

On the Fundamental Bifurcation Theorem for Semelparous Leslie Models

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Abstract This brief survey of nonlinear Leslie models focuses on the fundamental bifurcation that occurs when the extinction equilibrium destabilizes as R_0 increases through 1. Of particular interest is the bifurcation that occurs when only the oldest age class is reproductive, in which case the Leslie projection matrix is not primitive. This case is distinguished by the invariance of the boundary of the positive cone on which orbits contain temporally synchronized, missing age classes and by the bifurcation of oscillatory attractors, lying on the boundary of the positive cone, in addition to the bifurcation of positive equilibria. The lack of primitivity of the Leslie projection matrix, while seemingly only a mathematical technicality, corresponds to a fundamental life history strategy in population dynamics, namely, semelparity (when individuals have one reproductive event before dying). The study of semelparous Leslie models was historically motivated by the synchronized outbreak cycles of periodical insects, the most famous being the long-lived cicadas (*C. magicada* spp).

1 Introduction

Many mathematical models used to describe the dynamics of biological populations aggregate all individuals into a single state variable, such as population numbers, densities, biomass, etc. Structured population dynamics allows for differences among individuals by means of some designated characteristics. As models for the dynamics of structured populations, matrix models describe discrete time dynamical systems which advance a distribution vector $x = \text{col}(x_i)$ of numbers (or densities) x_i of individuals, assigned to a finite collection of (say m) specified classes, forward in time by a multiplication by a projection matrix P [4]. Typically the classification scheme is based on characteristics such as chronological age, a physiological trait (size, weight, etc.), life history stages (juvenile, adult, quiescent, etc.), the state of health (disease susceptible, infected, etc.), spatial location, and so on. Historically

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the first influential use of matrix models can be found in the seminal work of P.H. Leslie who studied populations structured by age [47, 48].

The projection matrix P has nonnegative entries that describe transition probabilities of individuals between classes and their mortality and fecundity rates. If these vital rates remain constant in time, then the resulting dynamic system is linear. Assuming no other processes (such as immigration or emigration, harvesting or seeding, etc.), the sequence of population densities is $x(t) = P^t x(0)$, $x(0) \geq 0$, and the study of this sequence is a beautiful application of Perron-Frobenius theory. This classic theory is applicable to the nonnegative matrix P when it is irreducible, an assumption generally made in applications to population dynamics. This amounts to requiring that there is a path that, in time, connects any two classes (through transitions or births). The vector $x(0) = 0$ remains fixed in time, a fixed point we refer to as the *extinction equilibrium*. Extinction is obviously of fundamental importance in population dynamics; thus the stability of the extinction equilibrium is of basic importance in mathematical models. If the dominant eigenvalue r (the spectral radius) of P is less than 1, then the extinction equilibrium is globally attracting. If $r > 1$ then the extinction equilibrium unstable (and repeller for $x(0) \geq 0$) and $x(t)$ grows exponentially without bound. If $r = 1$, there exist bounded non-extinction states, including equilibria given by constant multiples of the positive Perron eigenvector $v > 0$ of P associated with $r = 1$ (and, if P is not primitive, there can be other bounded dynamics such as periodic cycles [1, 36]). Thus, the destabilization of the extinction state at $r = 1$ results in a bifurcation phenomenon which creates bounded non-extinction states, but in this linear case only non-generically at exactly $r = 1$. We say this bifurcation is vertical and the spectrum associated with non-extinction states is a point spectrum.

Density-dependence is a term used in population dynamics to describe the situation when vital rates of a population depend on population density. For a matrix model this means $P = P(x)$ and the resulting discrete time dynamical system becomes nonlinear. That the extinction equilibrium $x = 0$ loses stability as r increases through 1, where now r is the dominant eigenvalue of the inherent (density free) projection matrix $P(0)$, is a consequence of the linearization principle for maps [34]. The nature of the bifurcation that results, at least in a neighborhood of the bifurcation point $(r, x) = (1, 0)$, is well-known provided $P(x)$ is primitive. By primitive is meant that $P(x)$ is nonnegative, irreducible and has a *strictly* dominant eigenvalue $r(x)$ (equivalently that some integer power $P^n(x)$ is positive). In this case, a continuum of positive equilibria bifurcates from $x = 0$ as r is increased through 1 whose stability depends on the direction of bifurcation (at least in a neighborhood of the bifurcation point): they are (locally asymptotically) stable if the bifurcation is forward (i.e. they correspond to $r > 1$) and unstable if it is backward (they correspond to $r < 1$) [8, 11]. Thus, for nonlinear models the bifurcation is not vertical and the spectrum is a continuum, unlike linear matrix models. This fundamental bifurcation result is described in more detail for nonlinear Leslie age-structured matrix models in Sect. 3.

The primitivity assumption, i.e. that the dominant eigenvalue r be a strictly dominant eigenvalue of $P(0)$, might seem a minor technicality in a rigorously stated mathematical theorem. Indeed, strict dominance is not needed for the nonlinear bifurcation results described in the previous paragraph but for one crucial exception, namely, that the direction of bifurcation determines the stability of the bifurcation. This is no longer true (in general) if $P(0)$ is imprimitive. The mathematical reason is that destabilization of the extinction equilibrium occurs not solely because the real, dominant eigenvalue r leaves the unit circle in the complex plane, but because other eigenvalues simultaneously leave the unit circle. This occurrence also leads to other possible bifurcation phenomenon from $x = 0$ at $r = 1$.

These mathematical details are not insignificant with regard to applications to structured population dynamics. The semelparous Leslie model discussed in Sect. 3 is, as we will see, an example possessing an imprimitive projection matrix. A population is semelparous if individuals have only one reproductive event before death. This life history strategy is used by numerous species across many taxa, including species of insects, arachnids, molluscs, and a few species of reptiles, amphibians, and marsupials, and many species plants (for which the strategy is also known as monocarpy). Perhaps the most famous examples are certain species of cicadas and salmon and, of course, annual plants. The opposite life history strategy of multiple reproductive events before death is called iteroparity. Semelparity and iteroparity, along with traits such as the timing of reproduction, resource allocation trade-offs, and number or size of offspring, play central roles in studies of life history strategies (see for example [60, 63]). A study of matrix models with imprimitive projection matrices is, therefore, of more than just mathematical interest.

Historically, the hallmark example of a matrix model with imprimitive projection matrix is the semelparous Leslie (age structured) model. This interest was particularly stimulated by studies of cicada population dynamics that utilized Leslie matrices [2, 3] and whose periodic, synchronized outbreaks have long fascinated biologists. In Sect. 3 we survey some recent results for this model with regard to the fundamental bifurcation that occurs when the extinction equilibrium is destabilized as r increases through 1. As we will see, certain basic features of the bifurcation are known in general, but a full understanding of the bifurcation has not yet been obtained except in lower dimensions $m = 2$ and 3. The complexity of the dynamic possibilities rapidly increases with the dimension m and a full accounting of the possibilities might be attainable only for specialized models. (The same conclusion, using methods other than those described in this paper, was reached in [30].) The dimension m can be thought of as the maturation time for individuals in the population, which for the long lived periodic cicada *Cicadidae Magicicada* (which in fact is the longest lived insect known) is 13 or 17 years ($m = 13$ or 17 in the Leslie model). This provides one stimulus for further study of higher dimensional semelparous Leslie models.

2 Preliminaries

Denote m -dimensional Euclidean space by R^m and its positive cone by

$$R_+^m \triangleq \{x = \text{col}(x_i) \in R^m \mid x_i > 0\}.$$

The closure and boundary of R_+^m are denoted by \bar{R}_+^m and $\partial R_+^m = \bar{R}_+^m \setminus R_+^m$ respectively. We consider discrete time dynamical systems defined by matrix multiplication

$$\begin{aligned} x(0) &= x_0 \in R_+^m \\ x(t+1) &= Px(t) \text{ for } t = 1, 2, \dots \end{aligned}$$

where the $m \times m$ matrix is called the projection P matrix. In population dynamic models, P generally has an additive decomposition

$$P = F + T$$

where F and T are the fertility and transition matrices respectively. Specifically

$$F = (f_{ij}), \quad T = (s_{ij})$$

$$f_{ij} \geq 0, \quad 0 \leq s_{ij} \leq 1, \quad \sum_{i=1}^m s_{ij} \leq 1 \text{ for } i, j = 1, 2, \dots, m$$

where f_{ij} is the per unit number of i -class offspring produced by a j -class individual during a time unit that survive to the end of the time unit.

An example is the (extended) Leslie matrix model based on age classes when the census time interval for t is equal to the length of the age classes. We denote the projection matrix for a Leslie model by $L = F + T$ where

$$F = \begin{pmatrix} 0 & 0 & \cdots & 0 & s_m \\ 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & 0 & 0 \end{pmatrix}, \quad T = \begin{pmatrix} 0 & 0 & \cdots & 0 & 0 \\ s_1 & 0 & \cdots & 0 & 0 \\ 0 & s_2 & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & s_{m-1} & s_a \end{pmatrix}$$

$$0 < s_i \leq 1 \text{ for } i = 1, 2, \dots, m-1 \tag{1}$$

$$s_m > 0, \quad 0 \leq s_a < 1.$$

Here the $i = 1, 2, \dots, m-1$ classes consist of juveniles (non-reproducing) individuals and the adult class x_m is not structured. The number s_a is the fraction of

adults who survive a time unit (and hence reproduce again). Assuming population counts are made at the end of each time step, the quantity s_m is the number of newborns produced per adult during a time unit that survive to the census time. In this way s_m contains both adult reproduction and newborn survivorship characteristics.

The famous Perron-Frobenius Theorem applies to the (nonnegative and irreducible) Leslie projection matrix L . Therefore, its spectral radius $r = \rho[L]$ is positive and is a simple eigenvalue of L with positive eigenvector

$$v(r) = \begin{pmatrix} p_1 \\ \vdots \\ \frac{p_i}{r^{i-1}} \\ \vdots \\ \frac{p_{m-1}}{r^{m-2}} \\ \frac{r}{s_m} \end{pmatrix} \tag{2}$$

where

$$p_i = \prod_{n=1}^{i-1} s_n \text{ for } i = 2, 3, \dots, m$$

is the probability of living to age i . For later notational convenience we define $p_1 = 1$. The dominant eigenvalue r satisfies the characteristic equation.

$$r^m - s_a r^{m-1} - p_m s_m = 0.$$

Moreover, no other eigenvalue has larger absolute value nor has a nonnegative right or left eigenvector.

If the population is iteroparous, i.e. $s_a > 0$, then the Leslie matrix L is primitive. That is to say r strictly dominates all other eigenvalues. A bifurcation of equilibria (fixed points) occurs at $r = 1$. The equilibrium $x(t) \equiv 0$ is a global attractor if $r < 1$ and is a repeller if $r > 1$. At $r = 1$ there is a continuum (of global extent) of positive equilibria, namely the positive scalar multiples of $v = v(1)$. This is a vertical transcritical bifurcation whose spectrum is a single point $r = 1$. At $r = 1$ all orbits with $x_0 \in \mathbb{R}_+^m \setminus \{0\}$ approach a multiple of v as $t \rightarrow +\infty$ and in this sense the bifurcating branch of positive equilibria is stable.

In these assertions we can replace r by the quantity

$$R_0 = s_m \frac{p_m}{1 - s_a}. \tag{3}$$

This follows from a basic theorem in [23] that guarantees r and R_0 (in general matrix models) equal 1 simultaneously or always lie on the same side of 1. Also see [8, 11, 15, 51]. This allows for a stability determination by a simple calculation from the

entries of L (no algebraic formula exists for r , in general). Biologically R_0 is the expected number of newborns per newborn over the course of its lifetime and is called the *net reproductive number* (or rate).

If the population is semelparous, i.e. $s_a = 0$, the Leslie matrix L is imprimitive. This is because r is no longer *strictly* dominant. Indeed, the eigenvalues of L are $\lambda = ru_k$ where

$$u_k \doteq \exp\left(\frac{2\pi(k-1)}{m}i\right), \quad k = 1, 2, \dots, m$$

are the m th roots of unity. In this case,

$$r = R_0^{1/m}, \quad R_0 = \prod_{i=1}^m s_i. \quad (4)$$

The vertical bifurcation of positive equilibria still occurs at $r = 1$, as in the primitive case, but it is no longer stable in the sense that all orbits with $x_0 \in R_+^m \setminus \{0\}$ approach a multiple of v as $t \rightarrow +\infty$. At $r = 1$ there also exists a continuum of periodic cycles. These cycles have a special form. Because $L^m = \text{diag}(R_0)$ and hence $L^m = I$ when $r = 1$ all points $x_0 \in R_+^m$ produce an m -cycle, i.e., a periodic orbit of period m (although m might not be the minimal period). This includes so called synchronous cycles, which are periodic orbits lying on the boundary ∂R_+^m of the positive cone. The boundary ∂R_+^m is straightforwardly seen to be forward invariant since a zero component in x_0 advances one entry (modulo m) at each time step. Similarly, positive components advance one entry at each step. These cycles have the same number of missing age classes (and positive age classes) at each point and they sequentially move between the coordinate hyperplanes. At the extreme are single class m -cycles in which only one entry is positive at each point of the cycle. In the case of semelparity we see, then, that continua of such so-called *synchronous m -cycles* also exist when $r = 1$. These synchronous cycles for the linear case can be the source of synchronous oscillations in nonlinear matrix models, to which we next turn our attention.

3 Nonlinear Leslie Matrix Models

The linear Leslie model predicts either extinction when $r < 1$ or unbounded (exponentially) unbounded growth when $r > 1$. Bounded population persistence can only occur at $r = 1$, the point spectrum of the bifurcating branch of equilibria and/or periodic cycles. The ecological notion of density dependence, i.e. the dependence of the components in F and T on population density, allows for population self regulation and bounded persistence on a spectrum of r values of positive measure (for example, all $r > 1$). This assumption results in a nonlinear matrix model of the

form

$$\begin{aligned}
 x(0) &= x_0 \in R_+^m \\
 x(t+1) &= L(x)x(t) \text{ for } t = 1, 2, \dots
 \end{aligned}
 \tag{5}$$

in which the age-specific entries in the fertility and transition matrices may depend on population density

$$L(x) = F(x) + T(x).$$

$$F(x) = \begin{pmatrix} 0 & 0 & \dots & 0 & s_m \sigma_m(x) \\ 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \dots & 0 & 0 \end{pmatrix}$$

$$T(x) = \begin{pmatrix} 0 & 0 & \dots & 0 & 0 \\ s_1 \sigma_1(x) & 0 & \dots & 0 & 0 \\ 0 & s_2 \sigma_2(x) & \dots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \dots & s_{m-1} \sigma_{m-1}(x) & s_a \sigma_a(x) \end{pmatrix}$$

where the fertility and survivorship parameters s_i (satisfying (1)) have been modified by density dependent, multiplicative factors $\sigma_i(x)$ normalized so that

$$\sigma_i(0) = 1 \text{ for all } i = 1, 2, \dots, m \text{ and } i = a. \tag{6}$$

In this way, the s_i are the *inherent* fertility and survivorship rates, by which we mean the rates in the absence of density effects. We refer to r and R_0 given by (3) and (4) as the *inherent population growth rate* and the *inherent net reproductive number* respectively. We must supply the multiplicative factors σ_i with some mathematical properties, which we do by assuming the following.

- A1: $\sigma_i \in C^2(D, \bar{R}_+^m)$ where D is an open set in R^m containing \bar{R}_+^m .
- In addition to the normalizations (6) we require, for $x \in \bar{R}_+^m$, that $s_m \sigma_m(x) > 0$ and $0 < s_i \sigma_i(x) \leq 1$ for $i = 1, 2, \dots, m - 1$ and $i = a$.

We denote partial derivatives by

$$\partial_j \sigma_i(x) \doteq \frac{\partial \sigma_i(x)}{\partial x_j}$$

and introduce the notation

$$\partial_j^0 \sigma_i \doteq \left. \frac{\partial \sigma_i(x)}{\partial x_j} \right|_{x=0}.$$

We denote the (row vector) gradient of σ_i with respect to x evaluated at $x = 0$ by

$$\nabla^0 \sigma_i \doteq \left(\partial_1^0 \sigma_i \cdots \partial_j^0 \sigma_i \cdots \partial_m^0 \sigma_i \right).$$

A negative derivative $\partial_j \sigma_m(x) < 0$ represents a *negative feedback* on fertility with respect to an increase in the density of the j^{th} age class when the population age distribution is x . A positive derivative represents a *positive feedback* (a so-called *component Allee effect*). Similarly for other survivorship factors $\sigma_i(x)$.

Functions commonly used by modelers for negative feedback factors include the rational function

$$\frac{1}{1 + \sum_{i=1}^m c_i x_i} \tag{7}$$

often referred to as a Leslie-Gower [49] (or Beverton-Holt or discrete Lotka-Volterra nonlinearity) and exponential function

$$\exp \left(-\sum_{i=1}^m c_i x_i \right) \tag{8}$$

(often called the Ricker model [57]). Functions that have been used for positive feedback include [7]

$$x_j \frac{1}{1 + \sum_{i=1}^m c_i x_i} \text{ or } x_j \exp \left(-\sum_{i=1}^m c_i x_i \right).$$

A basic biological question concerns the extinction or persistence of a population, which mathematically concerns the stability properties of the extinction equilibrium $x = 0$. The Jacobian of (5) at $x = 0$ is $L(0)$, which is the linear Leslie matrix in Sect. 1 with dominant eigenvalue r . The Linearization Principle [34] implies $x = 0$ is stable or unstable if $r < 1$ or $r > 1$ respectively, or mathematically more conveniently if $R_0 < 1$ or $R_0 > 1$.

Theorem 1 *Assume A1. If $R_0 < 1$ (equivalently $r < 1$) then the extinction equilibrium $x = 0$ is (locally asymptotically) stable. If $R_0 > 1$ (equivalently $r > 1$) then the extinction equilibrium is unstable.*

Theorems from persistence theory add to the dynamics near $x = 0$ when $r > 1$. Define

$$|x| \doteq \sum_{i=1}^m |x_i|.$$

The nonlinear Leslie model (5) is *uniformly persistent* with respect to $x = 0$ if there exists a $\delta > 0$ such that $\liminf_{t \rightarrow +\infty} |x(t)| > \delta$ for all $x(0) \in R_+^m \setminus \{0\}$. It is *dissipative* on \bar{R}_+^m if there is a compact subset of \bar{R}_+^m into which all orbits in \bar{R}_+^m enter and remain after a finite number of time steps. If (5) is both uniformly persistent with respect to $x = 0$ and dissipative, then it is called *permanent* on \bar{R}_+^m . That is to say, there exist constants $\delta_1, \delta_2 > 0$ such that

$$\delta_1 < \liminf_{t \rightarrow +\infty} |x(t)| \leq \limsup_{t \rightarrow +\infty} |x(t)| < \delta_2$$

for all $x(0) \in R_+^m \setminus \{0\}$. The following theorem is proved in [46] (also see Theorem 1.2.1 in [8] and, for the semelparous case $s_a = 0$, Proposition 3.3 in [45]).

Theorem 2 *Assume A1. If the nonlinear Leslie model (5) is dissipative on \bar{R}_+^m , then for $R_0 > 1$ it is permanent with respect to the extinction equilibrium $x = 0$ on \bar{R}_+^m .*

Under the conditions of this theorem not only is $x = 0$ unstable when $R_0 > 1$ (equivalently $r > 1$), but no orbit in $R_+^m \setminus \{0\}$ leads to extinction.

A sufficient condition for dissipativity is that there exists a number $k_0 > 0$ such that

$$\sigma_m(x)x_m, \sigma_a(x)x_m \leq k_0 \text{ for } x \in R_+^m. \tag{9}$$

These inequalities mean that the adult class self-regulates its vital rates. To see this we note, from the first component of the Leslie model (5), that

$$0 \leq x_1(t + 1) = b\sigma_m(x(t))x_m(t) \leq bk_0$$

for all $t \geq 0$ from which follow the inequalities

$$0 \leq x_i(t + 1) = s_{i-1}\sigma_{i-1}(x(t))x_{i-1}(t) \leq bk_0$$

for all $t \geq i - 1$ and $i = 1, 2, \dots, m - 1$. Finally

$$0 \leq x_m(t + 1) = s_{m-1}\sigma_{m-1}(x(t))x_{i-1}(t) + s_a\sigma_a(x(t))x_m(t) \leq bk_0 + s_ak_0$$

for all $t \geq m - 1$. Thus, all orbits in \bar{R}_+^m lie and remain in the rectangular region

$$B \doteq \{x \in \bar{R}_+^m \mid 0 \leq x_i \leq bk_0 \text{ for } i = 1, 2, \dots, m - 1 \text{ and } 0 \leq x_m \leq bk_0 + s_ak_0\}$$

after $m - 1$ time steps.

From the destabilization of the equilibrium $x \equiv 0$, as caused by an eigenvalue of the Jacobian increasing through 1 as R_0 (and hence r) increases through 1, we expect that a branch of non-zero equilibria will (transcritically) bifurcate from $x \equiv 0$ at $R_0 = 1$. That is to say, we expect there will exist a continuum of pairs (R_0, x) for which x is a nonzero equilibrium of (5) whose closure contains the bifurcation point

(1, 0). Theorems from bifurcation theory can be applied to validate this assertion. One way to do this is to write the equilibrium equation of (5), namely, the algebraic equation

$$x = L(x)x \tag{10}$$

as

$$(I - T(x))x = R_0\Phi(x)x \tag{11}$$

where

$$\Phi(x) = \begin{pmatrix} 0 & 0 & \cdots & 0 & \frac{1-s_a}{p_m} \sigma_m(x) \\ 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & 0 & 0 \end{pmatrix}.$$

Note that $s_a\sigma_a(x) < 1$ implies $I - T(x)$ has a nonnegative inverse

$$\begin{pmatrix} 1 & 0 & \cdots & 0 & 0 & 0 \\ s_1\sigma_1(x) & 1 & \cdots & 0 & 0 & 0 \\ s_1\sigma_1(x) & s_2\sigma_2(x) & \cdots & 0 & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots & \vdots \\ \prod_{j=1}^{m-2} s_j\sigma_j(x) & \prod_{j=2}^{m-2} s_j\sigma_j(x) & \cdots & s_{m-2}\sigma_{m-2}(x) & 1 & 0 \\ \frac{\prod_{j=1}^{m-1} s_j\sigma_j(x)}{1-s_a\sigma_a(x)} & \frac{\prod_{j=2}^{m-1} s_j\sigma_j(x)}{1-s_a\sigma_a(x)} & \cdots & \frac{\prod_{j=m-2}^{m-1} s_j\sigma_j(x)}{1-s_a\sigma_a(x)} & \frac{s_{m-1}\sigma_{m-1}(x)}{1-s_a\sigma_a(x)} & \frac{1}{1-s_a\sigma_a(x)} \end{pmatrix}.$$

We write the equilibrium equation (11) equivalently as

$$x = R_0M(x)x$$

where

$$\begin{aligned} M(x) &\stackrel{\circ}{=} (I - T(x))^{-1} \Phi(x) \\ &= \begin{pmatrix} 0 & 0 & \cdots & 0 & \frac{1-s_a}{p_m} \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & 0 & p_j \frac{1-s_a}{p_m} \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & 0 & 1 \end{pmatrix} \end{aligned}$$

which has the abstract form

$$x = R_0 M(0) x + R_0 h(x) \tag{12}$$

where

$$|R_0 h(x)| = O(|x|^2) \text{ near } x = 0$$

uniformly in R_0 on compact intervals.

Corresponding to a (nonzero, positive or negative) solution of Eq. (12) we refer to a (nonzero, positive or negative) equilibrium pair (R_0, x) . Equation (12) has the form of the nonlinear eigenvalue problem whose bifurcation properties are studied in [56] (also see [40]). A characteristic value of a matrix is the reciprocal of an eigenvalue. Note that $M(0)$ has one characteristic value, namely, 1 and that it is geometrically simple. Using Theorem 1.20 in [56] (see the Appendix) we find that there exists a continuum \mathcal{C}_+^e of positive equilibrium pairs (R_0, x) that contains $(1, 0)$ and is unbounded in $R_+^1 \times R_+^m$. (See the Appendix for further details.) It follows that either the spectrum of \mathcal{C}_+^e

$$\mathcal{S} \stackrel{\circ}{=} \{R_0 | (R_0, x) \in \mathcal{C}_+^e\} \subset R_+$$

is unbounded in R_+ or the range of \mathcal{C}_+^e

$$\mathcal{R} \stackrel{\circ}{=} \{x | (R_0, x) \in \mathcal{C}_+^e\} \subset R_+^m$$

of \mathcal{C}_+^e is unbounded in R_+^m or both. Both are continua.

Perturbation methods in classic bifurcation theory (e.g. Lyapunov-Schmidt techniques) allow for a parameterization of the bifurcating continuum \mathcal{C} of positive equilibria near the bifurcation point $(R_0, x) = (1, 0)$. The result is contained in the following theorem (see [8] for details). Let $v = v(1)$, i.e.

$$v = \begin{pmatrix} p_1 \\ \vdots \\ p_i \\ \vdots \\ p_{m-1} \\ \frac{1}{s_m} \end{pmatrix}$$

[see (2)].

Theorem 3 Assume A1 and $a_1 \neq 0$ where

$$a_1 \stackrel{\circ}{=} \sum_{i=1}^m \nabla^0 \sigma_i v + \frac{s_m}{1 - s_a} \nabla^0 \sigma_a v. \tag{13}$$

The nonlinear Leslie model (5) has a continuum \mathcal{C}_+^e of positive equilibrium pairs which bifurcates from $(R_0, x) = (1, 0)$, is unbounded in $R_+ \times R_+^m$ and, near the bifurcation point $(R_0, x) = (1, 0)$, has the parameterization

$$x = -\frac{1}{a_1}v\varepsilon + \eta\varepsilon^2 + O(\varepsilon^3), \quad R_0 = 1 + \varepsilon \tag{14}$$

for $\varepsilon \gtrsim 0$ if $a_1 < 0$ and $\varepsilon \lesssim 0$ if $a_1 > 0$.

Definition 1 The bifurcation of the continuum \mathcal{C}_+^e is forward (to the right or super-critical) if $(R_0, x) \in \mathcal{C}_+^e$ implies $R_0 > 1$ in a neighborhood of the bifurcation point $(1, 0)$. The bifurcation of the continuum \mathcal{C}_+^e is backward (to the left or sub-critical) if $(R_0, x) \in \mathcal{C}_+^e$ implies $R_0 < 1$ in a neighborhood of the bifurcation point $(1, 0)$.

Note that the *direction of bifurcation* of \mathcal{C}_+^e is determined by the sign of the quantity a_1 (if it is nonzero). If $a_1 < 0$ (which is certainly the case if there are no positive feedback components at $x = 0$) then \mathcal{C}_+^e bifurcates forward. On the other hand, if $a_1 > 0$ then the bifurcation is backward. An inspection of the formula for a_1 shows that the latter case requires positive feedback density effects at low population densities (i.e. component Allee effects [7]) and these must be of sufficient magnitude if negative feedback components are also present.

The set of R_0 values for which the nonlinear Leslie model (5) has a positive equilibrium is of obvious interest applications. This set includes the spectrum \mathcal{S} of the bifurcating continuum \mathcal{C}_+^e . \mathcal{S} is a continuum, i.e. is an interval in R_+ , whose closure contains 1. In an exceptional case, \mathcal{S} could be the singleton set $\{1\}$ as it is in the linear case. However, more generally \mathcal{S} is an interval of real numbers of positive measure. This is certainly the case if $a_1 \neq 0$ since, in that case, the bifurcation at $(1, 0)$ is not vertical by Theorem 3.

When can we expect there to exist a positive equilibrium for *all* values of $R_0 > 1$?

Corollary 1 ([17]) Assume A1. If there exists a function $k : R_+ \rightarrow R_+$, bounded on bounded sets in R_+ , such that

$$|x| \leq k(R_0) \text{ for all } (R_0, x) \in \mathcal{C}_+^e, \tag{15}$$

then the spectrum $\mathcal{S} \subset R_+$ of \mathcal{C}_+^e is unbounded and there exists (at least one) positive equilibrium for each $R_0 > 1$.

This corollary follows because (15) implies that a bounded spectrum \mathcal{S} would imply a bounded range \mathcal{R} , in contradiction to \mathcal{C}_+^e being unbounded.

As an example, suppose the inequalities (9) hold. We showed above that all orbits eventually lie and remain in the compact region B . It follows that any equilibrium must lie in this region and therefore (15) holds with

$$k(R_0) \doteq m \frac{R_0}{\prod_{j=1}^{m-1} s_j} k_0 + s_a k_0.$$

Note: A pair $(R_0, x) \in \mathcal{C}_+^e$ corresponds to a positive equilibrium $x \in R_+^m$ of the nonlinear Leslie model for parameters s_i that yield the corresponding R_0 value. The inherent projection matrix $L(0)$ of that model has a dominant eigenvalue r and we can, therefore, associate with each pair in \mathcal{C}_+^e a positive equilibrium pair (r, x) . If the R_0 spectrum \mathcal{S} of \mathcal{C}_+^e is unbounded, it follows from a theorem of Li and Schneider [51] that the spectrum of r values obtained from the corresponding equilibrium pairs (r, x) is also unbounded. ■

When might there be positive equilibria for $R_0 < 1$? This will certainly be the case when $a_1 > 0$ and the continuum \mathcal{C}_+^e bifurcates backward at $(1, 0)$. As we observe from the formula (13) for a_1 , this requires the presence of component Allee effects of sufficient magnitude. If $a_1 < 0$ then there are no positive equilibria for $R_0 < 1$ in a neighborhood of the bifurcation point $(1, 0)$, but this does preclude the possibility of equilibrium pairs (R_0, x) from the continuum \mathcal{C}_+^e outside a neighborhood of $(1, 0)$ for which $R_0 < 1$. One case in which this can be ruled out altogether is when

$$\sigma_i(x), \sigma_a(x) \leq 1 \text{ for } x \in \bar{R}_+^m \tag{16}$$

(which disallows any component Allee effects near $x = 0$). In this case we obtain from equilibrium equation (10) the inequality

$$0 \leq x = L(x) \leq L(0)x.$$

If $R_0 < 1$ then $r < 1$ [23] and all orbits of

$$\begin{aligned} y_0 &= x_0 \in R_+^m \\ y(t+1) &= L(0)y(t) \end{aligned}$$

satisfy $\lim_{t \rightarrow +\infty} y(t) = 0$. By a straightforward comparison argument, the orbits of the nonlinear Leslie model (5) satisfy $0 \leq x(t) \leq y(t)$ and hence also tend to the origin.

Corollary 2 *Assume A1 and (16). Then $R_0 < 1$ (equivalently $r < 1$) implies that the extinction equilibrium $x = 0$ is globally asymptotically stable.*

Combining these results we have the following result.

Corollary 3 *Assume A1, the adult self regulation assumption (9), and that the inequalities (16) hold. Then for the nonlinear Leslie model (5) we have that:*

- *the extinction equilibrium $x = 0$ is globally asymptotically stable for $R_0 < 1$;*
- *the model is permanent with respect to $x = 0$ for $R_0 > 1$;*
- *there exists at least one positive equilibrium for all values of $R_0 > 1$.*

Example sub-models for the vital rates $\sigma_i(x)$ and $\sigma_a(x)$ that satisfy (16) are the Leslie-Gower (7) and the Ricker (8) functions. The adult self regulation

inequalities (9) are satisfied if $c_m > 0$, and hence all the conclusions in Corollary 3 hold for models built using any combinations of these familiar nonlinearities.

We have not yet taken up the question of the stability or instability of the equilibria from the bifurcating continuum \mathcal{C}_+^e . In general such equilibria can be either stable or unstable, depending on the specifics of the nonlinearities used in the model. Some general conclusions can be made, however, in the neighborhood of the bifurcation point $(R_0, x) = (1, 0)$. Tractability of this question is obtained from the parameterization (14) of \mathcal{C}_+^e near $(1, 0)$. This parameterization allows for a parameterization of the Jacobian of (5) evaluated at the positive equilibrium and, in turn, a parameterization of the eigenvalues $\lambda = \lambda(\varepsilon)$ of the Jacobian.

If the population is iteroparous, i.e. if $s_a > 0$, then the Jacobian at the bifurcation point has a strictly dominant eigenvalue of 1. Thus, $\lambda_1(0) = 1$ and all other eigenvalues lie inside the unit circle. This means, in this case, that these eigenvalues will remain inside the complex unit circle for ε small (by continuity) and the stability of the bifurcating positive equilibria can be determined by the eigenvalue $\lambda_1(\varepsilon) = 1 + \lambda'_1(0)\varepsilon + O(\varepsilon^2)$ alone. A calculation of $\lambda'_1(0)$ can be made by perturbation or calculus methods and the result is (see Lemma 1.2.2 in [8] or, in a more general abstract setting, see the exchange of stability principle for transcritical bifurcations in [40])

$$\lambda_1(\varepsilon) = 1 - ca_1\varepsilon + O(\varepsilon^2)$$

for a positive constant $c > 0$. This leads to the following stability result for the equilibrium on the bifurcating continuum \mathcal{C}_+^e in a neighborhood of the bifurcation point.

Definition 2 The bifurcation of \mathcal{C}_+^e at $R_0 = 1$ is called stable (unstable) if, in a neighborhood of $(R_0, x) = (1, 0)$, the positive equilibria from the range of the continuum \mathcal{C}_+^e are locally asymptotically stable (unstable).

Theorem 4 Assume A1 and $s_a > 0$. If $a_1 < 0$ then the bifurcation of the continuum \mathcal{C}_+^e of positive equilibrium pairs of the nonlinear, iteroparous Leslie model (5) at $(R_0, x) = (1, 0)$ is forward and stable. If $a_1 > 0$ it is backward and unstable.

Taken together Theorems 3 and 4 constitute a fundamental bifurcation theorem for the iteroparous nonlinear Leslie model (5) that guarantees the occurrence of a transcritical bifurcation of positive equilibria at the destabilization of the extinction equilibrium when R_0 increases through 1 and the fact that the stability or instability of the bifurcation depends on the direction of bifurcation.

Example 1 The $m = 3$ stage nonlinear Leslie model with projection matrix

$$L(x) = \begin{pmatrix} 0 & 0 & be^{-c_1x_1(t)-c_3x_3(t)} \\ 1 - \mu_l & 0 & 0 \\ 0 & (1 - \mu_p)e^{-c_2x_3(t)} & 1 - \mu_a \end{pmatrix} \tag{17}$$

$$b > 0, 0 < \mu_l, \mu_p, \mu_a < 1 \text{ and } c_i > 0.$$

(known as the LPA model) was extensively used over a period of several decades in numerous experimental studies of nonlinear dynamics involving the insect *Tribolium castaneum* (aka flour beetles). See [24] and [6]. The three stages represent larval, pupal and adult stages in this insect and the unit of time is 2 weeks. This matrix model has the form (5) with parameters

$$s_3 = b, s_1 = 1 - \mu_l, s_2 = 1 - \mu_p, s_a = 1 - \mu_a$$

$$R_0 = b \frac{(1 - \mu_l)(1 - \mu_p)}{\mu_a}$$

and Ricker-type nonlinearities (8):

$$\sigma_1(x) \equiv 1, \quad \sigma_2(x) = e^{-c_2 x_3(t)}, \quad \sigma_3(x) = e^{-c_1 x_1(t) - c_3 x_3(t)}, \quad \sigma_a(x) \equiv 1$$

for which assumption A1 holds with $D = R^3$. There are no positive feedbacks and, indeed, the inequalities (16) hold. The population is iteroparous ($s_a > 0$). From these observations we conclude from Theorem 3, Corollary 2 and Theorem 4 that the extinction equilibrium is globally asymptotically stable for $R_0 < 1$, that the population permanent when $R_0 > 1$, and the bifurcation of positive equilibria at $R_0 = 1$ is forward and stable.

Although the inequalities (9) do not both hold ($\sigma_3(x) x_3$ is bounded for $x \in R^3_+$, but $s_a \sigma_a(x) x_3$ is not), an observation of the components of the equilibrium equations yields, for $x \in R^3_+$, the inequalities

$$0 \leq x_1 \leq b \frac{1}{c_1 e}$$

$$0 \leq x_2 \leq (1 - \mu_l) b \frac{1}{c_1 e}$$

$$0 \leq x_3 \leq (1 - \mu_p)(1 - \mu_l) b \frac{1}{c_1 e} + (1 - \mu_a) x_3$$

the latter of which implies

$$0 \leq x_3 \leq \frac{(1 - \mu_p)(1 - \mu_l)}{\mu_a} b \frac{1}{c_1 e}.$$

A summation shows that (15) holds with

$$k(R_0) = \frac{\mu_a + \mu_a(1 - \mu_l) + (1 - \mu_l)(1 - \mu_p)}{(1 - \mu_l)(1 - \mu_p)c_1 e} R_0.$$

It follows from Corollary 1 that there exists at least one positive equilibrium for all values of $R_0 > 1$.

The stability properties of the bifurcating positive equilibria, in a neighborhood of the bifurcation point, given in Theorem 4 might or might not persist globally

along the continuum \mathcal{C}_+^e . As is well known for nonlinear maps further bifurcations (numerous types), and even routes-to-chaos, can occur as R_0 is increased. This can indeed happen for the LPA model in Example 1, which formed the basis of the nonlinear studies described in [6, 24].

Strong Allee effects have been of increasing interest in theoretical ecology during the last couple of decades [7]. This is a dynamic scenario in which there exist multiple (nonnegative) attractors one of which is the extinction equilibrium, a scenario which in matrix models can only occur if $R_0 \leq 1$. One common way that a strong Allee effect arises in models is when a backward bifurcation occurs at $R_0 = 1$ and the spectrum \mathcal{S} of \mathcal{C}_+^e is infinite. In this case, $R_0 = 1$ necessarily lies in the spectrum \mathcal{S} which would imply the existence of a positive equilibrium for R_0 at and near 1 and, in particular for $R_0 \lesssim 1$. This occurs, for example if $a_1 > 0$ and the bound (15) hold (Theorem 3 and Corollary 1).

Geometrically, one can think of the backward bifurcating continuum \mathcal{C}_+^e as “turning around” at a point $(R_0^*, x^*) \in R_+^1 \times R_+^m$ (usually at a saddle-bifurcation) so as to have an infinite spectrum (or so as to at least include $R_0 = 1$). Thus, for $R_0 \lesssim 1$ the extinction equilibrium $x = 0$ is stable and there exist (at least) two other positive equilibria, one of which (near the bifurcation point) is unstable and the other on \mathcal{C}_+^e is potentially stable.

The turning point of \mathcal{C}_+^e usually occurs as a saddle-node (blue-sky) bifurcation which creates stable positive equilibria (and hence a strong Allee effect involving equilibria for at least $R_0 \gtrsim R_0^*$). If this stability of the positive equilibria persists along the continuum \mathcal{C}_+^e until $R_0 = 1$, then a strong Allee effect involving equilibria occurs for $R_0 \lesssim 1$. It can happen, however, that the stable positive equilibria created by the saddle-node bifurcation lose their stability at a spectrum point $R_0 < 1$, say by a period doubling or Neimark-Sacker bifurcation. In this case, a strong Allee effect occurs for $R_0 \lesssim 1$ that involve non-equilibrium attractors. For examples, see [17].

In this scenario, a strong Allee effect provides the possibility of population survival when environmental conditions degrade so as to produce $R_0 < 1$. It requires a backward bifurcation which, in turn, requires sufficiently strong positive feedbacks (component Allee effects) at low population densities. The caveat is, of course, that the population must remain out of the basin of attraction of the extinction state (the Allee basin).

4 Nonlinear Semelparous Leslie Models

All the theorems and corollaries in Sect. 3 are valid for the semelparous ($s_a = 0$) Leslie model

$$\begin{aligned}
 x(0) &= x_0 \in R_+^m \\
 x(t+1) &= L(x)x(t) \text{ for } t = 1, 2, \dots
 \end{aligned}
 \tag{18}$$

$$L(x) = T \begin{pmatrix} 0 & 0 & \cdots & 0 & s_m \sigma_m(x) \\ s_1 \sigma_1(x) & 0 & \cdots & 0 & 0 \\ 0 & s_2 \sigma_2(x) & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & s_{m-1} \sigma_{m-1}(x) & 0 \end{pmatrix}$$

with the exception of Theorem 4. For the semelparous Leslie model, as we will see, the stability of the bifurcating positive equilibria does not depend solely on the direction of bifurcation.

4.1 Bifurcating Equilibria

The mathematical reason underlying the failure of the direction of bifurcation to sufficiently determine the stability of the bifurcating continuum \mathcal{C}_+^e of positive equilibria at $R_0 = 1$ for semelparous Leslie models is the imprimitivity of the inherent projection matrix $L(0)$. The destabilization of the extinction equilibrium $x = 0$ in this case is not caused by the dominant eigenvalue $L(0)$ alone leaving the complex unit circle, but by all m eigenvalues simultaneously leaving the unit circle (at the m^{th} roots of unity) as R_0 increases through 1. As a consequence of this, when analyzing the parameterized branch of positive equilibria, as outlined in the paragraph preceding Theorem 4, one needs to calculate expansions of all m eigenvalues of the Jacobian in order to see whether they all move into the complex unit disk or whether at least one moves out of the circle as one follows the bifurcating branch of positive equilibria. These calculations are carried out in [18] where conditions for stability and instability are obtained that involve quantities in addition to a_1 . Define

$$a_k \stackrel{\circ}{=} \sum_{n=1}^m \sum_{j=1}^m p_j \delta_j^0 \sigma_n \operatorname{Re} u_k^{n-j} \text{ for } k = 1, 2, \dots, m_{1/2} + 1 \tag{19}$$

where

$$m_{1/2} \stackrel{\circ}{=} \begin{cases} \frac{m}{2} & \text{if } m \text{ is even} \\ \frac{m-1}{2} & \text{if } m \text{ is odd.} \end{cases}$$

Since $u_1 = 1$ the definition of a_1 is consistent with that in Sect. 3 when $s_a = 0$.

The following theorem provides stability and instability criteria for the bifurcating positive equilibria, in a neighborhood of the bifurcation point, in relation to the direction of bifurcation. It follows from the expansion

$$|\lambda_k| = 1 - \frac{1}{m a_1} a_k \varepsilon + O(\varepsilon^2), \quad \varepsilon = R_0 - 1 \tag{20}$$

of the eigenvalue magnitudes for the Jacobian evaluated at the bifurcating equilibria near the bifurcation point, as calculated in [18].

Theorem 5 ([18]) Assume **AI**. Let \mathcal{C}_+^e be the unbounded continuum of positive equilibrium pairs that bifurcates from $(R_0, x) = (1, 0)$ as given in Theorem 3.

- (a) If $a_1 < 0$ then the bifurcation of \mathcal{C}_+^e at $R_0 = 1$ is forward. If $a_k < 0$ for all $k = 1, 2, \dots, m_{1/2} + 1$ then the bifurcation of \mathcal{C}_+^e is stable. If at least one of these $a_k > 0$, then the bifurcation of \mathcal{C}_+^e is unstable.
- (b) If $a_1 > 0$ then the bifurcation \mathcal{C}_+^e at $R_0 = 1$ is backward and unstable.

Generically, in the sense that $a_1 \neq 0$, Theorem 5(b) implies the backward bifurcation of positive equilibria at $R_0 = 1$ ($a_1 > 0$) is always unstable.¹ However, Theorem 5(a) shows that a forward bifurcation is not necessarily stable, in contrast to the iteroparous case in Theorem 4. While analytically rather clear-cut, the stability criteria for a forward bifurcation, namely, that all a_k be negative, does not lend itself to an immediately obvious biological interpretation. They have to do with the relationship between the effects of density on vital rates among individuals within the same age class and those among individuals of different age classes.

For example, suppose there are no density effects between age classes; that is to say, suppose σ_i does not depend on x_j for all $j \neq i$. Then $\partial_j^0 \sigma_n = 0$ for all $j \neq n$ and $a_k = a_1$ for all k . It follows from Theorem 5 that a forward bifurcation is stable. More generally, write

$$a_k = a_1 + \sum_{n=1}^m \sum_{j=1}^m p_j \partial_j^0 \sigma_n \left(\operatorname{Re} u_k^{n-j} - 1 \right)$$

and note that the double sum on the right side contains no within-class density effects, i.e. no derivatives $\partial_j^0 \sigma_n$ with $j = n$. Thus, if $a_1 < 0$ and the magnitudes of all between-class density effects are sufficiently small, then $a_k < 0$ for all k .

Corollary 4 If $a_1 < 0$ and between-class density effects are weak, i.e. $\left| \partial_j^0 \sigma_n \right|$ are sufficiently small for all $j \neq n$, then the bifurcation of \mathcal{C}_+^e at $R_0 = 1$ is forward and stable for the semelparous model (18).

As we will see in Sect. 4.2, when between-class density effects become significant, the stability of the bifurcating branch of positive equilibria can be lost. For a further analysis of the relationship between between-class and within-class density effects, the direction of bifurcation, and the stability properties of the bifurcating positive equilibria see [18].

Note that Corollary 1 concerning an unbounded spectrum and the sufficiency of (9) for an unbounded spectrum both hold for the semelparous model (18).

¹This corrects an error in Theorem 4.1 of [10].

4.2 Bifurcating Synchronous Cycles

To investigate further the nature of the bifurcation at $R_0 = 1$ for the nonlinear semelparous Leslie model (18), we begin with the $m = 2$ dimensional case

$$L(x) = \begin{pmatrix} 0 & s_2\sigma_2(x_1, x_2) \\ s_1\sigma_1(x_1, x_2) & 0 \end{pmatrix}.$$

This semelparous, juvenile-adult model has been extensively studied by several authors [19–22, 32, 33, 55, 64, 66] (also see [54]).

If one begins with a population of only $x_1 > 0$ juveniles, then the resulting orbit

$$\begin{aligned} x(0) &= \begin{pmatrix} x_1 \\ 0 \end{pmatrix}, & x(1) &= \begin{pmatrix} 0 \\ s_1\sigma_1(x_1, 0)x_1 \end{pmatrix}, \\ x(2) &= \begin{pmatrix} R_0\sigma_2(0, s_1\sigma_1(x_1, 0)x_1) \\ 0 \end{pmatrix}, \dots \end{aligned}$$

sequentially visits the positive coordinate axes. This shows that the boundary of the positive cone is invariant and has a dynamic that can be understood by an analysis of the one-dimensional composite map

$$x_1(t + 1) = R_0\bar{\sigma}(x_1(t))x_1(t) \tag{21}$$

$$\bar{\sigma}(x_1) \stackrel{\circ}{=} \sigma_2(0, s_1\sigma_1(x_1, 0)x_1)\sigma_1(x_1, 0), \quad R_0 = s_1s_2$$

which describes the dynamics of every other point (the juvenile component) of the orbit. An equilibrium of this composite map corresponds to an orbit of period 2 of the semelparous model. This cycle is an example of a *single-class synchronous 2-cycle* by which is meant a periodic cycle in which the age classes are synchronized in a way that they are temporally separated and that only one class is present at each point in time.

One-dimensional maps, such as (21), have been well studied and there is a large literature, and a large quantity of analytic methods, available for their analysis. For example, one approach is to view (21) as an $m = 1$ dimensional matrix model to which we can apply the equilibrium bifurcation theorems in Sect. 3. Or, more straightforwardly, one can investigate the equilibrium equation for positive solution pairs (R_0, x_1) , which obviously are defined by the equation

$$1 = R_0\bar{\sigma}(x_1).$$

Noting that $\bar{\sigma}(x_1)$ is positive valued for $x_1 \geq 0$ and that $\bar{\sigma}(0) = 1$, we see that the pairs $(R_0, x_1) = (1/\bar{\sigma}(x_1), x_1)$ for $x_1 \in R^1_+$ define a continuum of equilibrium pairs that bifurcates from $(1, 0)$ at $R_0 = 1$ (whose range is R^1_+) and whose direction of

bifurcation is forward and stable or backward and unstable if

$$\partial_1^0 \bar{\sigma} < 0 \text{ (or } \partial_1^0 \bar{\sigma} > 0)$$

respectively. A calculation shows $\partial_1^0 \bar{\sigma} = c_w$ where

$$c_w \stackrel{\circ}{=} \partial_1^0 \sigma_1 + s_1 \partial_2^0 \sigma_2.$$

Each of these equilibrium pairs (R_0, x_1) corresponds to a single-class synchronous 2-cycle of the $m = 2$ of the dimensional semelparous Leslie model (18) as defined by the two points

$$\begin{pmatrix} x_1(1) \\ x_2(1) \end{pmatrix} = \begin{pmatrix} x_1 \\ 0 \end{pmatrix}, \quad \begin{pmatrix} x_1(2) \\ x_2(2) \end{pmatrix} = \begin{pmatrix} 0 \\ s_1 \sigma_1(x_1, 0) x_1 \end{pmatrix}$$

of the cycle. Identify this cycle by its pair of positive components $x_1(1), x_2(2)$ (which are the two cohort densities that temporally alternate) and denote the corresponding *single-class synchronous 2-cycle pair* by

$$(R_0, [x_1(1), x_2(2)]) \in R_+^1 \times R_+^2$$

where for every $x_1 \in R_+^1$

$$R_0 = \frac{1}{\bar{\sigma}_1(x_1)}, \quad x(1) = x_1, \quad x(2) = s_1 \sigma_1(x_1, 0) x_1.$$

The continuum of equilibrium pairs (R_0, x_1) of (21) produces a continuum \mathcal{C}_+^2 of these single-class synchronous 2-cycle pairs of the semelparous Leslie model (18). This continuum \mathcal{C}_+^2 bifurcates from $(1, 0, 0)$ at $R_0 = 1$ and it is a forward bifurcation if $c_w < 0$ and a backward bifurcation if $c_w > 0$.

That the stability of the $x(1) = x_1$ component as an equilibrium of the composite map (21) depends on the direction of bifurcation only tells us about the stability of the single-class 2-cycles with respect to the dynamics on the boundary ∂R_+^2 . The stability or instability of these cycles as cycles of the semelparous Leslie model (18) on \bar{R}_+^2 requires further analysis. This stability analysis involves the eigenvalues μ_1, μ_2 of the Jacobian of the composite map (which is the product of the Leslie model’s Jacobian evaluated at the two points of the 2-cycle). Making use of the parameterizations

$$\begin{pmatrix} x_1 \\ 0 \end{pmatrix} = \begin{pmatrix} -\frac{1}{c_w} \\ 0 \end{pmatrix} \varepsilon + O(\varepsilon^2), \quad \begin{pmatrix} 0 \\ s_1 \sigma_1(x_1, 0) x_1 \end{pmatrix} = \begin{pmatrix} 0 \\ -\frac{s_2}{c_w} \end{pmatrix} \varepsilon + O(\varepsilon^2),$$

$$R_0 = 1 + \varepsilon$$

of the synchronous 2-cycle points, one can calculate the parameterizations

$$\mu_1 = 1 - \varepsilon + O(\varepsilon^2), \quad \mu_2 = 1 + \frac{c_w - c_b}{c_w} \varepsilon + O(\varepsilon^2)$$

of these eigenvalues, where

$$c_b \stackrel{\circ}{=} a_1 - c_w = \partial_1^0 \sigma_2 + s_1 \partial_2^0 \sigma_1$$

measures the between-class density effects. Accompanying these bifurcating, single-class synchronous 2-cycles, are the bifurcating positive equilibria, which have, together with eigenvalues of the associated Jacobian, the expansions

$$\begin{pmatrix} x_1 \\ x_2 \end{pmatrix} = \begin{pmatrix} \frac{1}{c_w + c_b} \\ \frac{s_1}{c_w + c_b} \end{pmatrix} \varepsilon + O(\varepsilon^2), \quad R_0 = 1 + \varepsilon$$

$$\lambda_1 = 1 - \frac{1}{2} \varepsilon + O(\varepsilon^2), \quad \lambda_2 = -1 + \frac{c_w - c_b}{c_w + c_b} \varepsilon + O(\varepsilon^2).$$

From these expansions one can sort out the direction of bifurcation and stability properties of both the positive equilibria and synchronous 2-cycles. The results are summarized in the following theorem.

Theorem 6 ([22]) Consider the $m = 2$ dimensional, semelparous Leslie model (18) and assume AI holds. Also assume that $a_1 = c_w + c_b \neq 0$ and $c_w \neq 0$. Then a bifurcation of unbounded continua \mathcal{C}_+^e and \mathcal{C}_+^2 of positive equilibrium pairs and single-class, synchronous 2-cycles respectively occurs at $R_0 = 1$.

- (a) If $c_w + c_b < 0$ then the bifurcation of \mathcal{C}_+^e at $R_0 = 1$ is forward. The bifurcation is stable if $c_w - c_b < 0$ and unstable if $c_w - c_b > 0$.
- (b) If $c_w + c_b > 0$ then the bifurcation of \mathcal{C}_+^e at $R_0 = 1$ is backward and unstable.
- (c) If $c_w < 0$ then the bifurcation of \mathcal{C}_+^2 at $R_0 = 1$ is forward. The bifurcation is stable if $c_w - c_b > 0$ and unstable if $c_w - c_b < 0$.
- (d) If $c_w > 0$ then the bifurcation of \mathcal{C}_+^2 at $R_0 = 1$ is backward and unstable.

That a forward bifurcation in a nonlinear semelparous Leslie model (5) is not necessarily stable can be seen by cases (a) and (c). Also note that the positive equilibria and the synchronous 2-cycles can bifurcate in opposite directions, since $c_w + c_b$ and c_w do not necessarily have the same signs. In any case, however, a backward bifurcation is always unstable. Also note that it is never the case that both bifurcating continua are stable, although it is possible that both are unstable.

A natural question to ask is whether Theorem 6 can be extended in some manner to higher dimensional semelparous Leslie models with $m \geq 3$. The properties of the \mathcal{C}_+^e equilibrium bifurcation for $m \geq 3$, namely its occurrence, direction of bifurcation and stability properties, are described by Theorem 5. We next turn our attention to the bifurcation of single-class, synchronous m -cycles at $R_0 = 1$.

Periodic m -cycles are fixed points of the m -fold composite map obtained from (18) whose components satisfy equations of the form

$$\begin{aligned} x_1 &= R_0 \bar{\sigma}_1(x) x_1 \\ x_2 &= R_0 \bar{\sigma}_2(x) x_2 \\ &\vdots \\ x_m &= R_0 \bar{\sigma}_m(x) x_m \end{aligned} \tag{22}$$

where $\bar{\sigma}_i(x)$ is a composite made from the coefficients $\sigma_i(x)$ of the Leslie projection matrix $L(x)$. Single class synchronous cycles correspond to fixed points with $x_j = 0$ for $j = 2, 3, \dots, m$, and where $x_1 > 0$ is a positive fixed point of the one dimensional map

$$x_1 = R_0 \bar{\sigma}(x_1) x_1 \tag{23}$$

with

$$\bar{\sigma}(x_1) \doteq \bar{\sigma}_1(x)|_{x_j=0, j \neq 1} > 0, \quad \bar{\sigma}(0) = 1.$$

This one dimensional map can be treated in the manner that we treated the map (21) when $m = 2$. There is a continuum of equilibrium pairs (R_0, x_1) that bifurcates forward (backward) from $(1, 0)$ if $c_w < 0$ (or $c_w > 0$) where

$$c_w = \sum_{n=1}^m p_n \partial_n^0 \sigma_n. \tag{24}$$

Each equilibrium pair corresponds to a single-class, synchronous m -cycle of the semelparous Leslie model (18) and the bifurcating continuum of equilibrium pairs produces a continuum \mathcal{C}_+^m of single-class synchronous m -cycle pairs

$$(R_0, [x_1(1), x_2(2), \dots, x_m(m)]) \in R_+^1 \times R_+^m$$

of the semelparous Leslie model (18). This continuum \mathcal{C}_+^m bifurcates from $(1, [0, \dots, 0])$ at $R_0 = 1$ and it is a forward bifurcation if $c_w < 0$ and a backward bifurcation if $c_w > 0$.

Since positive fixed points of (23) satisfy the equation

$$1 = R_0 \bar{\sigma}(x_1)$$

the range of the continuum (i.e. of the set of x_1 values obtained from the continuum) is the half line R_+^1 , since there is a unique $R_0 = 1/\bar{\sigma}(x_1)$ for each $x_1 \in R_+^1$. With regard to the spectrum of R_0 values from the continuum \mathcal{C}_+^m , a little thought about

the composite $\bar{\sigma}(x_1)$ reveals that the adult regulation assumption (9) on σ_m implies $\bar{\sigma}(x_1)x_1$ is bounded for $x_1 \geq 0$. This in turn implies the spectrum of R_0 on the continuum is unbounded (and hence is a half line in R_+^1).

We summarize these results in the following theorem.

Theorem 7 Assume **A1** and $c_w \neq 0$. A continuum \mathcal{C}_+^m of single-class m -cycles for the semelparous Leslie model (18) bifurcates from the origin $x = 0$ at $R_0 = 1$. If $c_w < 0$ the bifurcation is forward. If $c_w > 0$ the bifurcation is backward. The range of the continuum, i.e. the set of first class cohort densities x_1 from the cycles, is the half line R_+^1 . If $\sigma_m(x)$ satisfies (9), then the spectrum of R_0 values is infinite (and hence is a positive half line whose closure contains 1).

By Theorem 3 the direction of the bifurcation at $R_0 = 1$ of the continuum \mathcal{C}_+^e of positive equilibria is determined by the sign of

$$a_1 = \sum_{n=1}^m \nabla^0 \sigma_n v, \quad v = \text{col}(p_i).$$

This quantity involves both between-class and within-class density effects $\partial_j^0 \sigma_n$. On the other hand, by Theorem 7 the direction of bifurcation at $R_0 = 1$ of the continuum \mathcal{C}_+^m of single class, synchronous m -cycles determined by the sign of the quantity c_w given by (24), which involves only within-class density effects $\partial_n^0 \sigma_n$. Since these quantities can have different signs, it follows that the two continuum can bifurcate in opposite directions.

Theorem 7 provides the existence of a bifurcating continuum of single-class, synchronous m -cycles. General stability and instability criteria for these cycles have yet to be obtained for dimensions $m \geq 3$ and this remains a challenging open problem. Some results are known, however, under special assumptions.

4.3 Negative Feedback Only

Most of the literature on nonlinear Leslie matrix focusses on the case of negative feedback density effects (negative derivatives $\partial_j^0 \sigma_n$) and the absence of positive density effects (no positive derivatives $\partial_j^0 \sigma_n$, i.e. no component Allee effects). Assume

$$\text{A2: } \partial_j^0 \sigma_n \leq 0 \text{ for all } 1 \leq j, n \leq m \text{ with at least one } \partial_n^0 \sigma_n < 0.$$

Then $a_1 < 0$ and $c_w < 0$ (and $c_b \leq 0$) and, by Theorems 3 and 7, both the bifurcating continua of positive equilibria and single-class m -cycle are forward.

In the $m = 2$ dimensional case we have the following corollary of Theorem 6.

Corollary 5 Assume $m = 2$ and that **A1** and A2 hold. The bifurcation at $R_0 = 1$ of the continua \mathcal{C}_+^e and \mathcal{C}_+^2 of positive equilibria and single-class, synchronous 2-cycles of semelparous Leslie model (18) are both forward and the following two

alternatives hold:

- (a) If $c_w < c_b$ then the bifurcation of \mathcal{C}_+^e is stable and the bifurcation of \mathcal{C}_+^2 is unstable;
 (b) If $c_w > c_b$ then the bifurcation of \mathcal{C}_+^e is unstable and the bifurcation of \mathcal{C}_+^2 is stable.

The two alternatives in Corollary 5 describe a *dynamic dichotomy* at the bifurcation point $R_0 = 1$: either the bifurcating positive equilibria or bifurcating the synchronous 2-cycles are stable, but not both. Which bifurcating branch is stable depends on the relative strength of between-class and in-class density effects, which we can express in terms of the ratio

$$\rho \doteq \frac{c_b}{c_w}. \quad (25)$$

If $\rho < 1$ then within-class effects outweigh between-class effects and the population equilibrates. On the other hand, if $\rho > 1$ then between-class effects outweigh between-class effects and the population tends towards synchronous 2-cycle oscillations in which the juveniles and adults are temporally separated.

It is interesting to notice that this dynamic dichotomy, in the case $m = 2$, bears a similarity with the classic two species competitive exclusion principle, except that in the case of semelparous Leslie populations the two dynamic outcomes have to do with age classes within a single population and not the presence or absence of species. (Mathematically, this relates to the fact that the composite of the semelparous model has the same mathematical form as a two species competition model.)

The dynamic dichotomy between the bifurcating positive equilibria and the single-class, synchronous 2-cycles described in Corollary 5 for $m = 2$ does not hold in higher dimensions $m \geq 3$. This can be seen, for example, in studies of the $m = 3$ dimensional case [9, 12, 18]. As we will see in Theorem 9, however, when $m = 3$ there is a dynamic dichotomy between the stability of the bifurcating positive equilibria and the boundary of the positive cone as an attractor or repeller.

The boundary ∂R_+^m of the positive cone is an *attractor* if there exists an open neighborhood $U \subset R_+^m$ of ∂R_+^m (in the relative topology of R^3) such that orbits with initial conditions in U have ω -limit sets in ∂R_+^m . The boundary ∂R_+^m of the positive cone is a *repeller* if there exists a neighborhood $U \subset R_+^m$ of ∂R_+^m such that for the orbit from each initial condition not in ∂R_+^m there exists a time $T > 0$ such that the orbit lies outside of U for all $t \geq T$.

The use of average Lyapunov functions for the study of nonlinear Leslie models was pioneered by Kon et al. [43, 45, 46]. This approach leads to criteria for the attracting and repelling properties of the boundary ∂R_+^m that require the calculation the maxima and minima of quantities taken along all orbits on ∂R_+^m (e.g. see Theorem 4.1 in [45]). This obviously requires some knowledge of the dynamics on ∂R_+^m , which in general can be complicated. Near the bifurcation point, however, the dynamics on ∂R_+^m is usually simpler and, in fact, usually involves attracting

(synchronous) cycles. Here, we will restrict attention to this case and assume all orbits on ∂R_+^m approach a cycle.

Theorem 8 ([18]) *In addition to A1 and A2, suppose the follow two assumptions hold for the semelparous model (18):*

A3: $\sigma_i(x) x_i$ is bounded for $x \in \bar{R}_+^m$ for all $1 \leq i \leq m$;

A4. every orbit on ∂R_+^m approaches a synchronous cycle as $t \rightarrow +\infty$.

The boundary ∂R_+^m of the positive cone is an attractor (repeller) if, for every periodic cycle $c(j)$ on ∂R_+^m , the quantity

$$\theta \doteq \sum_{j=1}^p \ln \left(R_0 \prod_{n=1}^m \sigma_n(c(j)) \right) \tag{26}$$

is negative (positive). Here p is the period of the cycle.

For dimension $m = 2$ we saw that the dynamics on ∂R_+^m were described by a (composite) one-dimensional map, which permitted us to address the assumption A4 near $R_0 = 1$. In higher dimensions, however, it is possible for an increasing number of different types of synchronous cycles to arise at bifurcation, namely *k-class synchronous cycles* with k positive entries at each time step. These cycles correspond to fixed points of the composite map (22) with k positive and $m - k$ zero entries. It is an open problem to obtain conditions under which the bifurcation of k -class synchronous cycles occurs at $R_0 = 1$, although one approach that uses Eq. (22) is clear. Select any subset of k of Eq. (22), set $x_i = 0$ for all other subscripts, and study the resulting system of equations using the bifurcation methods used above for single-class cycles.

Under assumption A2, the bifurcation of the single-class m -cycles is forward. Therefore, for $R_0 \gtrsim 1$ it is necessary, in order to apply Theorem 8, to calculate θ for the bifurcating single-class cycle. Since a parameterization of the cycle is possible by perturbation methods, one can calculate an approximation of θ for $R_0 \gtrsim 1$, which turns out to be

$$\theta = \left(m - 1 - \sum_{q=1}^{m-1} \rho_q \right) \varepsilon + O(\varepsilon^2)$$

where

$$\rho_q = \frac{\sum_{i=1}^m p_i \partial_i^0 \sigma_{i+q}}{\sum_{i=1}^m p_i \partial_i^0 \sigma_i}, \quad q = 1, 2, \dots, m - 1 \tag{27}$$

(subscripts on σ_i are calculated modulo m) [18]. Theorem 8 gives the following result.

Corollary 6 *Assume A1, A2 and A3 hold for the semelparous model (18). Assume for $R_0 \gtrsim 1$ that all boundary orbits tend to the single-class m -cycle as $t \rightarrow +\infty$.*

Then for $R_0 \gtrsim 1$

$$\sum_{q=1}^{m-1} \rho_q > m - 1 \text{ implies } \partial R_+^m \text{ is an attractor}$$

$$\sum_{q=1}^{m-1} \rho_q < m - 1 \text{ implies } \partial R_+^m \text{ is a repeller.}$$

The ratios ρ_q are measures of the relative strength of between-class density effects in comparison to within-class density effects. The denominator of ρ_q in (27) is a measure of within-class competition (at low population densities) as based on the derivatives $\partial_i^0 \sigma_i$. In the numerator, the derivative $\partial_i^0 \sigma_{i+q}$ measures the density effect that i^{th} age class has on the survivorship of age class $i + q$ modulo m . This means that the numerator of the ratio ρ_q is a measure of the density effects among these selected (but not all) unidirectional pairings of age classes. Thus, Corollary 6 generalizes the conclusion stated after Corollary 5 for $m = 2$, namely, that weak density effects between age classes promotes stabilization with all age classes present, while strong density effects between age classes promotes synchronized oscillations with missing age cohorts.

Suppose we strengthen the local monotonicity assumption A2 to the following global assumptions, which are satisfied, for example, by the Leslie-Gower type nonlinearities (7).

$$\text{A4: } \partial_i \sigma_j(x) < 0 \text{ and } \partial_i (\sigma_i(x) x_i) > 0 \text{ for } x \in \bar{R}_+^m.$$

In the $m = 2$ dimensional case, Eq. (22) reduce to a single (one dimensional) map

$$x_1 = R_0 \bar{\sigma}_1(x_1) x_1$$

which by A4 is a monotone map and, as a result, all orbits equilibrate as $t \rightarrow +\infty$. For $R_0 > 0$ assumption A4 also implies $x = 0$ is a repeller and there exists a unique positive fixed point $x_1 > 0$. All this goes to show that all boundary orbits tend to the single-class 2-cycle when $R_0 > 1$. Corollary 6 implies the boundary ∂R_+^2 is an attractor or repeller when ρ_1 is greater than or less than 1. Here ρ_1 is identical to ρ in (25) and this result provides an enhancement of Corollary 5.

Unlike the case $m = 2$, however, the monotonicity assumptions A4 do not guarantee that all boundary orbits tend to the single-class synchronous 3-cycle when $m = 3$. When $m = 3$ Eq. (22) defining the boundary cycles is a planar map, which under A4, is strictly competitive on \bar{R}_+^2 and strongly competitive on R_+^2 to which the powerful theory of planar monotone maps can be applied (e.g. Proposition 2.1 in [62]). The result is that if $R_0 > 1$ then all orbits converge to an equilibrium in \bar{R}_+^2 , specifically to a non-negative equilibrium lying on a positive axis ∂R_+^2 or possibly a positive equilibrium in R_+^2 . These fixed points correspond to a single-class synchronous 3-cycle and a two-class, synchronous 3-cycle respectively. Under our working assumptions we know that a single-class 3-cycle exists for $R_0 \gtrsim 1$. Using bifurcation theory it can be shown that positive two-class synchronous

3-cycles also bifurcate from the origin at $R_0 = 1$ if both $\rho_i > 1$ or both $\rho_i < 1$ [18]. A parameterization of these bifurcating two-class 3-cycles near $R_0 = 1$ leads to the expansion

$$\theta = \frac{\rho_1 + \rho_2 - \rho_1^2 - \rho_2^2 + \rho_1\rho_2 - 1}{\rho_1\rho_2 - 1} \varepsilon + O(\varepsilon^2)$$

which, coupled with the expansion (27), with $m = 3$, for the single-class 3-cycles lead to the following result.

Theorem 9 Assume A1, A2 and A3 hold for the semelparous model (18). For $R_0 \gtrsim 1$ we have the following alternatives for the cases $m = 2$ and $m = 3$.

Suppose $m = 2$. If $\rho_1 < 1$ then the bifurcating positive equilibria are stable and the boundary ∂R_+^2 is a repeller. If $\rho_1 > 1$, the bifurcating positive equilibria are unstable and ∂R_+^2 is an attractor.

Suppose $m = 3$. If $\rho_1 + \rho_2 < 2$ then the bifurcating positive equilibria are stable and the boundary ∂R_+^3 is a repeller. If $\rho_1 + \rho_2 > 2$ then the bifurcating positive equilibria are unstable and ∂R_+^3 is an attractor.

This theorem describes, for $R_0 \gtrsim 1$, a dynamic dichotomy between the boundary of the positive cone and a positive equilibrium. By this is meant, roughly speaking, that strong within-class (negative feedback) density effects, measured by the ratios ρ_i , promotes equilibration with over-lapping age classes while strong between-class density effects destabilize this equilibration and promotes oscillations with missing age classes present at each time step. In the latter case (i.e. when $\rho_1 + \rho_2 > 2$) for the $m = 3$, an orbit within the positive cone does not necessarily approach a synchronous cycle, or a periodic oscillation of any kind, even though it approaches the boundary of the cone on which orbits do approach the single-class 3-cycle. If, in addition to $\rho_1 + \rho_2 > 2$, one of the ratios ρ_i is less than 1, then the single-class synchronous 3-cycle is also unstable, namely it is a saddle (it is stable if both $\rho_i > 1$) [12]. In this case orbits in the positive cone that approach the boundary, approach a *cycle chain* on the boundary. This invariant set consists of the three phases of the synchronous 3-cycle together with heteroclinic connections among them. See Fig. 1. Other types of cycle chains (ones that also contain 2-cycle synchronous cycles and their phases) can also bifurcate from the origin, under different circumstances. For a list of the possibilities when $m = 3$ see [12]. Since $\rho_1 + \rho_2 > 2$ also implies that the positive equilibrium is unstable, we see that the dynamic dichotomy in the case $m = 3$ is not between the positive equilibrium and the single-class synchronous cycle, unlike the case $m = 2$.

In general, for dimensions $m \geq 4$ a description of the dynamic alternatives near the bifurcation point $R_0 = 1$ remains an open problem. It is not known in general if a dynamic dichotomy exists between the two alternatives of a stable positive equilibrium and an attracting boundary ∂R_+^m . Even if the boundary is known to be an attractor (from inside the positive cone), an understanding of the dynamics on the boundary is complicated by the possibility of many types of synchronous

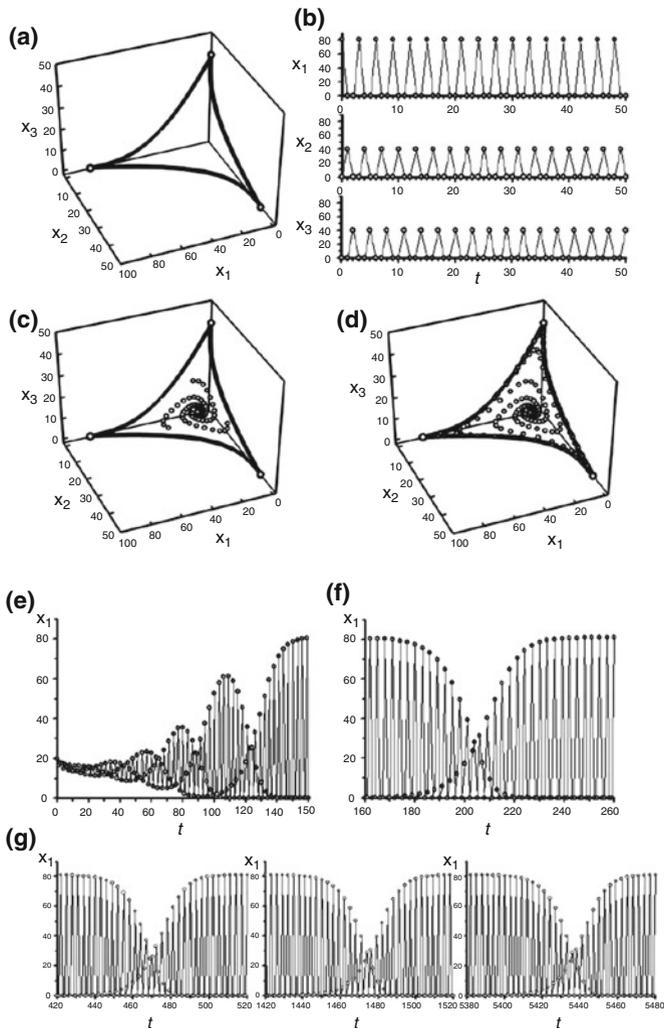


Fig. 1 These plots show orbits from the semelparous LPA model (17) with coefficients $\mu_a = 1$ and $b = 3$, $\mu_l = 0.5$, $\mu_p = 0$, $c_1 = c_3 = 0.1$, $c_2 = 0.2$. We calculate $\rho_1 = 0$ and $\rho_2 = 5$ and conclude that both continua of bifurcating positive equilibria and single-class synchronous cycles are unstable, but that the boundary ∂R_+^3 is an attractor. Note that $R_0 = 1.5$. (a) The open circles are the points of the single-class 3-cycle which are temporally visited counter-clockwise. Also shown are points on heteroclinic connecting orbits lying in the coordinate planes (which temporally are visited sequentially). (b) The time series of the single-class 3-cycle showing the synchrony of the age classes. (c) An orbit starting near the unstable positive orbits displays a spiral departure from the equilibrium. (d) This plot shows how the orbit approaches ∂R_+^3 , specifically the cycle chain shown in (a). (e) The x_1 component of this orbit appears to approach a period three oscillations by $t = 160$. (f) However, this component departs from this oscillation and undergoes a phase shift at around $t = 200$, after which it returns to a period three oscillation, but with its phase shifted by one time unit. (g) Three more such phase shifts are shown. They occur infinitely often, increasingly further apart, creating infinitely many longer and longer episodes of (near) single-class oscillations of period three.

m -cycles and connecting heteroclinics, i.e. types of cycle chains (to say nothing of other possible bifurcating invariant sets lying on the boundary). The dynamic complexity can greatly increase with the dimension $m \geq 4$, and it is likely that a complete and general description of the bifurcation at $R_0 = 1$ will not be possible for higher dimensions [30].

4.4 Backward Bifurcations

As mentioned at the end of Sect. 3 a strong Allee effect, that is to say, the occurrence of multiple attractors, one of which is the extinction equilibrium and another which is a non-extinction attractor, often (if not usually) arises in population models from a backward bifurcation. For nonlinear matrix models, a backward bifurcating continuum of positive equilibria (necessarily unstable for $R_0 \lesssim 1$) can “turn around” at a saddle-node bifurcation point $R_0^* < 1$, creating stable positive equilibria for $R_0 < 1$ when the extinction state is also stable. For the semelparous Leslie model (18) opportunities for a strong Allee effect arise from such an occurrence for both the continuum of positive equilibria and the continuum of single-class synchronous cycles (or more complicated cycle chains).

For example, we see from Theorem 6 that several bifurcation scenarios at $R_0 = 1$ are possible for the $m = 2$ dimensional case, due to the fact that the continua \mathcal{C}_+^e and \mathcal{C}_+^c can bifurcate in the same or different directions. Figure 2 shows orbits calculated from the semelparous Leslie model (18) with $m = 2$ and

$$\sigma_1(x) = \frac{1 + \alpha x_2}{1 + c_{21}x_1 + c_{22}x_2}, \quad \sigma_2(x) = \frac{1}{1 + c_{11}x_1 + c_{12}x_2}. \tag{28}$$

The parameter values chosen in Fig. 2, together with Theorem 6, imply that both continua \mathcal{C}_+^e and \mathcal{C}_+^c bifurcate backward. The result is a strong Allee effect in this model in which there are two non-extinction attractors for values of $R_0 < 1$, namely a positive equilibrium and a single-class, synchronous 2-cycle, as well as a stable extinction equilibrium. Among other things, this example shows that the dynamic dichotomy that occurs in the $m = 2$ dimensional semelparous Leslie model described in Corollary 5 does not occur when both continua bifurcate backwards.

5 Concluding Remarks

I have focussed in this paper on the dynamics of m dimensional, nonlinear semelparous Leslie models that arise from bifurcations that occur at $R_0 = 1$ due to the loss of stability of the extinction equilibrium. Under quite general conditions, methods from modern and classic bifurcation theory establish the existence of two basic continua that bifurcate from the extinction equilibrium at $R_0 = 1$, one \mathcal{C}_+^e

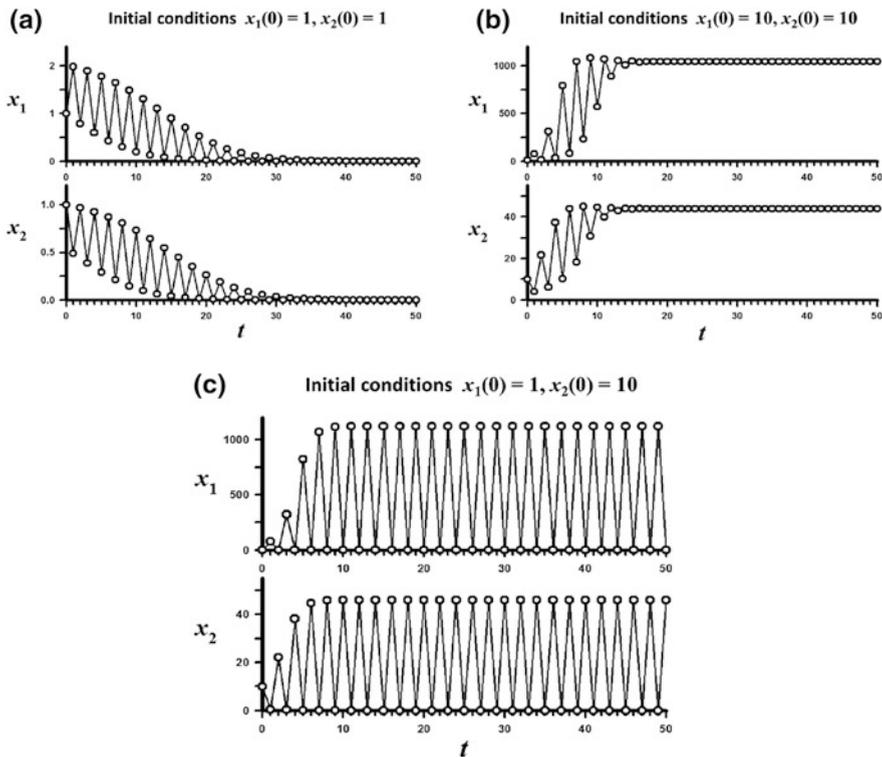


Fig. 2 These plots show three example orbits for the $m = 2$ semelparous Leslie model (18) with $\sigma_1(x)$ and $\sigma_2(x)$ given by (28) with parameter values $c_{11} = c_{12} = c_{22} = 0.01, c_{21} = 0, \alpha = 0.6, s_1 = 0.5,$ and $b = 1.25$. These values imply $R_0 = 0.625 < 1$ and $c_w = -0.015, c_b = 0.295, c_w + c_b = 0.280,$ and $c_w - c_b = -0.310$. By Theorem 6 both continua bifurcate backwards, which accounts for a strong Allee effect with two non-extinction attractors in the presence of an attracting extinction equilibrium. Some initial conditions lead to extinction as in plot (a), some to a positive equilibrium as in plot (b), and some to a single-class synchronous 2-cycle as in plot (c)

consisting of positive equilibrium pairs and the other \mathcal{C}_+^m consisting of single-class, synchronous m -cycle pairs. These continua have a global extent in the sense that they are unbounded, i.e. either their spectrum or range is unbounded. The directions of bifurcation, in a neighborhood of the bifurcation point $(R_0, x) = (1, 0)$, can be determined from the signs of the quantity a_1 in the case of \mathcal{C}_+^e and c_w in the case of \mathcal{C}_+^m . Both a_1 and c_w are linear combinations of the derivatives $\partial_j^0 \sigma_i$ (the sensitivities of the Leslie matrix entries σ_i to changes in low age-class densities). In models with no positive feedback density effects (i.e. no derivative $\partial_j^0 \sigma_i > 0$ or, in other words, no component Allee effects) the bifurcation of both continua is forward. Positive feedback effects can, if of sufficient magnitude, lead to backward bifurcations (which can, in turn, lead to strong Allee effects).

The question of what attractors arise from these bifurcations is a difficult one and has not been fully resolved in general, except in lower dimensions. The two dimensional case $m = 2$ is well understood (Theorem 6): backward bifurcations are unstable and, in the case of forward bifurcations, one but not both bifurcations of \mathcal{C}_+^e and \mathcal{C}_+^e is stable. The case $m = 3$ is also well-understood, at least in the absence of positive feedback terms, in that there is a dynamic dichotomy between \mathcal{C}_+^e and ∂R_+^3 (Theorem 9). In this case, the attractor is not necessarily a positive equilibrium or a single-class synchronous 3-cycle, but can be a cycle chain consisting of the three phases of the 3-cycle connected by heteroclinic orbits lying on ∂R_+^3 . This anticipates the complexity of the dynamics on ∂R_+^m , in particular the number and type of synchronous cycles, that can occur for higher dimensions m . The boundary dynamics significantly influence the dynamics and type of attractors for the semelparous Leslie model (5) on \bar{R}_+^m . It seems unlikely that a thorough accounting of the possibilities is possible for higher dimensions $m \geq 4$ without specialized and simplifying assumptions on the model. Using a different approach to the study of the dynamics of the Leslie model (5)—one based on a formal limiting procedure and comparison with associated differential equation models—Diekmann and van Gils come to the same conclusion, even with the specialized assumption they make that all density dependence is through a single weighted population size [30].

There is a large literature that investigates the dynamics of semelparous Leslie models from other points of view that do not restrict attention to a neighborhood of the bifurcation at $R_0 = 1$. These studies generally restrict the nonlinearities in the model in some way or another. Common assumptions include limiting density dependence to a few or even just one age class [50, 53, 61, 66], assuming density effects are through a dependence on one weighted population size $w = \sum_{j=1}^m w_j x_j$ (so that $\sigma_i = \sigma_i(w)$ for all i) [25–27, 29–31, 65–68], use of specific nonlinearities such as Leslie-Gower (7) [49] or Ricker (8) types [57], and an hierarchical structure to density dependence in which the vital rates of an age class depend only on densities of older (or younger) age classes [16, 37, 38]. These studies often are done with an eye towards the possibility of positive (non-synchronous) periodic cycles, invariant loops, and chaotic attractors. Given that one-dimensional maps $m = 1$ can, as is well known, exhibit complex dynamics, it is certainly to be expected that such attractors will occur in nonlinear Leslie models of dimension $m \geq 2$. They generally arise when R_0 is increased and a destabilization of the positive equilibria on \mathcal{C}_+^e occurs by means of a period-doubling or Neimark-Sacker (discrete Hopf) bifurcation, and subsequently by destabilizations of non-equilibrium attractors, all of which can lead to a so-called route-to-chaos. For semelparous Leslie models, since both the boundary ∂R_+^m and the interior R_+^m of the positive cone are invariant, it is possible for such bifurcation scenarios to occur in the interior and on the boundary positive cone. Thus, one can see complicated attractors on ∂R_+^m and/or in R_+^m . Biologically the former are distinguished by always having a missing age class while the latter never have a missing age class.

A theme that arises from the study of the semelparous Leslie model (5) is that strong competition (negative feedback density effects) between age-classes

(relative to within class competition) promotes synchronous oscillations. This is viewed as a kind of competitive exclusion principles among age-classes (in analogy to the competitive exclusion principle among different species). This idea forms one of the principle hypotheses offered to explain the synchronized, recurrent outbreaks of periodical insects, the periodical cicadas being the most famous example. Another competing hypothesis is predator saturation: by synchronizing their emergence adults overwhelm predators by their number and thereby assure successful reproduction of at least a fraction of their number (for a discussion see [52, 69]). Bulmer and Bencke [2, 3] concluded from their seminal model studies, in which predation and fungal infections of adult were included in a semelparous Leslie model, that between-class competitive effects (particularly in the youngest age classes) are the primary cause of synchronized cohort oscillations. Although there is some evidence of such competition among cicada nymphs [39], as they struggle for feeding locations on tree roots, it is difficult to obtain observational data about the interactions among age classes of nymphs.

There is, however, some striking experimental evidence of the phenomenon of competition induced synchronization of age classes. Decades long experimental studies of nonlinear dynamics conducted with *Tribolium castaneum* (flour beetles), reported in [5, 24, 28, 41], were not designed to study synchronized oscillations in a semelparous species. Indeed, *T. castaneum* is not naturally semelparous. However, the experimental protocol used in the keystone study of dynamic bifurcations and routes-to-chaos in effect made the experimental cultures of *T. castaneum* semelparous by imposing high adult mortality. (Theoretically $\mu_a = 0.96$ in the LPA model (17), although in practice 100% mortality was often imposed during the long term study.) With the cultures placed into an essentially semelparous life history, between-class density effects were increased in a sequence of replicated cultures (specifically, c_2 was increased from 0 to 1 in (17)). The goal of that experiment was to document a sequence of bifurcations and their resulting complicated attractors (including chaotic attractors) that were predicted to occur by the LPA model (17). For our purposes here, we point out that at the lowest level of between-class competition, $c_2 = 0$, there was observed an equilibrium state with all age-class present and at the highest level, $c_2 = 1$, single-class synchronous 3-cycles were observed. This is in agreement with the principle that strong between-class competition promotes synchronized oscillations. See Fig. 3. Furthermore, attracting cycle chains, as illustrated in Fig. 1b, offer a deterministic explanation of experimentally observed phase shifts in the synchronous 3-cycles (which were explained in [35] by stochastic jumps among the basins of attractions of the three phases).

In addition to many unanswered questions concerning the nature of the primary bifurcation at $R_0 = 1$ for the semelparous Leslie model in higher dimensions, there are extensions and elaborations of the model that also present interesting challenges. For example, the role of evolution in determining semelparity or iteroparity has long been of interest in life history theory [60, 63]. In this regard, the fundamental bifurcation at $R_0 = 1$ has been studied for evolutionary versions of matrix models primitive projection matrices [13, 14] and for semelparous Leslie models of dimension $m = 2$ [22]. As already mentioned, models that include the effects of

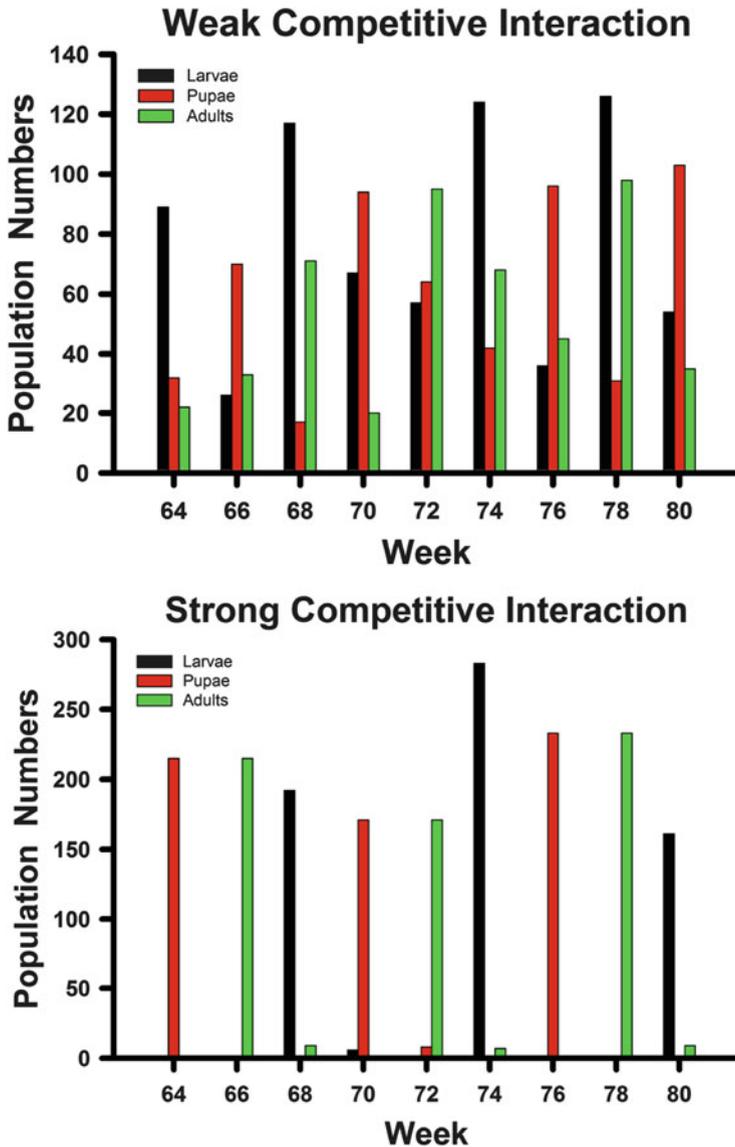


Fig. 3 Experimental evidence for single-class cycles induced by inter-class competition. The graphs show the age class histograms (at the end of 80 weeks when transients were dissipated) in the experimental treatments that underwent the weakest and strongest cannibalism rates. The former treatment shows overlapping age classes (larvae, pupae, adults), while the latter shows single cohorts of non-overlapping age classes. (The larval and pupal stages for *T. castaneum* are 2 weeks in length, which is the time unit used in the LPA model (17))

predation (and parasitism) have been formulated and studied [2, 3, 44], although not specifically with the bifurcation at $R_0 = 1$ in mind. The fundamental bifurcation at $R_0 = 1$ has also been studied for spatial versions of matrix models, but only for primitive projection matrices [58, 59].

The semelparous Leslie model is a notable and important example of a matrix population model that has an imprimitive projection matrix. A signature feature of this model is the presence of synchronous orbits, i.e. orbits with missing age classes. It has been shown that no matrix model, of any kind, with a primitive projection matrix can have synchronous orbits [42]. It would be interesting to study the fundamental bifurcation at $r = 1$ for general matrix models with imprimitive projection matrices and to ascertain the role that synchronous cycles play.

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Appendix

Theorem 1.20 in [56] implies the existence of two, globally distinct continua \mathcal{C}_+^e and \mathcal{C}_-^e of nonzero equilibrium pairs each of which satisfies the two alternatives, i.e. is unbounded in $R^1 \times R^m$ or contains a point $(\lambda, 0)$ where $\lambda \neq 1$ is a characteristic value of $M(0)$.² In a neighborhood of $(1, 0)$, \mathcal{C}_+^e and \mathcal{C}_-^e consist of positive and negative equilibrium pairs respectively. Since second alternative is ruled out by the fact that $M(0)$ has no characteristic value other than 1, \mathcal{C}_+^e and \mathcal{C}_-^e are globally distinct continua that are unbounded in $R \times R^m$. For purposes of contradiction we assume the unbounded continuum C_+^e , which in a neighborhood of $(1, 0)$ lies in $R_+^1 \times R_+^m$, does not remain in $R_+^1 \times R_+^m$. In this case, it must contain a point $(R_0^*, x^*) \in \partial(R_+ \times R_+^m)$ other than $(1, 0)$ and we can find a sequence of points $(R_{0n}, x_n) \in \mathcal{C}_+^e \cap (R_+ \times R_+^m)$ such that $\lim_{n \rightarrow \infty} (R_{0n}, x_n) = (R_0^*, x^*)$ where $R_0^* \geq 0$ and $x^* \in \bar{R}_+^m$. We want to arrive at a contradiction.

The points (R_{0n}, x_n) satisfy (12)

$$x_n = R_{0n}M(0)x_n + R_{0n}h(x_n). \tag{29}$$

First, suppose $x^* = 0$. We can extract a subsequence from the sequence of unit vectors

$$u_n = \frac{x_n}{|x_n|} \in R_+^m$$

²To apply Theorem 1.20 in [56] we extend the domain of the $\sigma_i(x)$ to R^m by re-defining them smoothly outside of the closure \bar{R}_+^m of the positive cone. This is possible by assumption A1.

that converges to a nonnegative unit vector u :

$$\lim_{n \rightarrow \infty} u_n = u \in \bar{R}_+$$

Passing to the limit in

$$\frac{x_n}{|x_n|} = R_{0n} M(0) \frac{x_n}{|x_n|} + R_{0n} \frac{h(x_n)}{|x_n|}.$$

we obtain $u = R_0^* M(0) u$. This leads to an immediate contradiction if $R_0^* = 0$. If $R_0^* \neq 0$ then since the only characteristic value of $M(0)$ is 1 we obtain another contradiction, namely, $R_0^* = 1$. Having ruled out $x^* = 0$, we conclude that $x^* \in \partial R_+^m \setminus \{0\}$. Passing to the limit in Eq. (29) we conclude that x^* is an equilibrium of the nonlinear Leslie model (with $R_0 = R_0^*$). However, an inspection of components of the equilibrium equation (10) shows that if one component equals 0 then all components equal 0, i.e. $x^* = 0$. This is a contradiction to $x^* \in \partial R_+^m \setminus \{0\}$.

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