J. Math. Biol. (2009) 59:75–104
DOI 10.1007/s00285-008-0208-9

Mathematical Biology

Three stage semelparous Leslie models

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Received: 26 October 2007 / Revised: 4 August 2008 / Published online: 6 September 2008

Abstract Nonlinear Leslie matrix models have a long history of use for modeling the dynamics of semelparous species. Semelparous models, as do nonlinear matrix models in general, undergo a transcritical equilibrium bifurcation at inherent net reproductive number $R_0 = 1$ where the extinction equilibrium loses stability. Semelparous models however do not fall under the purview of the general theory because this bifurcation is of higher co-dimension. This mathematical fact has biological implications that relate to a dichotomy of dynamic possibilities, namely, an equilibration with over lapping age classes as opposed to an oscillation in which age classes are periodically missing. The latter possibility makes these models of particular interest, for example, in application to the well known outbreaks of periodical insects. While the nature of the bifurcation at $R_0 = 1$ is known for two-dimensional semelparous Leslie models, only limited results are available for higher dimensional models. In this paper I give a thorough accounting of the bifurcation at $R_0 = 1$ in the three-dimensional case, under some monotonicity assumptions on the nonlinearities. In addition to the bifurcation of positive equilibria, there occurs a bifurcation of invariant loops that lie on the boundary of the positive cone. I describe the geometry of these loops, classify them into three distinct types, and show that they consist of either one or two three-cycles and heteroclinic orbits connecting (the phases of) these cycles. Furthermore, I determine stability and instability properties of these loops, in terms of model parameters, as well as those of the positive equilibria. The analysis also provides the global dynamics on the boundary of the cone. The stability and instability conditions are expressed in terms of certain measures of the strength and the symmetry/asymmetry of the inter-age class competitive interactions. Roughly speaking, strong inter-age class competitive

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interactions promote oscillations (not necessarily periodic) with separated life-cycle stages, while weak interactions promote stable equilibration with overlapping life-cycle stages. Methods used include the theory of planar monotone maps, average Lyapunov functions, and bifurcation theory techniques.

Keywords Nonlinear Leslie models · Semelparity · Bifurcation · Equilibria · Synchronous orbits · Periodic cycles · Invariant loops · Heteroclinic cycles · Over-lapping life cycle stages · Separated life cycle stages

Mathematics Subject Classification (2000) 92D25 · 92D40

1 Introduction

The goal of this paper is to describe the bifurcations that occur in three stage, nonlinear Leslie models for the dynamics of semelparous populations as the inherent net reproductive number R_0 passes through 1. Generally, as R_0 increases through 1 in a nonlinear matrix model, the extinction equilibrium destabilizes and there bifurcates from that equilibrium a (global) continuum branch of positive equilibria whose stability depends on the direction of bifurcation [3,6]. For semelparous Leslie models, however, the bifurcation scenario is not so simple.

It is known, for example, that a continuum branch of so-called synchronous cycles also bifurcates from the extinction equilibrium at $R_0 = 1$. Synchronous cycles reside on the boundary of the positive cone and visit coordinate hyperplanes sequentially. They describe temporally synchronized collections of age cohorts (with at least some missing cohorts at any point in time) that appear in periodic outbreaks. The most extreme case is when only one cohort is present at any point in time, which is called a *single-class cycle*. It is known, in some cases at least, that the synchronous cycles are embedded in invariant loops, lying on the boundary of the positive cone, that consist of orbits that heteroclinically connect the (phases) of the synchronous cycle [4,5,11–14].

The existence of these two bifurcating branches presents an alternative between two different dynamics for a semelparous population: one in which equilibration occurs with all generations present and another of non-equilibrating oscillations in which some age cohorts are absent at each point in time. A crucial problem, then, is to determine which of the two dynamics (if either) is stable or, more precisely, to determine conditions under which one or the other is stable. The answer to this question is, in general, a complicated one; it is not, for example, simply determined by the direction of bifurcation [5].

In [5] one can find a complete accounting of the bifurcation at $R_0 = 1$, including the stability question, for two-dimensional (2D) semelparous Leslie models, that is to say, for semelparous models that entail only a juvenile stage and an adult stage of equal time duration. It turns out that one and only one of the two bifurcating branches (positive equilibria or single-class synchronous two-cycles) is stable for R_0 near 1; which branch is stable is determined by certain measures of the intensity of inter-class and intra-class competition. Roughly speaking, intense inter-class competition between the juvenile and adult stages (relative to intra-class competition) promotes stability of the single-class two-cycle branch and hence temporally separated age classes, while less intense inter-class competition leads to equilibration with overlapping generations. One can find this theme throughout the literature on semelparous species [1,2,4,7,8,11–13,15,16,18,19,21–23,31]. It is one (but not the only) hypothesis put forth to explain the synchronization of the life cycles, and consequently the famous periodic outbreaks, of periodical insects (such as cicadas). Other studies of 2D semelparous models, but not from a bifurcation point-of-view, appear in [11,21,22].

The limited dynamics possible in the 2D case allow for a rather straightforward analysis of the bifurcation at $R_0 = 1$. In three or higher dimensions, however, the dynamics and their analyses become considerably more complicated. In this paper I will give a complete description of the bifurcation at $R_0 = 1$ for three-dimensional (3D) case under some monotonicity assumptions on the nonlinear interaction terms. I will show that the bifurcating single-class three-cycles are embedded in invariant loops lying on the boundary of the positive cone. I will characterize the geometry of (and the dynamics on) these bifurcating loops into three distinct types: A, SS, and WS (see Fig. 2). Each type consists of synchronous orbits that heteroclinically connect (the phases of) the single-class three-cycle, in the case of type A, or (the phases of) the single-class three-cycle and a two-class three-cycle, in the case of types SS and WS. In all cases, the bifurcating loop is a chain of synchronous three-cycles whose phases are heteroclinically connected by synchronous orbits, a structure I will call a *heteroclinic chain*.

I will also characterize the stability of the equilibria and the invariant loops in terms of model parameters. Crucial to this characterization are the definitions of two ratios ρ_1, ρ_2 that measure the relative effects of inter-class versus intra-class competition on class specific survivorships. The (ρ_1, ρ_2)-plane is sub-divided into regions of strong or weak (inter-class) competition and symmetric or asymmetric competition. Asymmetric competition occurs when younger (older) classes affect older (younger) classes but not vice versus. Based on the four possibilities of strong-symmetric, weak-symmetric, weak-asymmetric and strong-asymmetric competition, I characterize the stability properties of the bifurcating positive equilibria and characterize both the type and stability of the bifurcating invariant loops (heteroclinic chains).

The focus in this paper is on the bifurcation event at $R_0 = 1$, and the analysis and results are valid only for $R_0 \gtrapprox 1$ (R_0 greater than, but close to 1). The main result appears as Theorem 6 in Sect. 5. The dynamics on the boundary of the positive cone are studied in Sect. 3 and those on the interior of the cone in Sect. 4. The analysis makes use of bifurcation theory methods, the Implicit Function Theorem, the theory of planar monotone maps (as developed in [25] and [36]), and average Lyapunov functions. Mathematical details are placed in an appendix.

2 Preliminaries

Let R^3_+ denote the non-negative cone in 3D Euclidean space and let $int\left(R^3_+\right)$ denote its interior. A semelparous Leslie (age class) model

$$\hat{x}(t+1) = L\left(\hat{x}(t)\right)\hat{x}(t), \quad t = 0, 1, 2, \ldots \tag{1}$$

is characterized by a projection matrix of the form

$$L(\hat{x}) = \begin{pmatrix} 0 & 0 & b(\hat{x})\tau_3(\hat{x}) \\ \tau_1(\hat{x}) & 0 & 0 \\ 0 & \tau_2(\hat{x}) & 0 \end{pmatrix}$$

where $\hat{x} = \mathrm{col}(x, y, z) \in R^3_+$ and where the functions $\tau_i : R^3_+ \to (0, 1]$ and $b : R^m_+ \to int\left(R^1_+\right)$ describe age class specific (per unit time) survivorship and recruitment rates respectively. In this model there are two juvenile (non-reproductive) age classes x and y whose members survive one unit of time with probabilities τ_1 and τ_2. There is a single adult age class z whose members survive a unit of time with probability τ_3 at the end of which they produce offspring, at a per capita rate b, and then die. The eigenvalues of the inherent projection matrix $L(\hat{0})$ (here $\hat{0}$ denotes the origin col(0, 0, 0)) are the three cube roots of the *inherent net reproductive number*

$$R_0 \triangleq b(\hat{0})\tau_1(\hat{0})\tau_2(\hat{0})\tau_3(\hat{0}) > 0.$$

Thus, $L(\hat{0})$ is irreducible but not primitive. The linearization principle and Theorem 3 of [9] (also see Theorem 1.1.3 in [3] and [28]) imply that the *extinction equilibrium* $\hat{x} = \hat{0}$ is locally asymptotically stable (LAS) if $R_0 < 1$ and is unstable if $R_0 > 1$. This loss of stability suggests a bifurcation of nontrivial equilibria at $R_0 = 1$. This is confirmed by Theorem 1 below (and for higher dimensional models by the results in [5]).

Note that the boundary ∂R^3_+ of the cone is forward invariant under the map $L\left(\hat{x}\right)\hat{x}$. In fact, the non-negative coordinate axes, and their planar interiors, are each forward invariant. Indeed orbits visit the axes and the coordinate planes sequentially. Orbits on the boundary ∂R^3_+ are called *synchronous orbits* and periodic orbits on the boundary are called *synchronous cycles*. More specifically, *single-class* 3-*cycles* and *two-class* 3-*cycles* have the respective forms

$$\begin{pmatrix} * \\ 0 \\ 0 \end{pmatrix} \to \begin{pmatrix} 0 \\ * \\ 0 \end{pmatrix} \to \begin{pmatrix} 0 \\ 0 \\ * \end{pmatrix} \to \begin{pmatrix} * \\ 0 \\ 0 \end{pmatrix}, \quad \begin{pmatrix} * \\ * \\ 0 \end{pmatrix} \to \begin{pmatrix} 0 \\ * \\ * \end{pmatrix} \to \begin{pmatrix} * \\ 0 \\ * \end{pmatrix} \to \begin{pmatrix} * \\ * \\ 0 \end{pmatrix}.$$

where the asterisks indicate positive numbers.

Most structured population dynamic models assume that the dependence of vital rates on population densities is through a dependence on one or more weighted populations sizes. I make that assumption here and consider the 3D semelparous Leslie model (1) with survivorships

$$\tau_i(\hat{x}) = s_i g_i(w_i), \quad w_i \triangleq \beta_{i1}x + \beta_{i2}y + \beta_{i3}z, \quad 0 < s_i \leq 1$$

with weighted population sizes w_i defined by the *competition coefficients* $\beta_{ij} \geq 0$ in the *competition matrix* $B \triangleq \left(\beta_{ij}\right)$. I also assume the per capita birth rate of adults is a (density independent) constant $b(\hat{x}) \equiv b_0 > 0$. A normalization $g_i(0) = 1$ implies that s_i and b_0 are the inherent (density independent) survivorships and birth rate respectively. Without loss in generality, one can assume $g_i'(0) = -1$ (re-scaling the interaction coefficients β_{ij} if necessary). Finally, let $b \triangleq b_0 s_3$ denote the inherent per adult recruitment rate. Our interest lies in competition within and among age classes and accordingly the functions $g_i(w)$ are assumed monotone decreasing for $w \geq 0$ (Allee effects are ignored).

In summary, the basic assumptions made here for the 3D semelparous model equations

$$\begin{aligned} x(t+1) &= bg_3(w_3(t))\,z(t) \\ y(t+1) &= s_1 g_1(w_1(t))\,x(t) \\ z(t+1) &= s_2 g_2(w_2(t))\,y(t). \end{aligned} \tag{2}$$

are

$$\begin{aligned} &0 < s_i \leq 1, \quad b > 0 \\ &g_i \in C^1\left((-\gamma, +\infty) \to R_+^1\right), \quad g_i : R_+^1 \to (0, 1] \\ &g_i(0) = 1, \quad g_i'(0) = -1, \quad g_i'(w) < 0 \quad \text{for } w \in R_+^1 \end{aligned} \tag{3}$$

for some constant $\gamma > 0$. Note that the functions $h_i \in C^1\left((-\gamma, +\infty) \to R_+^1\right)$ defined by $h_i(w) \triangleq g_i(w)w$ are continuously differentiable and satisfy $h_i(0) = 0$, $h_i'(0) = 1$. It is further assumed that

$$h_i : R_+^1 \to R_+^1 \text{ is bounded and } h_i'(w) > 0 \quad \text{for } w \in R_+^1. \tag{4}$$

A prototypical example for which (3) and (4) hold is the discrete logistic (or Beverton-Holt) nonlinearity [26,27,32,33]

$$g_i(w) = \frac{1}{1+w} \tag{5}$$

for which $\gamma = 1$ and $h_i(w) = w/(1+w)$.

The monotonicity assumption on h_i in (4) rules out over-compensatory density feedback effects. This allows us to focus on the oscillatory implications of semelparity and inter-class competition while avoiding the potentially compounding factor of oscillations caused by over-compensatory effects (such as those that can occur, for example, by use of the well-known exponential Ricker nonlinearity). Mathematically, this assumptions allows use of the powerful theory of planar monotone maps.

In order to state a preliminary theorem concerning the bifurcation at $R_0 = 1$, we need some definitions. A *positive equilibrium pair* $(r, \hat{x}) \in R^1 \times R_+^3$ is a pair for which $\hat{x} \in int(R_+^3)$, the interior of the non-negative cone, and for which $\hat{x}$ is an equilibrium of (2) for inherent net reproductive value $R_0 = r$. A *three-cycle pair* $(r, \hat{x}) \in R^1 \times R_+^3$ is a pair for which $\hat{x} \neq \hat{0}$ and for which the initial condition $\hat{x}(0) = \hat{x}$ yields a three-cycle of (2) for inherent net reproductive value $R_0 = r$. If $\hat{x}$ lies on the positive coordinate axes (or in the positive coordinate planes), then $(r, \hat{x})$ is a *single-class* (*two-class*) *three-cycle pair*. An unbounded continuum of equilibrium pairs (or k-cycle pairs) is a connected set of equilibrium (or k-cycle) pairs $(r, \hat{x})$ that is unbounded in $R^1 \times R^3_+$. The *spectrum* of the continuum is the range of $r = R_0$ values associated with pairs from the continuum. A continuum *bifurcates from* $(r, \hat{x}) = (1, \hat{0})$ means that its closure contains $(1, \hat{0})$. Finally, (2) is *permanent* means there exist constants $\delta_1, \delta_2 > 0$ such that

$$\begin{aligned}&(x(0), y(0), z(0)) \in R^3_+ \backslash \hat{0} \Longrightarrow \\ &\quad 0 < \delta_1 \le \liminf_{t \to +\infty} (x(t) + y(t) + z(t)) \le \limsup_{t \to +\infty} (x(t) + y(t) + z(t)) \le \delta_2.\end{aligned}$$

Theorem 1 *Assume* (3) *holds for the three age class semelparous Leslie model* (2).

(a) *If* $R_0 < 1$ *then the origin* $\mathrm{col}(x, y, z) = \mathrm{col}(0, 0, 0)$ *is globally asymptotically stable* (*GAS*) *on* R^3_+.
Suppose in addition that (4) *holds and at least one intra-class competition coefficient* β_{jj} *is nonzero.*

(b) *If* $R_0 > 1$ *then* (2) *is permanent.*

(c) *There exists a compact, forward invariant set of the form*

$$C \triangleq \{(x, y, z) : 0 \le x \le c_1,\ 0 \le y \le c_2,\ 0 \le z \le c_3\}$$

for some constants $c_i > 0$.

(d) *There exist an unbounded continuum of positive equilibrium pairs and an unbounded continuum of single-class three-cycle pairs that bifurcate from* $(r, \hat{x}) = (1, \hat{0})$. *The spectrum of each continuum is unbounded. That is to say, for each* $R_0 > 1$ *there exists a positive equilibrium in* $int(R^3_+)$ *and a single-class three-cycle on* $\partial R^3_+ \backslash \hat{0}$ *of* (2).

Proof Part (a) of this theorem follows from Theorem 1.2.1 in [3] (also see Theorem 3 in [24] and Proposition 3.3 in [23]).

Part (b) also follows from Theorem 1.2.1 in [3] once we show (2) is dissipative, i.e., there exists a constant δ_2 such that $\limsup_{t \to +\infty} (x(t) + y(t) + z(t)) \le \delta_2$ for all orbits in the cone R^3_+. Suppose that $\beta_{33} \ne 0$ and let $h^0_3 \triangleq \sup_{w \ge 0} h_3(w)$, which is finite by assumption (4). (The cases $\beta_{11} \ne 0$ and $\beta_{22} \ne 0$ are handled similarly). The inequalities

$$\begin{aligned}0 &\le x(t+1) = b\beta_{33}^{-1} g_3(w_3(t))\, \beta_{33} z(t) \\ &\le b\beta_{33}^{-1} g_3(w_3(t))\, w_3(t) \le R_0 s_1^{-1} s_2^{-1} \beta_{33}^{-1} h^0_3 \\ 0 &\le y(t+1) \le s_1 x(t) \\ 0 &\le z(t+1) \le s_2 y(t)\end{aligned} \tag{6}$$

show that after at least three applications of the map defined by (2) any orbit in R^3_+ lies in the compact set $C \triangleq \{(x, y, z) : 0 \le x \le c_1,\quad 0 \le y \le c_2,\quad 0 \le z \le c_3\}$ where

$$c_1 \triangleq R_0 s_1^{-1} s_2^{-1} \beta_{33}^{-1} h^0_3, \quad c_2 \triangleq R_0 s_2^{-1} \beta_{33}^{-1} h^0_3, \quad c_3 \triangleq R_0 \beta_{33}^{-1} h^0_3.$$

Thus, we can take $\delta_2 \triangleq kR_0$ where $k \triangleq \beta_{33}^{-1} s_2^{-1} s_1^{-1} (1 + s_1 + s_1 s_2)\, h^0_3$.

The inequalities (7) also imply that C is forward invariant, which proves part (c).

Part (d) is a consequence of Theorems 2.2 and 3.1 in [5]. These theorems assert the existence of an unbounded continuum of positive equilibrium pairs $(R_0, \hat{x})$ and of an unbounded continuum of single-class three-cycle pairs $(R_0, \hat{x})$ both of which bifurcate from the origin at $R_0 = 1$. If the spectrum of the equilibrium continuum were bounded, then (since δ_2 is proportional to R_0) it would follow that all the equilibria associated with pairs from the continuum would also be bounded. Since this contradicts the unboundedness of the bifurcating continuum, we conclude that the spectrum is infinite, i.e., there is an equilibrium for every $R_0 > 1$. A similar argument holds for the continuum of three-cycles, since C contains any periodic cycle (it contains all orbits after three iterations). □

Theorem 1 lets us restrict our attention throughout the rest of the paper to $R_0 > 1$. The alternatives offered by the two bifurcating continua in part (d) correspond to the biological alternatives of equilibration with over-lapping age classes or period three oscillations with temporally separated age classes. The next section concerns the embedding of the single-class three-cycle on an invariant of one of three types and with the stability properties of the dynamics on the boundary of the cone.

3 Dynamics on the boundary of R^3_+

Denote the non-negative coordinate axes by A_+. Then $A^0_+ \triangleq A_+ \backslash \hat{0}$ and $P^0_+ \triangleq \partial R^3_+ \backslash A_+$ are the *positive* coordinate axes and *positive* coordinate planes respectively. It follows from the features of the semelparous Leslie model (2) that each of the sets in the decompositions $\partial R^3_+ = P^0_+ \cup A^0_+ \cup \{\hat{0}\}$ and $R^3_+ = int\left(R^3_+\right) \cup P^0_+ \cup A^0_+ \cup \{\hat{0}\}$ are forward invariant. Orbits lying in A^0_+ sequentially visit the coordinate axes and are single-age class orbits. Orbits lying in P^0_+ sequentially visit the coordinate planes and are two-age class orbits. Throughout this paper, the *composite map* refers to the map obtained by three applications of (2).

Consider first the dynamics on the positive coordinate axes A^0_+. A point col $(x, 0, 0) \in A^0_+$ on the positive x-axis is mapped by the composite map to a point on the positive x-axis. In other words, the composite map defines a scalar map from R^1_+ into itself, a fixed point of which is a single-class three-cycle of (2). This scalar map has the form

$$x(t+1) = R_0 \gamma\left(x(t)\right) x(t) \tag{7}$$

where, under the assumptions (3) and (4),

$$\gamma\left(x\right) \triangleq g_3\left(\beta_{33} s_2 g_2\left(\beta_{22} s_1 g_1\left(\beta_{11} x\right) x\right) s_1 g_1\left(\beta_{11} x\right) x\right) g_2\left(\beta_{22} s_1 g_1\left(\beta_{11} x\right) x\right) g_1\left(\beta_{11} x\right)$$

is a continuously differentiable function that maps $R^1_+ \to (0, 1]$ that satisfies $\gamma(0) = 1$. Also $\eta(x) \triangleq \gamma(x)x$ is monotone increasing and bounded for $x \geq 0$ and $\eta'(0) = 1$. It follows that for $R_0 > 1$ the Eq. (7) has a positive equilibrium x^* that is GAS on R^1_+. A similar analysis holds for points on the y-axis or on the z-axis. The positive fixed points x^*, y^*, z^* of the composite, lying on the three coordinate axes, make up the single-class three-cycle in Theorem 1:

$$\begin{pmatrix} x^* \\ 0 \\ 0 \end{pmatrix} \to \begin{pmatrix} 0 \\ y^* \\ 0 \end{pmatrix} \to \begin{pmatrix} 0 \\ 0 \\ z^* \end{pmatrix} \to \begin{pmatrix} x^* \\ 0 \\ 0 \end{pmatrix} \to \cdots . \tag{8}$$

Theorem 2 *Assume* (3) *and* (4) *hold and that* $R_0 > 1$. *The single-class three-cycles in Theorem* 1(d) *are GAS on the coordinate axes* A_+^0.

According to this theorem, when $R_0 > 1$ all populations founded with only one age class present will tend asymptotically to a periodic three-cycle with age classes temporally separated.

Consider now the dynamics on the positive coordinate planes P_+^0. The positive quadrant $int\left(R_+^2\right)$ of the x, y-plane is mapped into itself by the composite map. The resulting planar map has the form

$$\begin{aligned} x(t+1) &= R_0\gamma_1\left(x(t), y(t)\right) x(t) \\ y(t+1) &= R_0\gamma_2\left(x(t), y(t)\right) y(t). \end{aligned} \tag{9}$$

It is possible to write formulas for $\gamma_i(x, y)$ in terms of the g_i (as we did above for the scalar case), but it is not necessary to display them here. Suffice it to say that the monotonicity assumptions contained in (3) and (4) imply that the partial derivatives of the functions $\eta_1(x, y) \triangleq \gamma_1\left(x, y\right) x$ and $\eta_2(x, y) \triangleq \gamma_2\left(x, y\right) y$ satisfy

$$\partial_x\eta_1 > 0, \quad \partial_y\eta_1 < 0, \quad \partial_x\eta_2 < 0, \quad \partial_y\eta_2 > 0$$

on $int\left(R_+^2\right)$. Moreover, the inequalities we obtain by replacing the strict inequalities with $\leq$ and $\geq$ hold on the closure R_+^2. These inequalities imply the planar map on the cone is strictly competitive on the cone R_+^2 and strongly competitive on the interior $int\left(R_+^2\right)$ of the cone (Proposition 2.1 in [36]). Since there is a unique equilibrium on each axis and the origin is a repeller when $R_0 > 1$, it follows that hypotheses (H1–H4) in [36] hold for the planar map (9).

Lemma 1 [36] *Assume* (3) *and* (4) *hold and that* $R_0 > 1$. *The omega limit set of every orbit of the composite of the map* (9) *is contained in the closed square*

$$S^* \triangleq \left\{(x, y) \in R_+^2 \mid 0 \leq x \leq x^*,\ 0 \leq y \leq y^*\right\}$$

and exactly one of the following alternatives hold:

(a) *there is a positive fixed point* (x_+, y_+) *in the interior of the square* S^*;
(b) $(x_0, y_0) \in R^+$ *and* $x_0 > 0 \Longrightarrow \lim_{t\to+\infty}\left(x(t), y(t)\right) = (x^*, 0)$;
(c) $(x_0, y_0) \in R^+$ *and* $y_0 > 0 \Longrightarrow \lim_{t\to+\infty}\left(x(t), y(t)\right) = (0, y^*)$.

Analogous lemmas also hold for the other two coordinate planes. What these results tell us about the Leslie model (2) is the following.

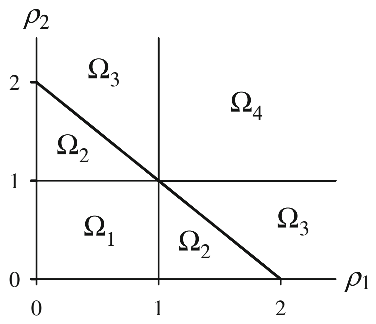

Fig. 1 The regions Ω_i for the parameters ρ_i in (10) are defined for $i = 1, 2, 3$, and 4 by the following inequalities respectively: (1) both $\rho_i < 1$; (2) $\rho_1 + \rho_2 < 2$ and either $\rho_1 < 1$, $\rho_2 > 1$ or $\rho_1 > 1$, $\rho_2 < 1$; (3) $\rho_1 + \rho_2 > 2$, and either $\rho_1 < 1$, $\rho_2 > 1$ or $\rho_1 > 1$, $\rho_2 < 1$; and (4) both $\rho_i > 1$

Lemma 2 *Assume* (3) *and* (4) *hold and that* $R_0 > 1$. *The omega limit set of every orbit on the boundary* ∂R^3_+ *of the Leslie model* (2) *lies on the boundary* ∂C^* *of the closed cube*

$$C^* \triangleq \left\{(x, y, z) \in R^3_+ \mid 0 \le x \le x^*, 0 \le y \le y^*, 0 \le z \le z^*\right\}$$

and exactly one of the following two alternatives hold for (2)*:*

(a) *there exists a* (*nontrivial*) *two-class three-cycle lying on* ∂C^*;
(b) *all orbits on* $\partial R^3_+ \backslash \hat{0}$ *tend to the single-age class three-cycle as* $t \to +\infty$.

Consider the first alternative (a) in Lemma 2. Specifically, consider the existence of two-class three-cycles when $R_0 > 1$ is near 1, i. e., for $R_0 \gtrapprox 1$. It turns out (Lemma 3) that whether or not there exists a non-negative two-class three-cycle for $R_0 \gtrapprox 1$ depends on parameter constraints that involve the ratios

$$\rho_1 = \frac{\beta_{21} + s_1\beta_{32} + s_1 s_2 \beta_{13}}{\beta_{11} + s_1\beta_{22} + s_1 s_2 \beta_{33}}, \quad \rho_2 = \frac{\beta_{31} + s_1\beta_{12} + s_1 s_2 \beta_{23}}{\beta_{11} + s_1\beta_{22} + s_1 s_2 \beta_{33}} \tag{10}$$

(for which we assume least one $\beta_{jj} \neq 1$). The denominator that appears in these ratios involves the intra-class competition coefficients β_{jj} while the numerators involve the inter-class competition coefficients β_{ij}, $i \neq j$. These ratios serve as measures of the intensity of inter-class competition (relative to the intensity of intra-class competition). Specifically, the ratio ρ_1 measures the total effect that each juvenile class has on the survivorships on the older classes and the effect that adults have on the survivorship of newborns. The ratio ρ_2 measures total effect that each juvenile class has on the survivorships on the younger classes and the effect that newborns have on the survivorship of adults.

The four parameter regions in the (ρ_1, ρ_2)-plane depicted in Fig. 1 will play decisive roles in determining in dynamics near the bifurcation point $R_0 = 1$. Region Ω_1 corresponds to weak inter-class competition and since by definition both $\rho_i < 1$ on this region, we call the competition *weak symmetric* (since competition with both older and younger age classes is weak). Similarly, we interpret region Ω_4 as a region of *strong symmetric* competition. Regions Ω_2 and Ω_4, on the other hand, correspond to *asymmetric competition*, since one ρ_i is less than 1 and the other is greater than 1, i.e., competition with older (younger) age classes is weak while competition with younger (older) age classes is strong. We refer to Ω_2 as the parameter region of *weak asymmetric competition* and to Ω_3 as the region of *strong asymmetric competition*.

The following lemma extends the basic bifurcation result in Theorem 1 by showing that, in addition to positive equilibria and single-class three-cycles, there is a branch of *two-class* three-cycles that also bifurcates at $R_0 = 1$. (The proof appears in the Appendix.)

Lemma 3 *Assume* (3) *and* (4) *hold and that at least one intra-class competition coefficient* β_{jj} *is nonzero. If* $\rho_1\rho_2 \neq 1$ *then a continuum of two-class three-cycles bifurcates from the origin at* $R_0 = 1$. *For* $R_0 \approx 1$ *these are the only two-class three-cycles near the origin, but they do not lie on* ∂R^3_+ *for* $R_0 \lessapprox 1$. *For* $R_0 \gtrapprox 1$, *on the other hand, we have the following alternatives:*

(a) *If* $(\rho_1, \rho_2) \in \Omega_1 \cup \Omega_4$ (*symmetric competition*) *then the bifurcating two-class three-cycles lie on* P^0_+;
(b) *If* $(\rho_1, \rho_2) \in \Omega_2 \cup \Omega_3$ (*asymmetric competition*) *then the bifurcating two-class three-cycles do not lie on* ∂R^3_+.

Lemmas 2 and 3 lead to the following result, which is the main theorem of this section (see the Appendix for a proof).

Theorem 3 *Assume that* (3) *and* (4) *hold, that at least one intra-class competition coefficient* β_{jj} *is nonzero, and that* $\rho_1\rho_2 \neq 1$. *For each* $R_0 \gtrapprox 1$ *the single-class three-cycle is GAS on the positive axes* A^0_+ *and the following alternatives hold, according to the parameter regions defined in Fig.* 1:

(a) *If* $(\rho_1, \rho_2) \in \Omega_1$ (*weak symmetric competition*) *then the two-class three-cycle is globally attracting on the positive coordinate planes* P^0_+;
(b) *If* $(\rho_1, \rho_2) \in \Omega_2 \cup \Omega_3$ (*asymmetric competition*) *then the single-class three-cycle is GAS on* $P^0_+ \cup A^0_+ = \partial R^3_+ \backslash \hat{0}$;
(c) *If* $(\rho_1, \rho_2) \in \Omega_4$ (*strong symmetric competition*) *then the single-class three-cycle attracts all initial points on* $P^0_+ \cup A^0_+ = \partial R^3_+ \backslash \hat{0}$ *except for the stable manifold of a saddle, two-class three-cycle lying on the* P^0_+. *In each coordinate plane, this stable manifold is the graph of a continuous increasing function of one variable and therefore has measure zero.*

On the parameter region $\Omega_2 \cup \Omega_3$ of asymmetric competition, the *composite* map yields planar maps on each of the coordinate planes, all of whose orbits tend to an equilibrium on the coordinate axes. This fact and the stable/unstable manifold theorem [17] lead to *heteroclinic manifolds* of orbits that heteroclinically connect the equilibria on adjacent coordinate axes. Altogether these equilibria and heteroclinic manifolds form an invariant loop of type *A* in Fig. 2. With regard to the *original* Leslie model (2), the three equilibria constitute the points of a single-class three-cycle and the orbits lying on the heteroclinic manifolds, which visit the coordinate planes (and hence the heteroclinic manifolds) sequentially, approach the three-cycle in both forward and

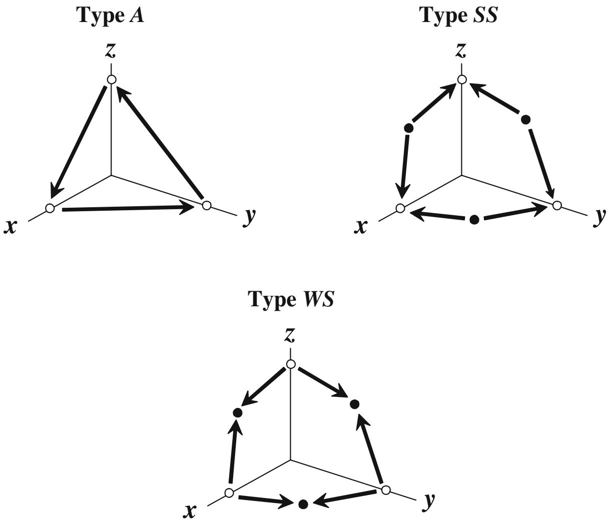

Fig. 2 For $R_0 \gtrapprox 1$ in the semelparous Leslie model (2) there exist invariant loops of one of the three geometries shown. In parameter region $\Omega_2 \cup \Omega_3$, the loop is an heteroclinic cycle of type A. In region Ω_4, the loop is of type SS and in region Ω_1 it is of type WS. The *open circles* on the coordinate axes A_+^0 are the points of the single-class three-cycle (the axes equilibria of the composite map). In types SS and WS, the *solid circles* interior to the coordinate planes P_+^0 are the points of the two-class three-cycle (the planar equilibrium of the composite). The oriented curves consist of heteroclinic orbits that connect the phase shifts of these three-cycles. The temporal motion is counter-clockwise, visiting the coordinate planes sequentially

reverse time. More specifically, these orbits approach different phases of the single-class three-cycle in forward and reverse time (which phases are determined by the coordinate plane in which the orbit's initial point lies).

In brief: on the parameter region $\Omega_2 \cup \Omega_3$ of *asymmetric competition* in the Leslie model (2), the bifurcating invariant loop is of *type A* in Fig. 2. The loop consists of a single-class three-cycle together with synchronous (i.e., two-class) orbits that heteroclinically and sequentially connect the phases of this three-cycle. Thus, all orbits on this *heteroclinic cycle* approach the single-class three-cycle. (For more on heteroclinic cycles see [4,12,13].)

On the parameter region Ω_4 of strong symmetric competition, all planar orbits of the composite map (except the planar equilibria and their stable manifolds) tend to one of the axes equilibria. This includes those orbits lying on the unstable manifolds of planar equilibria, which approach an axis equilibrium in forward time and a planar equilibrium in reverse time. These heteroclinic orbits form six heteroclinic manifolds which, together with the (six) equilibria, constitute an invariant loop of the composite map of type SS seen in Fig. 2. With regard to the *original* Leslie model (2), the three axes equilibria constitute the points of the single-class three-cycle and the three planar equilibria constitute the points of the two-class three-cycle. Orbits lying on the heteroclinic manifolds of the composite visit the coordinate planes (and hence the heteroclinic manifolds) sequentially, and they approach the single-class three-cycle in forward time and the two-class three-cycle in reverse time. More specifically, these heteroclinic orbits approach a phase of the single-class three-cycle in forward time and a phase of the two-class three-cycle in reverse time (which phases are determined by the coordinate plane in which the orbit's initial point lies).

In brief: on the parameter region Ω_4 of *strong symmetric competition* in the Leslie model (2), the bifurcating invariant loop is of *type* SS pictured in Fig. 2. The loop consists of a single-class three-cycle and a two-class three-cycle together with synchronous (i.e., two-class) orbits that heteroclinically connect a phase of the two-class three-cycle with a phase of the single-class three-cycle. Thus, all orbits on this *heteroclinic chain* (except the two-class three-cycle) approach the single-class three-cycle.

On the parameter region Ω_1 of *weak symmetric competition* in the Leslie model (2), a similar analysis shows the existence of an invariant loop of type WS shown in Fig. 2. The dynamic on this loop is the reverse time version of type SS. That is, this loop consists of a single-class three-cycle and a two-class three-cycle together with synchronous (two-class) orbits that heteroclinically connect a phase of the single-class three-cycle with a phase of the two-class three-cycle. Thus, all orbits on this heteroclinic chain (except the single-class three-cycle) approach the two-class three-cycle.

From a biological point of view the results in this section assert that a semelparous population described by Leslie models of the form (2) will, if initiated with at least one missing age class, asymptotically tend to an oscillation of period three in which either only one or only two age-classes are present at any point in time. More specifically, if inter-class competition is weak and symmetric (parameter region Ω_1) populations initiated with only one age class will tend to a three-cycle oscillation with age classes temporally separated while those initiated with two age classes present will tend to a three-cycle with exactly two age classes present at any time. However, if inter-class competition is increased (parameter region $\Omega_2 \cup \Omega_3 \cup \Omega_4$) then populations with at least one initially missing age class will tend to an oscillation of period three in which only one age class present at any time (except for those on the stable manifold of a saddle, two-class three-cycle which exists on parameter region Ω_4).

4 Dynamics on R_+^3

Theorem 3 describes the dynamics of the semelparous model (2) on the boundary of the non-negative cone when $R_0 \gtrapprox 1$. The focus of this section is on the dynamics in the interior of the cone R_+^3.

According to Theorem 1 there exists an equilibrium in the interior of the cone for $R_0 \gtrapprox 1$. Since there is no explicit formula for this positive equilibrium, it is not straightforward to perform a linearization stability analysis. However, for $R_0 \gtrapprox 1$ an approximation to the equilibrium is accessible by means of standard Lyapunov-Schmidt (or center manifold) calculations. This approximation in turn provides approximations to the Jacobian at the equilibrium and therefore to its eigenvalues. Similar calculations provide approximations to the bifurcating single-class three-cycle, to the Jacobian of the composite map, and to its eigenvalues. These approximation give information about the local asymptotic stability properties of the equilibria and of the single-class three-cycle by means of the linearization principle. The details appear in the Appendix.

Theorem 4 *Assume the semelparous Leslie model* (2) *satisfies* (3) *and* (4) *and assume that at least one* β_{jj} *is nonzero. For each* $R_0 \gtrapprox 1$ *we have on* R^3_+ *that*

(a) *the positive equilibrium is LAS if* $(\rho_1, \rho_2) \in \Omega_1 \cup \Omega_2$ (*weak competition*) *and is unstable* (*a saddle*) *if* $(\rho_1, \rho_2) \in \Omega_3 \cup \Omega_4$ (*strong competition*);
(b) *the single-class three-cycle is unstable if* $(\rho_1, \rho_2) \in \Omega_1 \cup \Omega_2 \cup \Omega_3$ (*asymmetric or weak symmetric competition*) *and LAS is* $(\rho_1, \rho_2) \in \Omega_4$ (*strong symmetric competition*).

Consider populations that initiate in $int(R^3_+)$, i.e., with all three age classes present. Theorem 4 suggests that when inter-class competition is weak (i.e., on regions Ω_1 or Ω_2) these population will equilibrate with overlapping generations. (I say "suggests" because, mathematically, this stability conclusion is only local in nature, although we conjecture that the positive equilibrium is globally attracting on $int(R^3_+)$.) On the other hand, when inter-class competition is strong and symmetric (i.e., on region Ω_4) Theorem 4 implies that such populations will not equilibrate with overlapping generations (part (a)); instead the theorem suggests these populations will asymptotically approach the single-class three-cycle with separated generations. (Similarly part (b) only asserts the local stability of the three-cycle.)

Note that on parameter region Ω_3 both the positive equilibrium and the single-class three-cycle are unstable. In this case of weak-asymmetric competition, the long term dynamics on R^3_+ are still unclear. Theorem 5 below shows that the boundary of the positive cone is an attractor in this case, which means that asymptotically orbits in $int(R^3_+)$ approach the heteroclinic cycle of type A lying on the boundary of the cone.

$\partial R^3_+ \backslash \hat{0}$ is an attractor if there exists an open neighborhood $U \subset R^3_+$ of $\partial R^3_+ \backslash \hat{0}$ (in the relative topology of R^3) such that orbits with initial conditions in U have ω-limit sets in $\partial R^3_+ \backslash \hat{0}$. On the other hand, ∂R^3_+ is a *repeller* if there exists a neighborhood $U \subset R^3_+$ of ∂R^3_+ such that for the orbit from each initial condition not in ∂R^3_+ there exists a time $T > 0$ such that the orbit lies outside of U for all $t \geq T$. A proof of the following theorem (that utilizes average Lyapunov function theory) appears in the Appendix.

Theorem 5 *Assume that the semelparous Leslie model* (2) *satisfies* (3) *and* (4), *that at least one* β_{jj} *is nonzero, and that* $R_0 \gtrapprox 1$.

(a) *For* $(\rho_1, \rho_2) \in \Omega_3 \cup \Omega_4$ (*strong competition*) *the boundary set* $\partial C \backslash \hat{0} \subset \partial R^3_+ \backslash \hat{0}$ *is an attractor.*
(b) *For* $(\rho_1, \rho_2) \in \Omega_1 \cup \Omega_2$ (*weak competition*) *the boundary set* $\partial C \subset \partial R^3_+$ *is a repeller.*

This theorem implies that for weak intra-class competition no temporal separation of age classes occurs (regardless of the nature of the global asymptotic attractor on $int(R^3_+)$). For strong competition age class separation and synchronization occurs (since orbits on ∂R^3_+ temporally visit the three coordinate planes sequentially), regardless of the nature of the asymptotic attractor on the boundary ∂R^3_+. On the region Ω_3 of weak asymmetric competition, the single-class three-cycle is unstable and the temporal segregation of age-class occurs as a result of the attracting heteroclinic cycle of type A lying on ∂R^3_+. That dynamic has the population sequentially visiting the neighborhood of successive phases of the single-class three-cycle (in episodes of increasing duration). See Fig. 5 below. On the region Ω_4 of strong symmetric competition, the attractor is the heteroclinic chain of type SS on which, however, the dynamic is asymptotically period-locked onto the single-class three-cycle.

5 Concluding remarks

With regard to the nature of the bifurcation that occurs at the origin at $R_0 = 1$, the following theorem is a corollary of Theorems 3, 4, and 5.

Theorem 6 *Consider the nonlinear semelparous Leslie model* (2) *under the assumptions* (3)–(4) *and assume at least one* $\beta_{jj} \neq 0$ *and* $\rho_1\rho_2 \neq 1$. *The extinction equilibrium loses stability as the inherent net reproductive number* R_0 *increases through* 1, *at which point transcritical bifurcations of both positive equilibria and invariant loops* (*heteroclinic chains*) *occur. The bifurcation is supercritical, i.e., the positive equilibria and heteroclinic chains exist for* $R_0 \gtrapprox 1$.

On the parameter region $\Omega_2 \cup \Omega_3$ *of asymmetric inter-class competition, the bifurcating invariant loops are heteroclinic cycles of type A* (*see Fig.* 2). *On the region* Ω_2 *of weak-asymmetric competition, the positive equilibria are* (*locally asymptotically*) *stable and the heteroclinic cycles are unstable. On the region* Ω_3 *of strong-asymmetric competition, the reverse is true, i.e., the positive equilibria are unstable and the heteroclinic cycles are locally attracting.*

On the parameter region $\Omega_1 \cup \Omega_4$ *of symmetric inter-class competition, the bifurcating invariant loops are heteroclinic chains of type WS or SS* (*see Fig.* 2). *On the region* Ω_1 *of weak-symmetric competition, the positive equilibria are* (*locally asymptotically*) *stable and the heteroclinic chains are of type WS and unstable. On the region* Ω_4 *of strong-symmetric competition, the positive equilibria are unstable and the heteroclinic chains are of type SS and locally attracting.*

The bifurcation of invariant loops for the semelparous Leslie model (2) is not unexpected because of the complex conjugate pair of eigenvalues that crosses the unit circle at $R_0 = 1$. In general this is predicted by the well-known Neimark-Sacker (or discrete Hopf bifurcation) Theorem [17,30,34]. However, that well-known theorem does not apply to (2) for two reasons: a real eigenvalue also leaves the unit circle at $R_0 = 1$ and the complex roots leave at a cube root of unity (a "resonance" case not covered by the Neimark–Sacker Theorem).

The bifurcation Theorem 6 concerns the stability on the cone R^3_+ of two bifurcating entities for $R_0 \gtrapprox 1$: positive equilibria (overlapping age cohorts) and heteroclinic chains (synchronized and non-overlapping age cohorts). The stability results are local and the global nature of the dynamics on the interior of the cone remains an open question. The results in Sect. 3, on the other hand, provide a complete accounting of the dynamics on the boundary of the cone and that analysis is global. The boundary dynamics are not only of mathematical interest. A population founded with a missing age cohort (for example, by a dispersing life cycle stage) will be subject to those dynamics. As we have seen, the boundary dynamics always lead asymptotically to

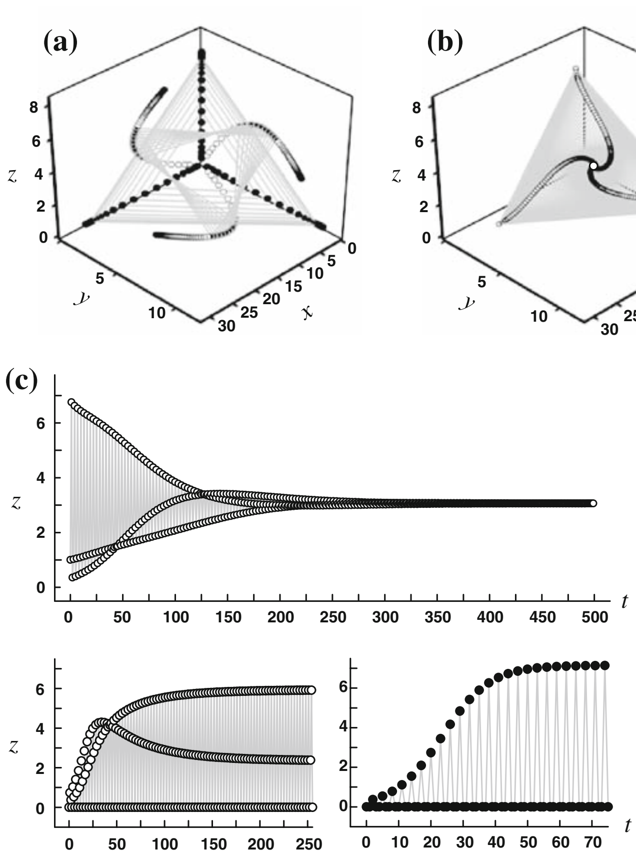

Fig. 3 Parameter Region Ω_1. This figure shows sample orbits for the model equations (2) with the non-linearities (5) and parameter values $b = 4$, $s_1 = 0.5$, $s_2 = 0.75$ and competition coefficient matrix $B = \begin{pmatrix} 0.01 & 0 & 0 \\ 0.01 & 0.01 & 0 \\ 0.01 & 0.01 & 0.01 \end{pmatrix}$. These parameters imply $R_0 = 1.5$ and $(\rho_1, \rho_2) = (0.800, 0.533) \in \Omega_1$. **a** An orbit with initial condition $(x_0, y_0, z_0) = (1, 0, 0)$ on the coordinate axes A_+^0 (*solid circles*) tends to a single-class three-cycle on the coordinate axes. An orbit with initial condition $(x_0, y_0, z_0) = (1, 1, 0)$ in the positive coordinate planes P_+^0 (*open circles*) tends to a two-class three-cycle on the planes. **b** An orbit with initial condition $(x_0, y_0, z_0) = (1, 10, 1)$ in the interior of R_+^3 tends to the positive equilibrium $(x_e, y_e, z_e) = (10.367, 4.693, 3.062)$. **c** Three plots illustrate the time series for the adult component z of the orbits in **a** and **b**. The *top plot* shows the equilibration of the orbit in the interior of R_+^3. The *lower left plot* shows the approach to a two class three-cycle by the orbit on the coordinate planes. The *lower right plot* shows the approach to the single-class three-cycle of the orbit on the coordinate axes

synchronized age cohorts (with either one or two missing age classes at every point in time). A perturbation which causes an occurrence of overlapping age cohorts (i.e., into $int(R_+^3)$) can break the synchronization, however, provided the inter-age class competition is sufficiently weak (so that the boundary is a repeller). Another interesting case for the importance of the boundary dynamics occurs when two (or more) semelparous species compete (a problem we do not consider here). The synchronized

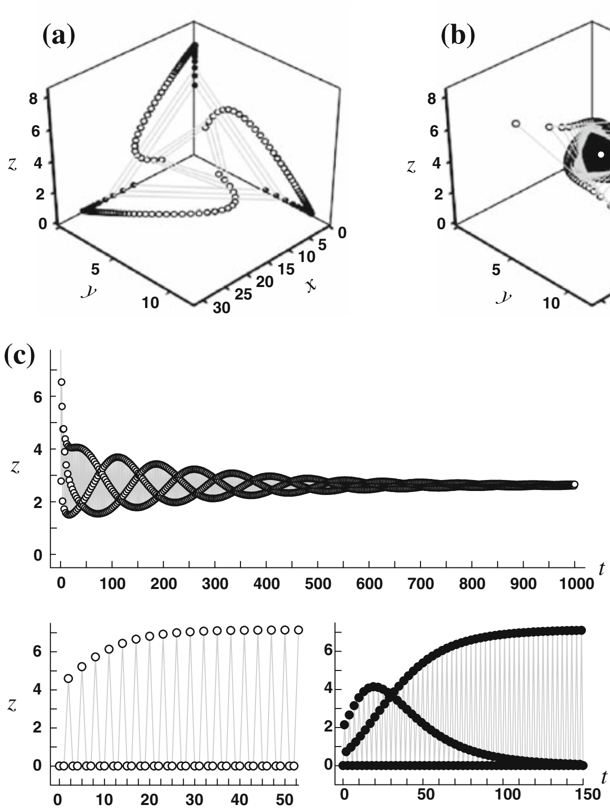

Fig. 4 Parameter Region Ω_2. This figure shows sample orbits for the model equations (2) with the nonlinearities (5) and the same parameter values as in Fig. 1 (and hence $R_0 = 1.5$) except with the competition coefficient matrix $B = \begin{pmatrix} 0.01 & 0 & 0 \\ 0.01 & 0.01 & 0 \\ 0.01 & 0.03 & 0.01 \end{pmatrix}$ which implies $(\rho_1, \rho_2) = (1.333, 0.5333) \in \Omega_2$. **a** An orbit $(x_0, y_0, z_0) = (15, 0, 0)$ on the coordinate axes A_+^0 (*solid circles*) and an orbit with initial condition $(x_0, y_0, z_0) = (2, 3, 0)$ in the positive coordinate planes P_+^0 (*open circles*) both tend to the single-class three-cycle on the coordinate axes. **b** An orbit with initial condition $(x_0, y_0, z_0) = (30, 5, 8)$ in the interior of R_+^3 tends to the positive equilibrium. $(x_e, y_e, z_e) = (8.458, 3.900, 2.655)$. **c** Three plots illustrate the time series for the adult component z of the orbits in **a** and **b**. The *top plot* shows the equilibration of the orbit in the interior of R_+^3. The *lower two plots* show the approach to the single-class three-cycle by both the coordinate axis and coordinate plane orbits in **a**

cycles for each species turn out to allow for competitive coexistence in circumstances that otherwise would be ruled out by the competitive exclusion principle [10].

Illustrative numerical examples of the dynamics on the cone and on its boundary appear in Figs. 3–6 for each of the parameter regions Ω_i.

The results in this paper rely on the monotonicity assumptions in (3)–(4). These assumptions allow for the application of monotone flow theory and an understanding of the global dynamics on the boundary of the positive cone. Consequently, the results do not apply to the exponential (Ricker) type nonlinearities that are often employed

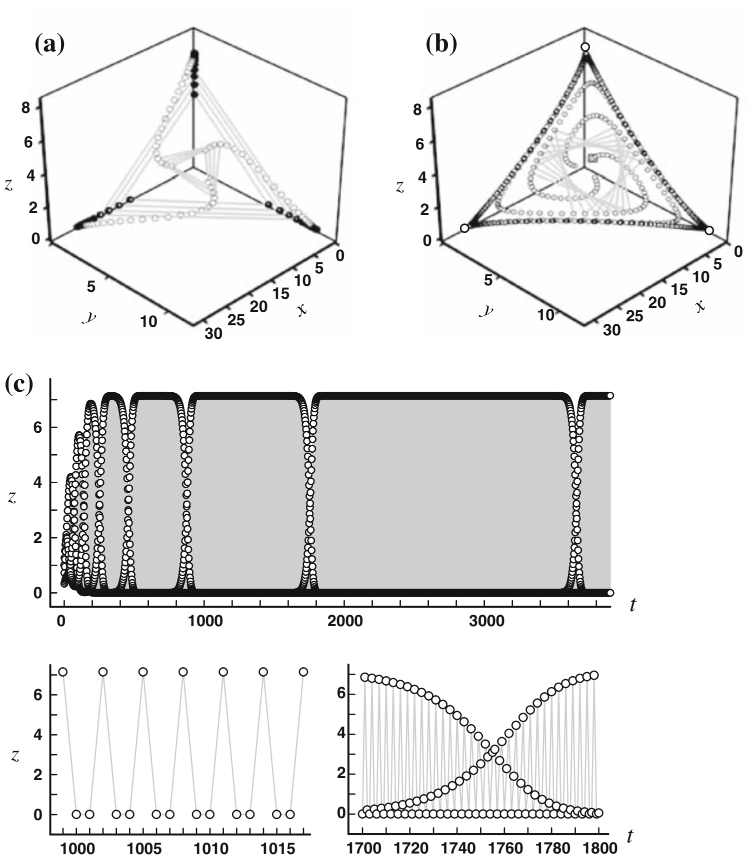

Fig. 5 Parameter region Ω_3. This figure shows sample orbits for the model equations (2) with the nonlinearities (5) and the same parameter values as in Fig. 1 (and hence $R_0 = 1.5$) except with the competition coefficient matrix $B = \begin{pmatrix} 0.01 & 0 & 0 \\ 0.03 & 0.01 & 0 \\ 0.01 & 0.02 & 0.01 \end{pmatrix}$. These parameters imply $(\rho_1, \rho_2) = (2.133, 0.5333) \in \Omega_3$. **a** An orbit with initial condition $(x_0, y_0, z_0) = (15, 0, 0)$ on the coordinate axes A_+^0 (*solid circles*) and an orbit with initial condition $(x_0, y_0, z_0) = (2, 3, 0)$ in the positive coordinate planes P_+^0 (*open circles*) both tend to the single-class three-cycle on the coordinate axes. **b** An orbit in the interior of R_+^3 with initial condition $(x_0, y_0, z_0) = (1, 1, 1)$ (*open square*) tends to the heteroclinic cycle of type A lying on the boundary ∂R_+^3. **c** Three plots illustrate the time series for the adult component z of the orbit in **b**. The lower two graphs show, left to right, an episode of three-cycle dynamics and a transitional shift from one phase to another respectively

in model studies of semelparous populations (e.g. see [4,11,12,21,22]). However, since all of the results in this paper are restricted to the case when R_0 is near 1 (and therefore for positive equilibria and synchronous cycles near the origin), it is natural to conjecture that they remain valid under only local monotonicity assumptions, namely, $g_i'(0) < 0$ and $h_i'(0) > 0$. If that conjecture is correct, then the results here would also apply to models with exponential nonlinearities for R_0 near 1.

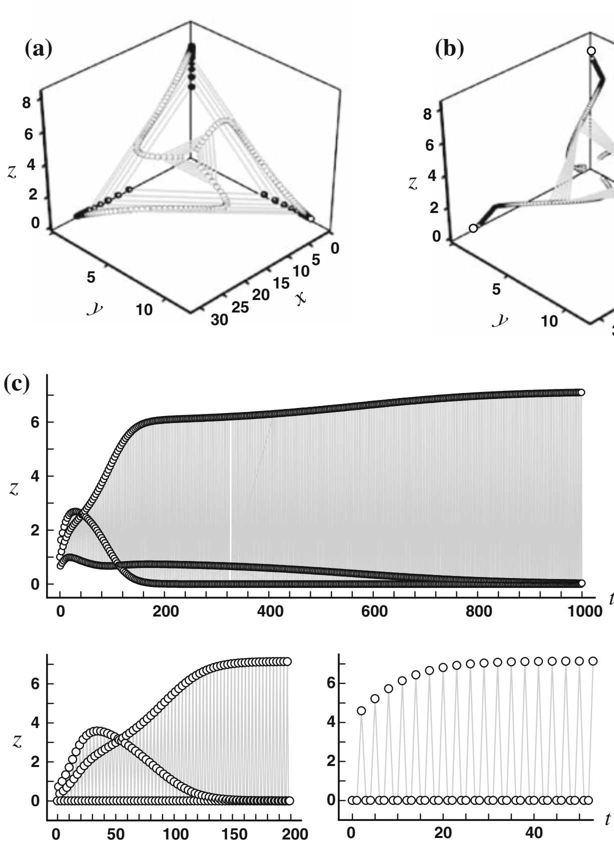

Fig. 6 Parameter Region Ω_4. This figure shows sample orbits for the model equations (2) with the nonlinearities (5) and the same parameter values as in Fig. 1 (and hence $R_0 = 1.5$) except with the competition coefficient matrix $B = \begin{pmatrix} 0.01 & 0 & 0 \\ 0.02 & 0.01 & 0 \\ 0.02 & 0.02 & 0.01 \end{pmatrix}$. These parameters imply $(\rho_1, \rho_2) = (1.600, 1.067) \in \Omega_4$. **a** An orbit with initial condition $(x_0, y_0, z_0) = (15, 0, 0)$ on the coordinate axes A_+^0 (*solid circles*) and an orbit with initial condition $(x_0, y_0, z_0) = (1, 1, 0)$ in the positive coordinate planes P_+^0 (*open circles*) both tend to the single-class three-cycle on the coordinate axes. **b** An orbit in the interior of R_+^3 with initial condition $(x_0, y_0, z_0) = (5, 1, 1)$ (*open square*) tends to single-class three-cycle on the coordinate axes. **c** Three plots illustrate the time series for the adult component z of the orbits in **a** and **b**. All three plots show approach to the single-class three-cycle

In a recent paper Kon and Iwasa [23] consider semelparous Leslie models of arbitrary dimension for general nonlinearities without the constraints of monotonicity or $R_0 \gtrapprox 1$. They obtain conditions that ensure the instability or local stability of single-class cycles. For the 3D models we consider in this paper (and for $R_0 \gtrapprox 1$) it turns out that their conditions are sufficient (although not necessary) to place (ρ_1, ρ_2) in regions Ω_1 and Ω_4, as is commensurate with our results here. While they consider more general models and consider arbitrary $R_0 > 1$, they do not consider the case of asymmetric competition, characterize the dynamics for symmetric competition, study two-class three-cycles, or consider the structure of the invariant loops (heteroclinic chains) on the boundary of the cone.

Since the approach in this paper is based on bifurcation theory methods and are restricted to $R_0 \gtrapprox 1$, it is not known to what extent the results remain valid for arbitrary $R_0 > 1$. In particular, the relevance of the parameter regions in characterizing the equilibrium and invariant loop dynamics is an open question for large $R_0 > 1$. A recent paper of Diekmann et al. [14] contains results concerning heteroclinic orbits for arbitrary $R_0 > 1$ (obtained by carrying simplex methods) for a special class of models, namely models with Beverton–Holt nonlinearities (5) and a restriction on the weighted population sizes w_i (which implies, among other things, that vital rates in the Leslie matrix remain constant on a planar simplex in R_+^3). For example, for such models of three dimension the authors obtain the existence of a heteroclinic cycle of type A for arbitrary $R_0 > 1$ (Corollary 1.3 in [14]). We can guarantee the latter requirement when R_0 is close to 1 for asymmetric competition (i.e., parameters in regions Ω_2 or Ω_3), but not for arbitrary $R_0 > 1$. (Other papers concerned with heteroclinic cycles are [4,12,13].)

Only models of dimensional three are studied in this paper. Semelparous Leslie models of dimension higher than three are also of interest [2,12,20,23,29,35,37]. This is particularly true for applications to the dynamics of periodical insects such as cicadas, whose synchronous outbreaks have historically been of interest because they are of such long periods. In principle, the mathematical analyses carried out in this paper are applicable to higher dimensional models, although the details of the approach taken here become computationally formidable. If that analyses were carried out, or if a different approach could be found to study the bifurcation at $R_0 = 1$, it is likely that invariant loops (possibly more than one) will be found to bifurcate at $R_0 = 1$, along with the positive equilibrium, and that these loops, although with increasingly complicated structure as the dimension increases, will consist of heteroclinic connections to the phases of synchronous cycles (in an increasing complexity of possible combinations). It is also to be anticipated that the stability issue will reduce to a choice between the positive equilibrium (overlapping age classes) and the boundary of the cone on which the invariant loops reside (synchronized age cohorts) and that this choice will be determined by some measure of the intensity of inter-class competition expressed by analogs of the ratios ρ_1 ,ρ_2 for the 3D case studied here.

Acknowledgments I would like to thank the anonymous referees for their very constructive comments and suggestions. This material is based upon work supported by the National Science Foundation under Grant No. 0414212.

Appendix

Proof of Lemma 3 The composition map has the form

$$\begin{pmatrix} x \\ y \\ z \end{pmatrix} \to \begin{pmatrix} R_0\gamma_1(x, y, z)\, x \\ R_0\gamma_2(x, y, z)\, y \\ R_0\gamma_3(x, y, z)\, z \end{pmatrix}$$

where

$$\begin{aligned}\gamma_1(x,y,z) &\triangleq g_3(\beta_{31}x_2+\beta_{32}y_2+\beta_{33}z_2)\, g_2(\beta_{21}x_1+\beta_{22}y_1+\beta_{23}z_1)\\ &\quad \times g_1(\beta_{11}x+\beta_{12}y+\beta_{13}z)\\ \gamma_2(x,y,z) &\triangleq g_1(\beta_{11}x_2+\beta_{12}y_2+\beta_{13}z_2)\, g_3(\beta_{31}x_1+\beta_{32}y_1+\beta_{33}z_1)\\ &\quad \times g_2(\beta_{21}x+\beta_{22}y+\beta_{23}z)\\ \gamma_3(x,y,z) &\triangleq g_2(\beta_{21}x_2+\beta_{22}y_2+\beta_{23}z_2)\, g_1(\beta_{11}x_1+\beta_{12}y_1+\beta_{13}z_1)\\ &\quad \times g_3(\beta_{31}x+\beta_{32}y+\beta_{33}z)\end{aligned}$$

and $x_i = x_i(x,y,z),\ y_i = y_i(x,y,z),\ z_i = z_i(x,y,z)$ are defined by

$$\begin{aligned}x_1(x,y,z) &\triangleq bg_3(\beta_{31}x+\beta_{32}y+\beta_{33}z)\,z,\\ x_2(x,y,z) &\triangleq bg_3(\beta_{31}x_1+\beta_{32}y_1+\beta_{33}z_1)\,z_1\\ y_1(x,y,z) &\triangleq s_1g_1(\beta_{11}x+\beta_{12}y+\beta_{13}z)\,x,\\ y_2(x,y,z) &\triangleq s_1g_1(\beta_{11}x_1+\beta_{12}y_1+\beta_{13}z_1)\,x_1\\ z_1(x,y,z) &\triangleq s_2g_2(\beta_{21}x+\beta_{22}y+\beta_{23}z)\,y,\\ z_2(x,y,z) &\triangleq s_2g_2(\beta_{21}x_1+\beta_{22}y_1+\beta_{23}z_1)\,y_1.\end{aligned}$$

Two-class three-cycles correspond to fixed points of this map with exactly one zero component. It is sufficient to study the map in the (x, y)-plane. In the (x, y)-plane such fixed points satisfy

$$x = R_0\gamma_1(x,y,0)\,x, \quad y = R_0\gamma_2(x,y,0)\,y \tag{11}$$

with nonzero x and y or equivalently

$$\Gamma_1(x,y,R_0) \triangleq R_0\gamma_1(x,y,0) - 1 = 0, \quad \Gamma_2(x,y,R_0) \triangleq R_0\gamma_2(x,y,0) - 1 = 0. \tag{12}$$

One can solve these equations in the neighborhood of the origin and $R_0 = 1$ by use of the Implicit Function Theorem. For that purpose we need the Jacobian of the pair Γ_1, Γ_2 evaluated at $x = y = 0$ and $R_0 = 1$. Note that $\gamma_i(0,0,0) = 1$ and hence $\Gamma_i(0,0,1) = 0$. Define

$$d \triangleq \beta_{11} + s_1\beta_{22} + s_1s_2\beta_{33}$$

and let ∂_x^0 and ∂_y^0 denote partial differentiation followed by evaluation at $x = y = 0$ and $R_0 = 1$. Using the assumptions $g_i(0) = 1$ and $g_i'(0) = -1$ in (3), we calculate the derivatives $\partial_x^0 y_1 = s_1,\ \partial_y^0 y_1 = 0,\ \partial_x^0 z_1 = 0,\ \partial_y^0 z_1 = s_2$ and $\partial_x^0 x_2 = 0,\ \partial_y^0 x_2 = s_1^{-1}$,

$\partial_x^0 z_2 = s_1 s_2$, $\partial_y^0 z_2 = 0$, and then

$$\partial_x^0 \Gamma_1 = -d, \quad \partial_y^0 \Gamma_1 = -\beta_{12} - s_2\beta_{23} - s_1^{-1}\beta_{31},$$
$$\partial_x^0 \Gamma_2 = -\beta_{21} - s_1\beta_{32} - s_1 s_2\beta_{13}, \quad \partial_y^0 \Gamma_2 = -s_1^{-1} d.$$

Thus,

$$\det \begin{pmatrix} \partial_x^0 \Gamma_1 & \partial_y^0 \Gamma_1 \\ \partial_x^0 \Gamma_2 & \partial_y^0 \Gamma_2 \end{pmatrix} = s_1^{-1} d^2 (1 - \rho_1 \rho_2)$$

and, if $\rho_1\rho_2 \neq 1$, then the Implicit Function Theorem implies the existence of a unique branch of solutions

$$x = x_+ (R_0), \quad y = y_+ (R_0) \tag{13}$$

of (12) which is defined and continuously differentiable for R_0 near 1 and that satisfies $x_+ (1) = 0$, $y_+ (1) = 0$. An implicit differentiation of the two equations $\Gamma_i (x_+ (R_0), y_+ (R_0)) = 0$ with respect to R_0 leads to equations that one can solve for

$$x_+'(1) = d^{-1} \frac{1 - \rho_2}{1 - \rho_1\rho_2}, \quad y_+'(1) = s_1 d^{-1} \frac{1 - \rho_1}{1 - \rho_1\rho_2}.$$

A study of these formulas shows that $x_+ (R_0)$ and $y_+ (R_0)$ are both positive if and only if both $\rho_i < 1$ or both $\rho_i > 1$, i.e., on regions Ω_1 and Ω_4.

All that remains to prove is the last sentence in the statement of Lemma 3. This follows from the uniqueness assertion of the Implicit Function Theorem which implies, in a neighborhood of the origin and $R_0 = 1$, that the only solutions of (12) lie on the branch (13). For R_0 sufficiently close to 1 we know from Lemma 1 that any possible positive equilibrium must lie in the square $(0, x^*) \times (0, y^*)$. For R_0 even closer to 1 if necessary this square lies in the neighborhood of uniqueness guaranteed by the Implicit Function Theorem (since both x^* and y^* tend to 0 as R_0 tends to 1). □

Proof of Theorem 3 That the single-class three-cycle is GAS on the positive axes A_+^0 follows from Theorem 2. The dynamics of the composite map on the (forward invariant) positive quadrant of the (x, y)-plane are described by the equations

$$\begin{aligned} x_{t+1} &= R_0 \gamma_1 (x_t, y_t, 0)\, x_t \\ y_{t+1} &= R_0 \gamma_2 (x_t, y_t, 0)\, y_t \end{aligned} \tag{14}$$

$$\gamma_1 (x, y, 0) \triangleq g_3 (\beta_{31} x_2 + \beta_{33} z_2)\, g_2 (\beta_{22} y_1 + \beta_{23} z_1)\, g_1 (\beta_{11} x + \beta_{12} y)$$
$$\gamma_2 (x, y, 0) \triangleq g_1 (\beta_{11} x_2 + \beta_{13} z_2)\, g_3 (\beta_{32} y_1 + \beta_{33} z_1)\, g_2 (\beta_{21} x + \beta_{22} y).$$

There are two axes equilibria

$$\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} x^* \\ 0 \end{pmatrix} \text{ and } \begin{pmatrix} 0 \\ y^* \end{pmatrix}$$

where x^* and y^* are points on the single-class three-cycle (8). A linearization analysis requires the dominant eigenvalue of the Jacobian of (14) evaluated at each of these two equilibria, namely,

$$J_2(x^*, 0) = \left.\begin{pmatrix} R_0\partial_x\left(x\gamma_1(x,0,0)\right) & R_0 x\partial_y\gamma_1\left(x,0,0\right) \\ 0 & R_0\gamma_2\left(x,0,0\right)\end{pmatrix}\right|_{x=x^*}$$

$$J_2(0, y^*) = \left.\begin{pmatrix} R_0\gamma_1\left(0,y,0\right) & 0 \\ R_0 y\partial_x\gamma_2\left(0,y,0\right) & R_0\partial_y\left(y\gamma_2(0,y,0)\right)\end{pmatrix}\right|_{y=y^*}.$$

The eigenvalues of these triangular matrices appear along the diagonals. Two of the eigenvalues are those of the one dimensional maps on the forward invariant x-axis and y-axis and satisfy

$$0 < R_0\partial_x\left(x\gamma_1(x,0,0)\right)|_{x=x^*} < 1, \quad 0 < R_0\partial_y\left(y\gamma_2(0,y,0)\right)|_{y=y^*} < 1.$$

(Recall that the equilibria of the composite are stable on the coordinate axes.) The stability determining eigenvalues are the positive real numbers $R_0\gamma_2\left(x^*, 0, 0\right)$ and $R_0\gamma_1\left(0, y^*, 0\right)$. We can approximate the magnitudes of these quantities for $R_0 \gtrapprox 1$ by using the (Lyapunov-Schmidt) expansions

$$x^*(\varepsilon) = d^{-1}\varepsilon + O\left(\varepsilon^2\right), \quad y^*(\varepsilon) = s_1 d^{-1}\varepsilon + O\left(\varepsilon^2\right), \quad z^*(\varepsilon) = s_1 s_2 d^{-1}\varepsilon + O\left(\varepsilon^2\right) \tag{15}$$

where $\varepsilon \triangleq R_0 - 1$. (Here we used $\partial_x^0 F = s_1 s_2 \partial_z^0 g_3 + \partial_x^0 g_1 + s_1 \partial_y^0 g_2$ in correction to the formula for this derivative that appears in [5].) To first order in ε we have that

$$g_1\left(\beta_{13}z^*\right) = 1 - \beta_{13}s_1 s_2 d^{-1}\varepsilon + O\left(\varepsilon^2\right), \quad g_2\left(\beta_{21}x^*\right) = 1 - \beta_{21}d^{-1}\varepsilon + O\left(\varepsilon^2\right),$$
$$g_3\left(\beta_{32}y^*\right) = 1 - \beta_{32}s_1 d^{-1}\varepsilon + O\left(\varepsilon^2\right)$$

(recall $g_i'(0) = -1$) and thus arrive at the expansions

$$R_0\gamma_2\left(x^*, 0, 0\right) = R_0 g_1\left(\beta_{13}z^*\right) g_3\left(\beta_{32}y^*\right) g_2\left(\beta_{21}x^*\right) = 1 + (1-\rho_1)\varepsilon + O\left(\varepsilon^2\right)$$
$$R_0\gamma_1\left(0, y^*, 0\right) = R_0 g_3\left(\beta_{31}x^*\right) g_2\left(\beta_{23}z^*\right) g_1\left(\beta_{12}y^*\right) = 1 + (1-\rho_2)\,\varepsilon + O\left(\varepsilon^2\right)$$

for the stability determining eigenvalues. It follows that the composite equilibrium $(x^*, 0)$ is LAS for $R_0 \gtrapprox 1$ if $\rho_1 > 1$ and unstable if $\rho_1 < 1$, and the composite equilibrium $(0, y^*)$ is LAS for $R_0 \gtrapprox 1$ if $\rho_2 > 1$ and unstable if $\rho_2 < 1$. Similar calculations lead to analogous results for the composite dynamics on the y, z-plane and the z, x-plane. Specifically, $\rho_1 > 1$ (respectively $\rho_1 < 1$) implies

$$
\begin{array}{l}
(x^*, 0) \text{ is LAS (respectively unstable) in the } x, y\text{-plane} \\
(y^*, 0) \text{ is LAS (respectively unstable) in the } y, z\text{-plane} \\
(z^*, 0) \text{ is LAS (respectively unstable) in the } z, x\text{-plane}
\end{array}
$$

and $\rho_2 > 1$ (respectively $\rho_2 < 1$) implies

$$
\begin{array}{l}
(0, y^*) \text{ is LAS (respectively unstable) in the } x, y\text{-plane} \\
(0, z^*) \text{ is LAS (respectively unstable) in the } y, z\text{-plane} \\
(0, x^*) \text{ is LAS (respectively unstable) in the } z, x\text{-plane.}
\end{array}
$$

Part (a). In the parameter region $(\rho_1, \rho_2) \in \Omega_1$ the axes equilibria of the composite are unstable (saddles whose stable manifolds are the coordinate axes) and therefore it follows from Theorem 5.3 [36] that the positive planar equilibrium (x_+, y_+) is globally attracting on the coordinate planes P_+^0. To finish the proof of part (a) we need to show that (x_+, y_+) is LAS. The proof of Lemma 3 implies

$$
x_+ = d^{-1}\frac{1-\rho_2}{1-\rho_1\rho_2}\varepsilon + O\left(\varepsilon^2\right), \quad y_+ = s_1 d^{-1}\frac{1-\rho_1}{1-\rho_1\rho_2}\varepsilon + O\left(\varepsilon^2\right).
$$

A straightforward, but tedious, calculation shows that the Jacobian of (14), to first order, is

$$
\begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix} + \begin{pmatrix} -\frac{1-\rho_2}{1-\rho_1\rho_2} & -\frac{1}{s_1}\rho_2\frac{1-\rho_2}{1-\rho_1\rho_2} \\ -s_1\rho_1\frac{1-\rho_1}{1-\rho_1\rho_2} & -\frac{1-\rho_1}{1-\rho_1\rho_2} \end{pmatrix}\varepsilon + O\left(\varepsilon^2\right) \tag{16}
$$

and that the eigenvalues are real and, to first order, have expansions

$$
\lambda_1 = 1 - \varepsilon + O\left(\varepsilon^2\right), \quad \lambda_2 = 1 + \frac{(\rho_1 - 1)(\rho_2 - 1)}{\rho_1\rho_2 - 1}\varepsilon + O\left(\varepsilon^2\right). \tag{17}
$$

On parameter region Ω_1 where both $\rho_i < 1$ we see that both eigenvalues satisfy $0 < \lambda_i < 1$. It follows that the fixed point (x_+, y_+) of the composite is LAS. Similar analyses carried out on the other two coordinate planes lead to the same result. Consequently, the two-age class three-cycle is LAS on the boundary ∂R_+^3.

Part (b). In the parameter regions Ω_2 and Ω_3 there exist no planar equilibria of the composite and therefore no two-class three-cycles on the boundary ∂R_+^3 (Lemma 3(b)). It follows from Lemma 2(b) that the single-class three-cycle is globally attracting on $P_+^0 \cup A_+^0 = \partial R_+^3 \backslash \hat{0}$.

Part (c). Consider the parameter region $(\rho_1, \rho_2) \in \Omega_4$. Since both $\rho_i > 1$, it follows from the analysis of the coordinate axes equilibria of the composite map above that the single-class three-cycle is LAS on the boundary ∂R_+^3. Also in this case we see from (17) that the composite fixed point (x_+, y_+) in the (x, y)-coordinate plane is a saddle. Moreover, from the expansion (16) we find that the Jacobian of (14), evaluated at the fixed point (x_+, y_+), has a positive determinant for $\varepsilon \gtrapprox 0$. Part (c) follows from Theorem 5 in [25].

Proof of Theorem 4(a) From Theorem 2.1 in [5] follows, for $\varepsilon \triangleq R_0 - 1 > 0$ sufficiently small, the equilibrium expansion

$$\begin{pmatrix} x_e(\varepsilon) \\ y_e(\varepsilon) \\ z_e(\varepsilon) \end{pmatrix} = \frac{1}{\Delta} \begin{pmatrix} 1 \\ s_1 \\ s_1 s_2 \end{pmatrix} \varepsilon + O\left(\varepsilon^2\right) \tag{18}$$

where

$$\Delta \triangleq (\beta_{31} + \beta_{11} + \beta_{21}) + s_1 (\beta_{32} + \beta_{12} + \beta_{22}) + s_1 s_2 (\beta_{33} + \beta_{13} + \beta_{23}) > 0.$$

From this follow ε-expansions for the Jacobian of (2) evaluated at (18) and its eigenvalues λ:

$$J(x_e(\varepsilon), y_e(\varepsilon), z_e(\varepsilon)) = J_0 + J_1\varepsilon + O\left(\varepsilon^2\right), \quad \lambda(\varepsilon) = \lambda_0 + \lambda_1\varepsilon + O\left(\varepsilon^2\right).$$

Here

$$J_0 = \begin{pmatrix} 0 & 0 & \frac{1}{s_1 s_2} \\ s_1 & 0 & 0 \\ 0 & s_2 & 0 \end{pmatrix}$$

and hence λ_0 is one of the cube roots of unity: $\lambda_0 = 1$ and $(-1 \pm \sqrt{3}i)/2$. Stability for $\varepsilon \gtrapprox 0$ is determined by $\lambda_0 + \lambda_1\varepsilon$. Let v_0 and w_0 denote the right and left eigenvectors of J_0 associated with λ_0 normalized so that $w_0 v_0 = 1$. To first order we have $J_0 v_1 = \lambda_0 v_1 + (\lambda_1 v_0 - J_1 v_0)$ and hence $\lambda_1 = w_0 J_1 v_0$. A straightforward expansion of each term in the Jacobian results in

$$J_1 = \frac{1}{\Delta} \begin{pmatrix} -\beta_{31} & -\beta_{32} & \begin{matrix} \frac{\beta_{11}+\beta_{21}}{s_1 s_2} + \frac{\beta_{12}+\beta_{22}}{s_2} \\ +\beta_{13} + \beta_{23} - \beta_{33} \end{matrix} \\ \begin{matrix} -2s_1\beta_{11} \\ -s_1^2\beta_{12} - s_1^2 s_2 \beta_{13} \end{matrix} & -\beta_{12} s_1 & -\beta_{13} s_1 \\ -\beta_{21} s_1 s_2 & \begin{matrix} -s_2\beta_{21} \\ -2s_1 s_2 \beta_{22} - s_1 s_2^2 \beta_{23} \end{matrix} & -\beta_{23} s_1 s_2 \end{pmatrix}.$$

For $\lambda_0 = 1$ these formulas yield the first order coefficient $\lambda_1 = -1/3$. For $\lambda_0 = \left(-1 + i\sqrt{3}\right)/2$ they yield a complex coefficient $\lambda_1 = a_1 + ib_1$ where

$$a_1 \triangleq \frac{1}{6\Delta} (\beta_{11} + \beta_{21} - 2\beta_{31} - 2s_1\beta_{12} + s_1\beta_{22} + s_1\beta_{32} + s_1 s_2 \beta_{13} - 2s_1 s_2 \beta_{23} + s_1 s_2 \beta_{33})$$

$$b_1 \triangleq \frac{\sqrt{3}}{6\Delta} (\beta_{21} - \beta_{11} - s_1\beta_{22} + s_1\beta_{32} + s_1 s_2 \beta_{13} - s_1 s_2 \beta_{33}).$$

For $\lambda_0 = \left(-1 + i\sqrt{3}\right)/2$ the coefficient is the conjugate $\lambda_1 = a_1 - ib_1$.

For $\varepsilon \gtrapprox 0$ the eigenvalue $\lambda(\varepsilon) = 1 - \varepsilon/3 + O\left(\varepsilon^2\right)$ satisfies $0 < \lambda(\varepsilon) < 1$. As a result the stability of the positive equilibrium depends on the magnitude of the complex eigenvalue

$$\lambda(\varepsilon) = (a_0 + b_0 i) + (a_1 + i b_1)\,\varepsilon + O\big(\varepsilon^2\big), \quad a_0 \triangleq -1/2, \quad b_0 \triangleq \sqrt{3}/2$$

for $\varepsilon \gtrapprox 0$. Since $|\lambda(\varepsilon)|^2 = 1 + 2\varepsilon\,(a_0 a_1 + b_0 b_1) + O\left(\varepsilon^2\right)$ we see that $a_0 a_1 + b_0 b_1 < 0 \Longrightarrow |\lambda(\varepsilon)| < 1$ and $a_0 a_1 + b_0 b_1 > 0 \Longrightarrow |\lambda(\varepsilon)| > 1$ for $\varepsilon \gtrapprox 0$. A calculation shows $a_0 a_1 + b_0 b_1 = d\,(\rho_1 + \rho_2 - 2)\,/6\varDelta$ and hence $\rho_1 + \rho_2 < 2 \Longrightarrow |\lambda(\varepsilon)| < 1$ and $\rho_1 + \rho_2 > 2 \Longrightarrow |\lambda(\varepsilon)| > 1$ for $\varepsilon \gtrapprox 0$. Note that when the equilibrium is unstable it is a saddle with a one dimensional stable manifold. □

Proof of Theorem 4(b) To lowest order for $\varepsilon \gtrapprox 0$, the points on the single-class three-cycle (8) are (15). For $\varepsilon \gtrapprox 0$ we can determine the local stability of the three-cycle from the eigenvalues $\lambda_i(\varepsilon) = \lambda_i(0) + \lambda_i'(0)\varepsilon + O\left(\varepsilon^2\right)$ of the Jacobian $\varPhi(\varepsilon)$ of the composite, which is equal to the triple product

$$\varPhi(\varepsilon) = J\left(0, 0, z^*(\varepsilon)\right) J\left(0, y^*(\varepsilon), 0\right) J\left(x^*(\varepsilon), 0, 0\right). \tag{19}$$

A straightforward calculation shows $\varPhi(0) = I$ and $\lambda_i(0) = 1$. Thus $\varPhi(\varepsilon) = I + \varPhi'(0)\varepsilon + O\left(\varepsilon^2\right)$ and $\lambda_i(\varepsilon) = 1 + \lambda_i'(0)\varepsilon + O\left(\varepsilon^2\right)$. The eigenvalue equation $\varPhi(\varepsilon)\,v(\varepsilon) = \lambda(\varepsilon)\,v(\varepsilon)$, to lowest order, shows that $\lambda_i'(0)$ is an eigenvalue of $\varPhi'(0)$ which (a tedious calculation done with the aid of a computer algebra program) turns out to be a triangular matrix of the form

$$\varPhi'(0) = \begin{pmatrix} -1 & * & * \\ 0 & 1-\rho_1 & 0 \\ 0 & 0 & 1-\rho_2 \end{pmatrix}.$$

The asterisks represent unneeded terms, since the eigenvalues if $\varPhi'(0)$ appear along the diagonal. The eigenvalues of $\varPhi(\varepsilon)$ are, to first order in ε,

$$\lambda_1(\varepsilon) = 1 - \varepsilon + O\big(\varepsilon^2\big), \quad \lambda_2(\varepsilon) = 1 + (1-\rho_1)\,\varepsilon + O\big(\varepsilon^2\big),$$
$$\lambda_3(\varepsilon) = 1 + (1-\rho_2)\,\varepsilon + O\big(\varepsilon^2\big).$$

For $\varepsilon \gtrapprox 0$ it follows that $0 < \lambda_1(\varepsilon) < 1$ and the stability of the single-class three-cycle depends on $\lambda_2(\varepsilon)$ and $\lambda_3(\varepsilon)$. For $\varepsilon \gtrapprox 0$ the only case when both satisfy $0 < \lambda_i(\varepsilon) < 1$ is when both $\rho_i > 1$ (i.e., on region $\varOmega_4$). If at least one $\rho_i < 1$ (i.e., for parameters from region $\varOmega_1 \cup \varOmega_2 \cup \varOmega_3$), then the three-cycle is unstable. □

Proof of Theorem 5 See Theorems A.1 and A.2 in [23] (and relevant earlier references) for the following theorem concerning a continuous map $T : X \to X$ on a metric space X.

Theorem 7 *Suppose $S \subset X$ is a compact subset such that S and $X \backslash S$ are forward invariant under a mapping T. Then S is a repeller if there exists a continuous function $P : X \to R_+$ such that*

(a) $P(\hat{x}) = 0 \Longleftrightarrow \hat{x} \in S$
(b) *for all* $\hat{x} \in S$

$$\sup_{t \geq 1} \prod_{i=0}^{t-1} \psi\left(T^i(\hat{x})\right) > 1 \tag{20}$$

where $\psi : X \to R_+$ *is a continuous function satisfying* $P\left(T\left(\hat{x}\right)\right) \geq \psi\left(\hat{x}\right) P\left(\hat{x}\right)$. *If, on the other hand,* $P\left(T\left(\hat{x}\right)\right) \leq \psi\left(\hat{x}\right) P\left(\hat{x}\right)$ *and*

$$\inf_{t \geq 1} \prod_{i=0}^{t-1} \psi\left(T^i(\hat{x})\right) < 1 \tag{21}$$

then S *is an attractor.*

The following lemma helps to define X and S for an application of Theorem 7 to (2).

Lemma 4 *Assume* (3) *and* (4) *hold, that at least one* $\beta_{ii} \neq 0$, *and that* $R_0 > 1$ *for* (2). *There exist positive constants* k_1, k_2, δ_0 *such* $C \backslash E(\delta)$ *is forward invariant for all positive* $\delta \leq \delta_0$ *, where* $E(\delta)$ *is the ellipsoid*

$$E(\delta) \triangleq \left\{(x, y, z) \in R_+^3 : \left(\frac{x}{k_1\delta}\right)^2 + \left(\frac{y}{k_2\delta}\right)^2 + \left(\frac{z}{\delta}\right)^2 < 1\right\}.$$

Proof We need to show that $(x, y, z) \in C \backslash E(\delta)$ implies $(x', y', z') \in C \backslash E(\delta)$ where (x', y', z') is the image of (x, y, z) under (2). In spherical coordinates $x = \rho \sin\varphi \cos\theta,\ y = \rho \sin\varphi \sin\theta,\ z = \rho\cos\varphi,\ \rho \geq 0, (\theta, \varphi) \in D \triangleq \{(\theta, \varphi) : 0 \leq \theta \leq \pi/2,\ 0 \leq \varphi \leq \pi/2\}$ the goal is to pick k_1, k_2, δ so that

$$\left(\frac{\rho \sin\varphi \cos\theta}{k_1\delta}\right)^2 + \left(\frac{\rho \sin\varphi \sin\theta}{k_2\delta}\right)^2 + \left(\frac{\rho\cos\varphi}{\delta}\right)^2 \geq 1 \tag{22}$$

implies $\sigma\left(\rho, \theta, \varphi\right) \geq 1$ where

$$\sigma\left(\rho, \theta, \varphi\right) \triangleq \left(\frac{b\hat{g}_3\left(\rho, \theta, \varphi\right)\rho\cos\varphi}{k_1\delta}\right)^2 + \left(\frac{s_1\hat{g}_1\left(\rho, \theta, \varphi\right)\rho\sin\varphi\cos\theta}{k_2\delta}\right)^2 + \left(\frac{s_2\hat{g}_2\left(\rho, \theta, \varphi\right)\rho\sin\varphi\sin\theta}{\delta}\right)^2$$

and $\hat{g}_i\left(\rho, \theta, \varphi\right) \triangleq bg_i\left(w_3\left(\rho, \theta, \varphi\right)\right),\ w_i\left(\rho, \theta, \varphi\right) \triangleq \beta_{i1}\rho\sin\varphi\cos\theta + \beta_{i2}\rho\sin\varphi \sin\theta + \beta_{i3}\rho\cos\varphi$. Inequality (22) is equivalent to

$$\rho \geq \eta(\delta, \theta, \varphi) \triangleq \frac{k_1k_2\delta}{\left(\left(k_2^2\cos^2\theta + k_1^2\sin^2\theta\right)\sin^2\varphi + k_1^2k_2^2\cos^2\varphi\right)^{1/2}}. \tag{23}$$

The monotonicity assumptions (3)-(4) imply that $\sigma(\rho, \theta, \varphi)$ is non-decreasing in ρ and as a result

$$m(\delta, \theta, \varphi) \triangleq \min_{\rho \geq \eta(\delta,\theta,\varphi)} \sigma(\rho, \theta, \varphi) = \sigma(\eta(\delta, \theta, \varphi), \theta, \varphi).$$

To lowest order in δ it turns out that $m(\delta, \theta, \varphi) = m_0(\theta, \varphi) + O(\delta)$ where

$$m_0(\theta, \varphi) \triangleq \frac{b^2 k_2^2 \cos^2 \varphi + k_1^2 \left(s_1^2 \cos^2 \theta + s_2^2 k_2^2 \sin^2 \theta\right) \sin^2 \varphi}{k_1^2 k_2^2 \cos^2 \varphi + \left(k_2^2 \cos^2 \theta + k_1^2 \sin^2 \theta\right) \sin^2 \varphi}.$$

A calculation yields

$$\frac{dm_0(\theta, \varphi)}{d\varphi} = \Big[k_2^2 \left(k_1^2 s_1 - bk_2\right)\left(bk_2 + k_1^2 s_1\right) \cos^2 \theta + k_1^2 k_2^2 (k_1 k_2 s_2 - b)(b + k_1 k_2 s_2) \sin^2 \theta\Big] \sin 2\varphi.$$

This derivative is nonnegative on D provided both terms in the coefficient are positive. This occurs if k_1 and k_2 are chosen so that

$$bk_1^{-1} s_2^{-1} < k_2 < b^{-1} k_1^2 s_1. \tag{24}$$

Then $\min_{0 \leq \varphi \leq \pi/2} m_0(\theta, \varphi) = m_0(\theta, 0) = b^2 k_1^{-2}$ which in turn implies $\min_D m_0(\theta, \varphi) = b^2 k_1^{-2}$. Hence $\min_D m_0(\theta, \varphi) > 1$ provided $k_1 < b$. In summary, choose k_1 so that $\left(b^2 s_1^{-1} s_2^{-1}\right)^{1/3} < k_1 < b$ and then k_2 so that (24) holds. Then $\sigma(\rho, \theta, \varphi) \geq m(\delta, \theta, \varphi) = m_0(\theta, \varphi) + O(\delta) > 1$ for all $\delta > 0$ sufficiently small. □

For the semelparous Leslie model (2) we define the functions

$$P(\hat{x}) \triangleq xyz$$

$$\psi(\hat{x}) \triangleq \frac{P(T(\hat{x}))}{P(\hat{x})} = R_0 g_3(\beta_{31} x + \beta_{32} y + \beta_{33} z) g_1(\beta_{11} x + \beta_{12} y + \beta_{13} z) \times g_2(\beta_{21} x + \beta_{22} y + \beta_{23} z)$$

for use in Theorem 7. The map T is that defined by the semelparous Leslie model equations (2). Assume $R_0 > 1$ so that the system is permanent (Theorem 1).

Lemma 5 *Assume* (3) *and* (4). *For any orbit on* $\partial R_+^3 \backslash \hat{0}$

$$\liminf_{t \to \infty} \frac{1}{t} \sum_{i=0}^{t-1} \ln \psi\left(T^i(\hat{x})\right) \geq \ln R_0 \prod_{i=1}^{3} g_i\left(\beta_{i1} x^* + \beta_{i2} y^* + \beta_{i3} z^*\right). \tag{25}$$

Proof By Lemma 2 the ω-limit set of any orbit on the forward invariant set $\partial R^3_+ \backslash \hat{0}$ lies in the cube C^*. Therefore, for an arbitrary but fixed number $\delta > 0$ any orbit on $\partial R^3_+ \backslash \hat{0}$ satisfies $0 \leq x(t) \leq x^* + \delta, \quad 0 \leq y \leq y^* + \delta, \quad 0 \leq z \leq z^* + \delta$ for t sufficiently large. Since $g_i(u)$ is decreasing, it follows for any orbit on $\partial R^3_+ \backslash \hat{0}$ that

$$\psi\left(T^i(\hat{x})\right) = R_0 \prod_{i=1}^{3} g_i\left(\beta_{i1}x(i) + \beta_{i2}y(i) + \beta_{i3}z(i)\right)$$
$$\geq R_0 \prod_{i=1}^{3} g_i\left(\beta_{i1}\left(x^* + \delta\right) + \beta_{i2}\left(y^* + \delta\right) + \beta_{i3}\left(z^* + \delta\right)\right).$$

Since $\delta > 0$ is arbitrary (25) follows. □

From (15) and (25) we have $\ln R_0 \Pi^3_{i=1} g_i\left(\beta_{i1}x^* + \beta_{i2}y^* + \beta_{i3}z^*\right) = 1 + (2 - \rho_1 - \rho_2)\,\varepsilon + O\left(\varepsilon^2\right)$ and

$$\liminf_{t\to\infty} \frac{1}{t} \sum_{i=0}^{t-1} \ln \psi\left(T^i(\hat{x})\right) \geq \ln\left[1 + (2 - \rho_1 - \rho_2)\,\varepsilon + O\left(\varepsilon^2\right)\right]. \tag{26}$$

This inequality holds for any orbit in $\partial R^3_+ \backslash \hat{0}$ when $\varepsilon \gtrapprox 0$ (i.e., $R_0 \gtrapprox 1$).

Let $X \triangleq C \backslash E(\delta)$. By Lemma 4 this compact set is forward invariant for all positive $\delta \leq \delta_0$. The same is true of the (compact) boundary set $S \triangleq X \cap \partial R^3_+$ (since C and ∂R^3_+ are forward invariant). We choose these sets in Theorem 7.

(a) On the parameter regions Ω_3 and Ω_4 (i.e., for $\rho_1 + \rho_2 > 2$), inequality (26) implies, for $\varepsilon \gtrapprox 0$, that $\liminf_{t\to\infty} t^{-1} \Sigma^{t-1}_{i=0} \ln \psi\left(T^i(\hat{x})\right) < 0$ for any orbit on ∂R^3_+ (and hence on S). Thus, there exists a sequence $t_j \to +\infty$ such that $\Sigma^{t_j-1}_{i=0} \ln \psi\left(T^i(\hat{x})\right) < 0$ and hence $\Pi^{t_j-1}_{i=0} \psi\left(T^i(\hat{x})\right) < 1$. This implies the inequality (21) holds and Theorem 7 implies S is an attractor. Since the neighborhood N is arbitrarily small, it follows that $\partial C \backslash \hat{0}$ is an attractor.

(b) On the parameter regions Ω_1 and Ω_2 (i.e., for $\rho_1 + \rho_2 < 2$), $\varepsilon \gtrapprox 0$ implies $\liminf_{t\to\infty} t^{-1} \Sigma^{t-1}_{i=0} \ln \psi\left(T^i(\hat{x})\right) > 0$ for any orbit on ∂R^3_+ (and hence on S). Thus, for large t it follows that $\Sigma^{t-1}_{i=0} \ln \psi\left(T^i(\hat{x})\right) > 0$ and hence $\Pi^{t-1}_{i=0} \psi \left(T^i(\hat{x})\right) > 1$. This means the inequality 20) holds and Theorem 7 implies S is a repeller. Since N is an arbitrarily small neighborhood of the origin, ∂C is a repeller.

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