Z := \{\, b : \ b_1 + b_3 < -b_2 < 0 \ \&\ (b_1 - b_3)^2 + b_2(b_1 + b_3) < 0 \,\}.$$

For the first of these, Theorem 5.1(i) establishes a very strong form of permanence. So we focus our attention on Z. We use the following result [5, Theorem 13.6.1].

Theorem 5.15. *The replicator system* (2.1) *is permanent if there exists a* $p \in \operatorname{int}\Sigma$ *such that*

$$p \cdot Bu < u \cdot Bu \tag{5.19}$$

holds for all rest points $u \in \operatorname{bd}\Sigma$.

The proof of this theorem utilizes the function $V^{\frac{1}{4}}$, with V defined by (5.6) as an average Lyapunov function. This is reflected in the following auxiliary result.

Lemma 5.16. *Let* $p = E_4$. *Then* $-p \cdot Bu + u \cdot Bu = \frac{1}{4}\frac{\dot V}{V}$.

Theorem 5.17. *The replicator equation* (2.1) *with* B *given in* (5.1) *is permanent in the region* Z.

Proof. From (5.7) we deduce

$$\frac{\dot V}{V}\rfloor_{E_1} = -b_1 - b_2 - b_3,$$
$$\frac{\dot V}{V}\rfloor_{E_{2s}} = -b_1 + b_2 - b_3,$$

and both right-hand sides are positive in the parameter region Z. Next we compute

$$\frac{\dot V}{V}\rfloor_{E_{2a}} = -b_1 - b_2 - b_3 + \frac{4b_1b_3}{b_1 + b_3},$$

which is also positive in the region Z. Finally, we turn our attention to the equilibrium E_3. Recall that the formula for E_3 is

$$E_3 = \left(\frac{b_1^2 - b_1b_3 + b_2b_3}{R}, \frac{b_2(b_1 - b_2 + b_3)}{R}, \frac{b_2b_1 - b_1b_3 + b_3^2}{R}, 0\right) = \frac{1}{R}(Q_1, Q_2, Q_3, 0).$$

If $b_2 > 0$ and $b_1 + b_3 - b_2 < 0$, then E_3 is a point on the simplex iff $R < 0$, $Q_1 < 0$, $Q_3 < 0$. Consequently

$$Q_1 + Q_3 = b_1^2 + b_3^3 - 2b_1b_3 + b_2(b_1 + b_3) < 0.$$

Hence, in the region Z there is no equilibrium E_3. ■

5.8. Attractor diagrams. We have collected quite a bit of local and global information. Figures 8 and 9 provide an overview of the parameter regions corresponding to the various kinds of attractors. Note that we do not know whether there is a unique periodic attractor in the region denoted "permanent" in Figure 8. Neither can we exclude that in other regions periodic attractors coexist with the indicated attractors.

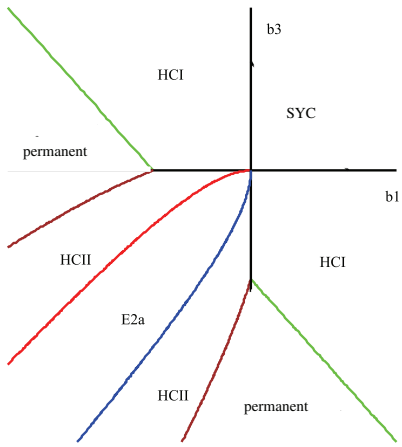


Figure 8. *Attractor diagram for b_2 positive.*

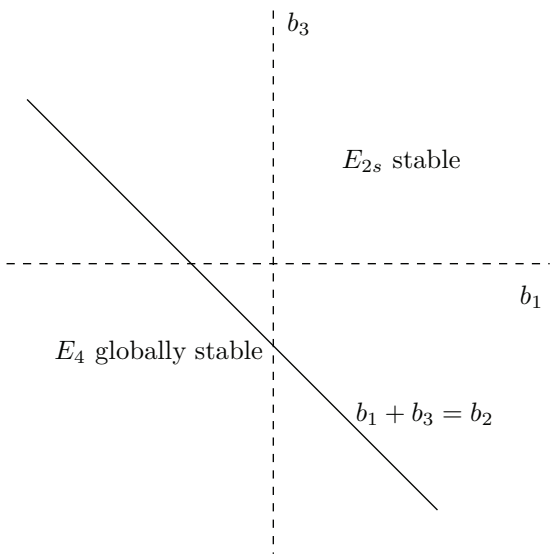


Figure 9. *Attractor diagram for b_2 negative.*

6. Discussion. The emergences of the 13- and 17-year periodical cicadas of eastern North America have intrigued many people. What mechanisms lead to such long life cycles? Is it significant that both 13 and 17 are prime? Why does only one brood exist?

To find answers, one should ultimately make quantitative models that incorporate known biological detail. But in order to interpret the dynamical features that such models exhibit, it will be helpful to relate to a catalogue of stylized dynamics in simple caricature models. The present paper has as its aim to contribute to such a catalogue.

It is very natural to order the catalogue by the length k of the life cycle, as lower dimensional systems are easier to analyze and have fewer parameters. But low dimensional models are misleadingly simple, so one should aspire to move on to longer and longer life cycles, accepting that the work gets harder and harder, if only due to the sheer number of possibilities.

To make progress, simplifications are called for. Here we have introduced a scaling that, in the limit, leads to a continuous time description of the dynamics generated by the full-life-cycle-map for basic reproduction numbers R_0 just above one. We like to think of the limiting system as a normal form for the highly degenerate bifurcation at $R_0 = 1$, characterized by all roots of unity being multipliers. But it remains to be verified that the limiting system does indeed give a faithful description of the dynamics for the original discrete time system.

The ordinary differential equation system is, we think, mathematically interesting. It is a Lotka–Volterra system with cyclic symmetry, which can be rewritten as a replicator equation with that same symmetry. As a consequence of the symmetry, various types of heteroclinic cycles occur robustly, and one can even derive conditions for the (in)stability of such cycles.

If one restricts one's attention to life cycles of three or fewer years, one finds a strict dichotomy: either all year classes coexist in a symmetric steady state or orbits approach the boundary, meaning that some (and maybe all) year classes go through periods of very low abundance. The transition between the two possibilities is by way of a vertical bifurcation. Here we have shown that for $k = 4$ the transition is not necessarily that rigid. More precisely, if the transition to instability of the coexistence steady state is by way of a Hopf bifurcation, it is not vertical. Stable interior periodic orbits may arise by Hopf bifurcation, exist in certain open regions of parameter space, and vanish in a boundary heteroclinic cycle. If the transition is by way of a real eigenvalue, it is vertical.

For $k \geq 3$ one can have stable heteroclinic cycles in which the year classes are chasing each other, in the sense that one is growing while its predecessor declines, and so on and so forth, with the periods of hegemony of a year class becoming longer and longer. For $k = 4$ another type of stable heteroclinic cycle is possible, viz. one in which coalitions of two year classes are chasing each other, in the sense that a year class interchanges its old "partner" for a new one, to be subsequently dropped itself, and so on and so forth, with the periods of hegemony of a coalition becoming longer and longer. Field observations of these phenomena have, as far as we know, never been made for semelparous populations, but given the time scales involved and the noisiness of the real world, it would be surprising if they were.

We do not believe that a complete classification for arbitrary k is feasible. Yet it must be possible to reveal certain patterns, partly determined by the prime decomposition of k. Whether or not we are overly optimistic remains to be seen.

Appendix.

A.1. A global Lyapunov function. To simplify some of the lengthy formulas we introduce the basis for the Z_4 invariant polynomials of degree ≤ 3:

$$
\begin{aligned}
\pi_1 &= u_1 + u_2 + u_3 + u_4,\\
\pi_2 &= u_1^2 + u_2^2 + u_3^2 + u_4^2,\\
\pi_3 &= u_1u_2 + u_2u_3 + u_3u_4 + u_4u_1,\\
\pi_4 &= u_1^3 + u_2^3 + u_3^3 + u_4^3,\\
\pi_5 &= u_1^2u_2 + u_2^2u_3 + u_3^2u_4 + u_4^2u_1,\\
\pi_6 &= u_1^2u_3 + u_2^2u_4 + u_3^2u_1 + u_4^2u_2,\\
\pi_7 &= u_1u_2u_3u_4.
\end{aligned}
\tag{A.1}
$$

In addition we have invariant polynomials of degree ≤ 3 that can be expressed in those given above:

$$
\begin{aligned}
r_1 &= u_1u_3 + u_2u_4 = \tfrac{1}{2}(\pi_1^2 - \pi_2) - \pi_3,\\
r_2 &= u_1^2u_4 + u_2^2u_1 + u_3^2u_2 + u_4^2u_3 = \pi_1\pi_2 - \pi_4 - \pi_5 - \pi_6,\\
r_3 &= u_1u_2u_4 + u_2u_3u_1 + u_3u_4u_2 + u_4u_1u_3 = \tfrac{1}{6}\pi_1^3 - \tfrac{1}{2}\pi_1\pi_2 + \tfrac{1}{3}\pi_4.
\end{aligned}
\tag{A.2}
$$

Theorem A.1. *If $b_2 > b_3 + b_1 > 0$ ($b_2 < b_1 + b_3 < 0$), then $r_1 = u_1u_3 + u_2u_4$ is a global Lyapunov function in the following sense: $\frac{dr_1}{dt} < 0$ (> 0) except at the points E_4, E_{2s}, and HCI, where $\frac{dr_1}{dt} = 0$.*

Proof. A straightforward computation gives that

$$
\begin{aligned}
\frac{dr_1}{dt} &= (b_1 + b_3)(-r_3 + 2\pi_3 r_1) + b_2(4r_1^2 - \pi_6)\\
&= (b_1 + b_3)(-r_3 + 2\pi_3 r_1 + 4r_1^2 - \pi_6)\\
&\quad + (b_2 - (b_3 + b_1))(4r_1^2 - \pi_6).
\end{aligned}
$$

We claim that both $t_1 = -r_3 + 2\pi_3 r_1 + 4r_1^2 - \pi_6$ and $t_2 = 4r_1^2 - \pi_6$ are nonpositive on the simplex. As on the simplex

$$
-r_3 + 2\pi_3 r_1 + 4r_1^2 - \pi_6 = -r_1((u_1 - u_3)^2 + (u_2 - u_4)^2),
$$

the statement for t_1 is immediate. In addition, a straightforward inspection shows that the vector field transversally intersects the line $\mathcal{P}$ where $u_1 = u_3$ and $u_2 = u_4$ except in E_4 and E_{2s}. To show that $t_2 \leq 0$, we perform the transformation

$$
\begin{aligned}
v &= u_1u_3,\\
w &= u_2u_4,\\
x &= u_1 + u_3
\end{aligned}
\tag{A.3}
$$

to obtain $t_2 = 4(v + w)^2 - vx - w(1 - x)$. We find a critical point for $v = w = \frac{1}{32}$ and $x = \frac{1}{2}$. In this point $t_2 = -\frac{1}{64}$. At the boundary of Σ either $v = 0$ or $w = 0$. For $w = 0$ we find that $t_2 = 4v^2 - vx$ has a critical point $v = x = 0$ with $t_2 = 0$. By symmetry t_2 has another boundary maximum $t_2 = 0$ for $v = 0$.

The transformation (A.3) is singular if either $u_1 = u_3$ or $u_2 = u_4$. If $u_1 = u_3$, then $x = 2\sqrt{v}$, and hence $t_2 = 4(v + w)^2 - 2v\sqrt{v} - w(1 - 2\sqrt{v})$. We find a critical point for $\sqrt{v} = \frac{1}{16}(1 + \frac{1}{3}\sqrt{57})$, $w = 5v - \sqrt{v}$ with a corresponding $t_2 = -\frac{23}{512} + \frac{19}{4608}\sqrt{57} < 0$.

The case $u_2 = u_4$ is symmetric to the case $u_1 = u_3$.

If both $u_1 = u_3$ and $u_2 = u_4$, then

$$
t_2 = 4(u_1^2 + (\tfrac{1}{2} - u_1)^2)^2 - \tfrac{1}{2}u_1^2 - \tfrac{1}{2}(\tfrac{1}{2} - u_1)^2,
$$

and there is a critical point for $u_1 = \frac{1}{4}$ with corresponding $t_2 = 0$. The final conclusion is that indeed $t_2 \leq 0$. This shows that when $b_2 > b_1 + b_3 > 0$, r_1 is a Lyapunov function. ■

A.2. Derivation of the Lotka–Volterra system from the Leslie-matrix model. We derive the replicator equation (1.1) from the nonlinear Leslie-matrix model:

$$\begin{cases} x_i(t+1) = h^\epsilon_{i-1}(I(t))x_{i-1}(t), \quad i = 0, \dots, k-1, \quad \text{mod } k, \\ \qquad I(t) = \displaystyle\sum_{l=1}^{k} c_l x_l(t), \end{cases} \tag{A.4}$$

where the mappings h^ϵ_i depend smoothly on ϵ. For the vector $x = (x_0, \dots, x_{k-1})^T$ we have the nonlinear mapping

$$x(t+1) = L_\epsilon(I(t))x(t). \tag{A.5}$$

The kth iterate of the mapping is then given by

$$x_i(t+k) = \prod_{j=0}^{k-1} h^\epsilon_{i+j}(I(t+j))\, x_i(t). \tag{A.6}$$

We assume that

H1 $$\textstyle\prod_{j=0}^{k-1} h^0_i(0) = 1.$$

Let $\epsilon y = x$, $\tau = \frac{\epsilon t}{k}$, and $\tilde{y}(\tau) = y(t)$. Then

$$\frac{\tilde{y}_i(\tau+\epsilon) - \tilde{y}_i(\tau)}{\epsilon} = \frac{1}{\epsilon}\left\{ \prod_{j=0}^{k-1} h^\epsilon_{i+j}(\epsilon\, c \cdot y(t+j)) - 1 \right\} \tilde{y}_i(\tau). \tag{A.7}$$

The Taylor series in ϵ of the term between brackets is given by

$$\prod_{j=0}^{k-1} h^\epsilon_{i+j}(0) - 1 + \prod_{j=0}^{k-1} h^0_{i+j}(0) \sum_{j=0}^{k-1} \frac{Dh^0_{i+j}(0)}{h^0_{i+j}(0)} \epsilon\, c \cdot y(t+j) + \mathcal{O}(\epsilon^2).$$

It is a consequence of H1 that we may write

$$\prod_{j=0}^{k-1} h^\epsilon_{i+j}(0) - 1 = a\epsilon + \mathcal{O}(\epsilon^2).$$

As we have that $y(t+1) = L_0 y(t) + \mathcal{O}(\epsilon)$, we obtain in the limit for $\epsilon \to 0$ the differential equation

$$\dot{\tilde{y}}_i(\tau) = \left(a + \sum_{j=0}^{k-1} \frac{Dh^0_{i+j}(0)}{h^0_{i+j}(0)} c \cdot L_0^j \tilde{y}(\tau) \right) \tilde{y}_i(\tau). \tag{A.8}$$

When we rescale the time $t = a\tau$, we find

$$\dot{\tilde{y}}_i(t) = \left(1 + \frac{1}{a} \sum_{j=0}^{k-1} \frac{Dh^0_{i+j}(0)}{h^0_{i+j}(0)} c \cdot L_0^j \tilde{y}(\tau) \right) \tilde{y}_i(t). \tag{A.9}$$

We omit the tildes and we define $\sigma^i = \frac{1}{a}\sum_{j=0}^{k-1} \frac{Dh^0_{i+j}(0)}{h^0_{i+j}(0)}(L_0^T)^j c$ in order to write the equation in the more compact form

$$\dot{y}_i(t) = (1 + \sigma^i y(t))y_i(t).$$

Note that

$$\begin{aligned} L_0^T \sigma^i &= \frac{1}{a}\sum_{j=0}^{k-1} \frac{Dh^0_{i+j}(0)}{h^0_{i+j}(0)} L_0^{T^{j+1}} c \\ &= \frac{1}{a}\sum_{j=1}^{k} \frac{Dh^0_{i+j-1}(0)}{h^0_{i+j-1}(0)} L_0^{T^{j}} c \\ &= \frac{1}{a}\sum_{j=0}^{k-1} \frac{Dh^0_{i+j-1}(0)}{h^0_{i+j-1}(0)} L_0^{T^{j}} c = \sigma^{i-1}. \end{aligned}$$

Finally, we will apply a rescaling so that the transformed vector field commutes with S. Let $y_i = \theta_i z_i$, which leads to the equation

$$\dot{z}_i(t) = (1 + \tilde{\sigma}^i \cdot z(t))z_i(t), \tag{A.10}$$

where $(\tilde{\sigma}^i)_j = (\sigma^i)_j \theta_j$. It is possible to choose θ such that

$$S^{-1}\tilde{\sigma}^i = \tilde{\sigma}^{i-1}, \tag{A.11}$$

i.e.,

$$(\tilde{\sigma}^i)_{j+1} = (\tilde{\sigma}^{i-1})_j \Leftrightarrow (\sigma^i)_{j+1}\theta_{j+1} = (\sigma^{i-1})_j \theta_j.$$

As we know that $h^0_j(0)(\sigma^i)_{j+1} = (\sigma^{i-1})_j$, it follows that we achieve this by choosing

$$\frac{\theta_{j+1}}{\theta_j} = h^0_j(0).$$

As the last equation involves the quotients of θ_j, we may in addition assume that

$$\sum_{j=1}^{k} (\sigma^i)_j = 1. \tag{A.12}$$

For the Ricker nonlinearity $h_i^\epsilon(x) = (1+\epsilon)^{\frac{1}{k}} e^{-g_i x}$, we compute

$$\begin{aligned} B_i^{Ricker}(y) &= \sum_{j=0}^{k-1} \frac{d}{d\epsilon} h^0_{i+j}(0) + \sum_{j=0}^{k-1} Dh^0_{i+j}(0)(S^{-j})c \cdot y(\tau) \\ &= 1 - \sum_{l=0}^{k-1}\sum_{j=0}^{k-1} g_{i+j} c_{l+j} y_l(t). \end{aligned} \tag{A.13}$$

Lemma A.2. *Let, for positive integers t, and for $0 < |\epsilon|$, $x(t,\epsilon)$ be the itinerary defined by* (A.4) *that starts at x_0 at $t = 0$, let N be a given natural number, and let $\tilde{y}(t)$ be the solution of the differential equation* (A.8) *with initial condition $\tilde{y}(0) = \frac{1}{\epsilon}x_0$; then $|x(nk,\epsilon) - \epsilon\tilde{y}(n\epsilon)| = \mathcal{O}(\epsilon)$, for $n \leq N$.*

Proof. Without loss of generality, we prove the result for $k = 1$. The mapping (A.4) is of the form

$$x(t+1) = F(x(t),\epsilon)x(t)$$

for a smooth mapping $F : \mathbb{R}^k \times \mathbb{R} \longrightarrow \mathbb{R}^{k\times k}$ that satisfies $F(0,0) = \mathrm{Id}$. With the rescaling $x(\epsilon t) = \epsilon\tilde{y}(\tau)$ the mapping in $\tilde{y}$ is given by

$$\tilde{y}(\tau+\epsilon) = F(\epsilon\tilde{y}(\tau),\epsilon)\tilde{y}(\tau).$$

For this mapping we find

$$\begin{aligned}\tilde{y}(\tau+\epsilon) &= \tilde{y}(\tau) + (F(\epsilon\tilde{y}(\tau),\epsilon) - \mathrm{Id})\tilde{y}(\tau)\\ &= \tilde{y}(\tau) + \epsilon(D_1F(0,0)\tilde{y}(\tau) + D_2F(0,0))\tilde{y}(\tau) + \mathcal{O}(\epsilon^2).\end{aligned}$$

This mapping differs in order $\mathcal{O}(\epsilon^2)$ of the Euler approximation with stepsize ϵ of the differential equation

$$\dot{\tilde{y}} = (D_1F(0,0)\tilde{y}(\tau) + D_2F(0,0))\tilde{y},$$

which is the analogue of (A.8). This proves the theorem. ■

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REFERENCES

[1] A. A. Andronov, E. A. Leontovich, I. I. Gordon, and A. G. Maier, *Qualitative Theory of Second-Order Dynamic Systems*, Wiley, New York, 1973.

[2] M. G. Bulmer, *Periodical insects*, Am. Nat., 111 (1977), pp. 1099–1117.

[3] E. C. Zeeman, *Population dynamics from game theory*, in Global Theory of Dynamical Systems (Proc. Internat. Conf., Northwestern Univ., Evanston, IL, 1979), Lecture Notes in Math. 819, Springer, Berlin, 1980, pp. 471–479.

[4] J. Hofbauer, P. Schuster, K. Sigmund, and R. Wolff, *Dynamical systems under constant organization* II: *Homogeneous growth functions of degree $p = 2$*, SIAM J. Appl. Math., 38 (1980), pp. 282–304.

[5] J. Hofbauer and K. Sigmund, *The Theory of Evolution and Dynamical Systems: Mathematical Aspects of Selection*, London Mathematical Society Student Texts 7, Cambridge University Press, Cambridge, UK, 1988.

[6] A. Edalat and E. C. Zeeman, *The stable classes and the codimension-one bifurcations of the planar replicator system*, Nonlinearity, 5 (1992), pp. 921–939.

[7] M. L. Zeeman, *Hopf bifurcations in competitive three-dimensional Lotka–Volterra systems*, Dynam. Stability Systems, 8 (1993), pp. 189–217.

[8] M. Plank, *Hamiltonian structures for the n-dimensional Lotka–Volterra equations*, J. Math. Phys., 36 (1995), pp. 3520–3534.

[9] M. Plank, *Bi-Hamiltonian systems and Lotka-Volterra equations: A three-dimensional classification*, Nonlinearity, 9 (1996), pp. 887–896.

[10] M. Plank, *Some qualitative differences between the replicator dynamics of two player and n player games*, Nonlinear Anal., 30 (1997), pp. 1411–1417.

[11] M. Plank, *On the dynamics of Lotka–Volterra equations having an invariant hyperplane*, SIAM J. Appl. Math., 59 (1999), pp. 1540–1551.
[12] J. Hofbauer and K. Sigmund, *Evolutionary Games and Population Dynamics*, Cambridge University Press, Cambridge, UK, 1998.
[13] H. Behncke, *Periodical insects*, J. Math. Biol., 40 (2000), pp. 413–431.
[14] N. V. Davydova, O. Diekmann, and S. A. van Gils, *Year class competition or competitive exclusion for strict biennials?*, J. Math. Biol., 46 (2003), pp. 95–131.
[15] 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, pp. 141–150.
[16] 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.
[17] N. V. Davydova, O. Diekmann, and S. A. van Gils, *On circulant populations.* I. *The algebra of semelparity*, Linear Algebra Appl., 398 (2005), pp. 185–243.
[18] E. Mjolhus, A. Wikan, and T. Solberg, *On synchronization in semelparous populations*, J. Math. Biol., 50 (2005), pp. 1–21.
[19] J. M. Cushing, *Nonlinear semelparous Leslie models*, Math. Biosci. Eng., 3 (2006), pp. 17–36.
[20] R. Kon and Y. Iwasa, *Single-class orbits in nonlinear Leslie matrix models for semelparous populations*, J. Math. Biol., 55 (2007), pp. 781–802.