

Andrews University

Digital Commons @ Andrews University

Faculty Publications

9-1-2012

Stable Bifurcations in Semelparous Leslie Models

J. M. Cushing

The University of Arizona

Shandelle M. Henson

Andrews University, henson@andrews.edu

Follow this and additional works at: <https://digitalcommons.andrews.edu/pubs>



Part of the [Biology Commons](#)

Recommended Citation

Cushing, J. M. and Henson, Shandelle M., "Stable Bifurcations in Semelparous Leslie Models" (2012). *Faculty Publications*. 1678.

<https://digitalcommons.andrews.edu/pubs/1678>

This Article is brought to you for free and open access by Digital Commons @ Andrews University. It has been accepted for inclusion in Faculty Publications by an authorized administrator of Digital Commons @ Andrews University. For more information, please contact repository@andrews.edu.



Stable bifurcations in semelparous Leslie models

J. M. Cushing & Shandelle M. Henson

To cite this article: J. M. Cushing & Shandelle M. Henson (2012) Stable bifurcations in semelparous Leslie models, *Journal of Biological Dynamics*, 6:sup2, 80-102, DOI: [10.1080/17513758.2012.716085](https://doi.org/10.1080/17513758.2012.716085)

To link to this article: <https://doi.org/10.1080/17513758.2012.716085>



Copyright J.M. Cushing



Published online: 31 Aug 2012.



Submit your article to this journal [↗](#)



Article views: 648



View related articles [↗](#)



Citing articles: 19 View citing articles [↗](#)

Stable bifurcations in semelparous Leslie models[†]

J.M. Cushing^{a*} and Shandelle M. Henson^b

^a*Department of Mathematics and Interdisciplinary Program in Applied Mathematics, 617 N Santa Rita, University of Arizona, Tucson, AZ 85721, USA;* ^b*Department of Mathematics, Andrews University, Berrien Springs, MI 49104, USA*

(Received 20 March 2012; final version received 24 July 2012)

In this paper, we consider nonlinear Leslie models for the dynamics of semelparous age-structured populations. We establish stability and instability criteria for positive equilibria that bifurcate from the extinction equilibrium at $R_0 = 1$. When the bifurcation is to the right (forward or super-critical), the criteria consist of inequalities involving the (low-density) between-class and within-class competition intensities. Roughly speaking, stability (respectively, instability) occurs if between-class competition is weaker (respectively, stronger) than within-class competition. When the bifurcation is to the left (backward or sub-critical), the bifurcating equilibria are unstable. We also give criteria that determine whether the boundary of the positive cone is an attractor or a repeller. These general criteria contribute to the study of dynamic dichotomies, known to occur in lower dimensional semelparous Leslie models, between equilibration and age-cohort-synchronized oscillations.

Keywords: nonlinear age-structured population dynamics; Leslie matrix; semelparity; bifurcation; equilibrium; synchronous cycles; stability

1. Introduction

The inherent net reproductive number R_0 is a basic quantity that can determine the viability of a biological population. The typical scenario is that a population at low density is threatened with extinction when $R_0 < 1$ and can persist if $R_0 > 1$. Mathematically, an equilibrium in which the population is absent is (locally asymptotically) stable if $R_0 < 1$ and is unstable if $R_0 > 1$. (Indeed, it is generally the case that uniform persistence or permanence, with respect to the extinction state, occurs when $R_0 > 1$.) The result of this destabilization as R_0 increases through 1 is a transcritical bifurcation in which a branch of non-extinction equilibria intersects the extinction equilibrium at $R_0 = 1$. For $R_0 \approx 1$, this intersecting branch of non-trivial equilibria decomposes into two sub-branches, corresponding to $R_0 \lesssim 1$ and $R_0 \gtrsim 1$, respectively, one of which consists of positive equilibria (the other consists of non-positive, and therefore biologically irrelevant, equilibria).

The general exchange of stability principle implies that stability is passed from the extinction equilibrium to the non-extinction equilibria as R_0 increases through 1. We say that the bifurcating

*Corresponding author. Email: cushing@math.arizona.edu, cushing@email.arizona.edu

[†]Dedicated to Simon Levin on the occasion of his 70th birthday.
Author Email: henson@andrews.edu

branch of positive equilibria is stable or unstable if the positive equilibria on that branch are (locally asymptotically) stable or unstable, respectively.

Typically in population models, the stability of the branch of positive equilibria depends on the direction of bifurcation. That is to say, the branch of positive equilibria is stable if it corresponds to $R_0 \gtrsim 1$, in which case the bifurcation is said to be ‘to the right’ (or forward or super-critical). If the opposite is true, that is, if the positive equilibria correspond to $R_0 \lesssim 1$, then the bifurcating branch of positive equilibria is unstable and the bifurcation is ‘to the left’ (or backward or sub-critical). In other words, bifurcations to the right at $R_0 = 1$ are stable and bifurcations to the left are unstable. Bifurcations to the right occur when, at low population densities, the effects of negative density feedback terms predominate over those of positive density feedback terms (Allee effects). If Allee effects are sufficiently strong, then a left bifurcation occurs. Since it is usually assumed that negative feedback density effects predominate at high population levels, it typically occurs, in the case of a left bifurcation, that the bifurcating branch of unstable positive equilibria ‘turns around’ and stabilizes at a critical value of $R_0 < 1$ (at a saddle-node bifurcation point), thereby creating the familiar bistable phenomenon often associated with strong Allee effects. For more details, see [6,9].

This fundamental bifurcation scenario has been established in numerous types of mathematical models for population dynamics, including single-species and multi-species models described by autonomous ordinary differential equations, discrete time matrix models and continuous time partial differential equation models for structured populations, non-autonomous models for populations in periodically fluctuating environments, and partial differential equation and integro-difference equation spatial models. See, for example, [5,6,9,26] and the references cited therein. The plethora of models for the spread of diseases also exhibits this basic transcritical bifurcation phenomenon, where the disease-free state is the extinction state of the pathogen and the epidemic equilibrium arises from the bifurcation as R_0 passes through 1. (In these applications, R_0 often has a different biological interpretation.)

The mathematical theorems that support the fundamental bifurcation theorem have, of course, hypotheses that must be fulfilled. One of these hypotheses is that the dominant eigenvalue of the linearization at the extinction equilibrium be strictly dominant (i.e. strictly larger in magnitude than all other eigenvalues). In this paper, we consider an important class of models for which this condition fails. Our goal is to study the nature of the bifurcation that results in this case.

Specifically, we will consider a special case of the famous Leslie age-structured model that describes a semelparous life history. For discrete time matrix models, the requirement of a strictly dominant eigenvalue for the linearization at the extinction equilibrium is the requirement that the projection matrix describing the model dynamics be primitive. The projection matrix of the semelparous Leslie model, however, is not primitive; indeed, all its eigenvalues have the same magnitude. This class of models, therefore, constitutes the extreme opposite of the primitivity required by the fundamental bifurcation theorem; namely, upon destabilization of the extinction state, *all* eigenvalues leave the unit circle in the complex plane.

It is known for semelparous Leslie models that a transcritical bifurcation of positive equilibria does occur at $R_0 = 1$ [7]. It is also known, however, that the stability of the bifurcating positive equilibria is *not* determined solely by the direction of bifurcation as it is for primitive matrix models [7,8,11]. The bifurcation at $R_0 = 1$ is complicated by the simultaneous bifurcation of periodic cycles.

For semelparous Leslie models, the boundary of the positive cone is invariant. Orbits on the boundary of the cone have missing age classes at each point in time. Indeed, in semelparous Leslie models, each empty class moves ahead one class per time step and the empty age classes are in this sense synchronized (orbits on the boundary, other than the extinction equilibrium at the origin, are therefore referred to as synchronous orbits). It is known that a single-class cycle lying on the boundary of the cone (with only one non-empty age class, or age cohort,

present at each point in time) always bifurcates from the extinction state at $R_0 = 1$, along with the positive equilibria [7]. This dynamic – periodic oscillations with non-overlapping age classes – is obviously quite different from that of the positive equilibrium – equilibration with all age classes present. Moreover, other cycles with two or more non-empty classes per time step can, under some circumstances, also bifurcate at $R_0 = 1$ [8]. Although the dynamics on the boundary of the cone can be quite complicated, they nonetheless represent oscillations with missing age classes, which is in stark contrast to equilibration with all age classes present.

The number of age classes in the semelparous Leslie model (i.e. the dimension of the model) is essentially the length of the maturation period. For short maturation periods, that is, for semelparous Leslie models of dimension 2 or 3, it is known that a dynamic dichotomy exists between the bifurcation branch of positive equilibria and the boundary of the positive cone; namely, when one is attracting, the other is repelling [7,8,11]. For longer maturation periods (higher dimensional semelparous Leslie models), such a dynamic dichotomy has not been established.

There is a considerable literature on semelparous Leslie models [1,2,7,8,11,13–15,17–19,22,23,25,27–29]. A substantial amount of this literature was stimulated by investigations into the long cyclic outbreaks of periodical insects (the highlight example being the famous periodical cicadas), which is exactly the dynamic of the synchronous cycles on the boundary of the positive cone of the semelparous Leslie model. Therefore, it is of interest to consider higher dimensional models and the alternatives between the boundary of the positive cone being an attractor and the positive equilibria being an attractor.

Our main goal in this paper is to derive stability and instability criteria for the bifurcating positive equilibria for general semelparous Leslie models of any dimension. These criteria appear in Theorem 3. Also in Section 3, we provide a biological interpretation for these criteria in the case of negative density feedback (i.e. the absence of Allee effects). Although we do not establish a dynamic dichotomy between the positive equilibria and the boundary of the positive cone in higher dimensions (indeed we give a numerical simulation that suggests that it might not necessarily occur in dimensions greater than 3), in Section 4, we give some criteria under which the boundary of the cone is attracting or repelling (Theorem 5).

2. Preliminaries

Let R^m denote m -dimensional Euclidean space and R_+^m the positive cone:

$$R_+^m \doteq \{\hat{x} = \text{col}(x_n) : x_n > 0, n = 1, 2, \dots, m\}.$$

Denote the closure of R_+^m by \bar{R}_+^m and its boundary by $\partial R_+^m \doteq \bar{R}_+^m \setminus R_+^m$. Let Ω be an open set in R^m that contains \bar{R}_+^m . We assume

A1: $\sigma_n \in C^2(\Omega, R_+^1)$, $\sigma_n(\hat{0}) = 1$ and $s_n > 0$ for $n = 1, \dots, m$ and $0 < s_n < 1$ for $n = 1, \dots, m - 1$.

A semelparous Leslie model is a map from Ω to \bar{R}_+^m defined by

$$\hat{x} \longrightarrow S(\hat{x})\hat{x} \tag{1}$$

with a Leslie projection matrix

$$S(\hat{x}) = \begin{pmatrix} 0 & 0 & 0 & \cdots & 0 & s_m \sigma_m(\hat{x}) \\ s_1 \sigma_1(\hat{x}) & 0 & 0 & \cdots & 0 & 0 \\ 0 & s_2 \sigma_2(\hat{x}) & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & 0 & \cdots & s_{m-1} \sigma_{m-1}(\hat{x}) & 0 \end{pmatrix}. \tag{2}$$

Note that Equation (1) maps R_+^m into itself and ∂R_+^m into itself.

We introduce the notation

$$p_j = \begin{cases} 1 & \text{for } j = 1, \\ \prod_{n=1}^{j-1} s_n & \text{for } j = 2, 3, \dots, m \end{cases} \tag{3}$$

and define

$$R_0 \doteq \prod_{n=1}^m s_n,$$

the inherent net reproductive number (i.e. the expected number of offspring per newborn per life time in the absence of density effects). We can introduce R_0 explicitly into the model equations by writing

$$S(\hat{x}) = \begin{pmatrix} 0 & 0 & 0 & \dots & 0 & R_0 p_m^{-1} \sigma_m(\hat{x}) \\ s_1 \sigma_1(\hat{x}) & 0 & 0 & \dots & 0 & 0 \\ 0 & s_2 \sigma_2(\hat{x}) & 0 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & 0 & \dots & s_{m-1} \sigma_{m-1}(\hat{x}) & 0 \end{pmatrix}.$$

Note that the inherent projection

$$S(\hat{0}) = \begin{pmatrix} 0 & 0 & 0 & \dots & 0 & R_0 p_m^{-1} \\ s_1 & 0 & 0 & \dots & 0 & 0 \\ 0 & s_2 & 0 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & 0 & \dots & s_{m-1} & 0 \end{pmatrix}$$

has characteristic equation $\lambda^m - R_0 = 0$ and eigenvalues

$$\lambda_k = R_0^{1/m} u_k, \quad k = 1, 2, \dots, m,$$

where

$$u_k \doteq \exp\left(\frac{2\pi(k-1)}{m}i\right), \quad k = 1, 2, \dots, m, \tag{4}$$

are the m th roots of unity. All eigenvalues λ_k have the same magnitude: $|\lambda_k| = R_0^{1/m}$. Since $S(\hat{0})$ is the Jacobian of the map (1) evaluated at the extinction equilibrium $\hat{x} = \hat{0}$, we see, by the linearization principle, that the extinction equilibrium loses stability as R_0 increases through 1.

THEOREM 1 *Assume A1. For the semelparous Leslie model (1) and (2), the extinction equilibrium $\hat{x} = \hat{0}$ is (locally asymptotically) stable if $R_0 < 1$ and is unstable if $R_0 > 1$.*

Remark 1 If $\sigma_n(\hat{x}) \leq 1$ for $n = 1, \dots, m$, then a straightforward comparison argument shows that $R_0 < 1$ implies the extinction equilibrium $\hat{x} = \hat{0}$ is a global attractor on R_+^m [6].

Remark 2 If the map (1) and (2) is dissipative, then $R_0 > 1$ implies that the map is uniformly persistent (permanent) with respect to $\hat{x} = \hat{0}$ (i.e. all orbits in the positive cone R_+^m ultimately are at a finite distance from $\hat{x} = \hat{0}$) [6,21,24]. A sufficient condition for dissipativity is A4 in Section 4.

Using the notation

$$\partial_j^0 \sigma_n \doteq \left. \frac{\partial \sigma_n}{\partial x_j} \right|_{\hat{x}=\hat{0}}$$

and

$$m_{1/2} \doteq \begin{cases} \frac{m}{2} & \text{if } m \text{ is even,} \\ \frac{m-1}{2} & \text{if } m \text{ is odd,} \end{cases}$$

we define the quantities

$$a_k \doteq \sum_{n=1}^m \sum_{j=1}^m p_j \partial_j^0 \sigma_n \operatorname{Re} u_k^{n-j} \quad \text{for } k = 1, 2, \dots, m_{1/2} + 1 \tag{5}$$

and assume

$$\text{A2: } a_1 \doteq \sum_{n=1}^m \sum_{j=1}^m p_j \partial_j^0 \sigma_n \neq 0.$$

THEOREM 2 ([7, Theorem 2.1]) *Assume A1 and A2 hold. A (unique) branch of equilibria of the semelparous Leslie model (1) and (2) bifurcates (transcritically) from the extinction equilibrium $\hat{x} = \hat{0}$ at $R_0 = 1$, which has the form*

$$\hat{x} = -\hat{v}a_1^{-1}\varepsilon + O(\varepsilon^2), \quad \hat{v} = \operatorname{col}(p_n)$$

for $\varepsilon \approx 0$ where

$$R_0 = 1 + \varepsilon.$$

Near the bifurcation point, the sub-branch of positive equilibria corresponds to positive $-a_1^{-1}\varepsilon \gtrless 0$. Thus, the bifurcation is to the right (i.e. $R_0 \gtrless 1$) if $a_1 < 0$. It is to the left (i.e. $R_0 \lesssim 1$) if $a_1 > 0$.

The bifurcation of positive equilibria is to the right if, at low population densities, negative effects on survival and reproduction, due to increased population density, predominate over any positive (Allee) effects as measured by $a_1 < 0$. If, on the other hand, positive feedback (Allee) effects are of sufficient strength (as measured by $a_1 > 0$), then the bifurcation is to the left.

For matrix models with primitive projection matrices, the stability of the bifurcating positive equilibria depends on the direction of bifurcation: the positive equilibria are stable if the bifurcation is to the right and unstable if it is to the left [6,9]. This is an example of the well-established exchange of stability principle for transcritical bifurcations [20]. The projection matrix of the Leslie semelparous model (1) and (2) is not primitive, however, so this principle is not applicable. In fact, it is known from studies of the $m = 2$ and 3 dimensional cases that equilibrium stability does not in general depend only on the direction of bifurcation [7,8,11]. What determines stability in these low-dimensional cases is the relative strength of within-class versus between-class competition as measured by the quantities $\partial_n^0 \sigma_n$ and $\partial_n^0 \sigma_j$, $n \neq j$, respectively.

The main result of this paper is the establishment of stability and instability criteria for the general m -dimensional case. These criteria, which appear in Theorem 3, show in what manner the within-class and between-class competition intensities $\partial_n^0 \sigma_n$ and $\partial_n^0 \sigma_j$ determine the stability of the bifurcating positive equilibria in Theorem 2.

3. Stability criteria for bifurcating positive equilibria

Our main result is in the following theorem, the proof of which is given in Appendix 1.

THEOREM 3 *Assume A1 and A2 hold. We have the following bifurcation results for the semelparous Leslie model (1) and (2) at $R_0 = 1$:*

- (a) *In the case of a right (super-critical) bifurcation (i.e. when $a_1 < 0$), the bifurcating positive equilibria in Theorem 2 are, for $R_0 \gtrsim 1$, (locally asymptotically) stable if all $a_k < 0$ for $k = 2, 3, \dots, m_{1/2} + 1$. They are unstable if $a_k > 0$ for at least one $k = 2, 3, \dots, m_{1/2} + 1$.*
- (b) *In the case of a left (sub-critical) bifurcation (i.e. when $a_1 > 0$), the bifurcating positive equilibria in Theorem 2 are, for $R_0 \lesssim 1$, unstable.*

For a left bifurcation to occur, sufficiently strong positive feedback or Allee effects are required (as represented by the derivatives $\partial_n^0 \sigma_j > 0$ appearing in a_1). We see from Theorem 3 that the bifurcating positive equilibria are always unstable in this case. In the case of a right bifurcation, however, the bifurcating positive equilibria might or might not be stable. That is to say, the direction of bifurcation does not always determine stability, as occurring in models with primitive projection matrices [6,9]. One case in which the direction of bifurcation does determine the stability is that when there is no between-class competition, since then we have $a_k = a_1$ for all k .

COROLLARY 1 *Assume A1 and A2 hold and that no between-class competition occurs. If $a_1 = \sum_{n=1}^m p_n \partial_n^0 \sigma_n < 0$, then the (super-critically) bifurcating positive equilibria in Theorem 2 are, for $R_0 \gtrsim 1$, (locally asymptotically) stable. If $a_1 > 0$, then the (sub-critically) bifurcating positive equilibria in Theorem 2 are, for $R_0 \lesssim 1$, unstable.*

A sufficient condition for the stability criteria $a_k < 0$ to hold in the case of a right (super-critical) bifurcation is that there be weak between-class (relative to within-class) competition intensity, since in that case $a_k \approx a_1 < 0$ for all k .

COROLLARY 2 *Assume A1 and A2 hold and $a_1 < 0$. If $\sum_{n=1}^m p_n \partial_n^0 \sigma_n < 0$, then the bifurcating positive equilibria in Theorem 3 are, for $R_0 \gtrsim 1$, (locally asymptotically) stable if between-class competition is sufficiently weak in the sense that $\sum_{j=1}^m \sum_{q=1}^{m-1} p_j |\partial_j^0 \sigma_{j+q}|$ is sufficiently small.*

Sufficient, but not necessary, for a right bifurcation to occur ($a_1 < 0$) is that no density-dependent feedback be positive, that is, that no partial derivative satisfy $\partial_j^0 \sigma_n > 0$. We now restrict our attention to this case, that is, we assume

$$A3: \partial_j^0 \sigma_n \leq 0 \text{ for all } 1 \leq j, n \leq m \text{ and at least one } \partial_n^0 \sigma_n < 0.$$

Note that A1 and A3 imply A2 and $a_1 < 0$ and therefore (by Theorem 2) a right bifurcation occurs. Moreover, A1 and A3 imply $\sum_{n=1}^m p_n \partial_n^0 \sigma_n < 0$ and therefore that Corollary 2 applies.

Our next goal is to provide, under assumption A3, further interpretation of the stability–instability criteria in Theorem 3(a) in terms of within-class and between-class competition intensities [8]. To analyse the stability–instability criteria in Theorem 3(a), it is convenient to

calculate subscripts mod m and write

$$a_k = \sum_{n=1}^m p_n \partial_n^0 \sigma_n + \sum_{j=1}^m \sum_{q=1}^{m-1} p_j \partial_j^0 \sigma_{j+q} \operatorname{Re} u_k^q. \tag{6}$$

We find it convenient to define the quantities

$$\rho_q \doteq \frac{\sum_{j=1}^m p_j \partial_j^0 \sigma_{j+q}}{\sum_{n=1}^m p_n \partial_n^0 \sigma_n}, \quad q = 1, 2, \dots, m - 1.$$

The denominator is a measure of within-class competition (at low population densities) as based on the derivatives $\partial_n^0 \sigma_n$. The derivative $\partial_j^0 \sigma_{j+q}$ in the numerator measures the effect that the density of the j th age class has on the survivorship of age class $j + q$ modulo m . This means that the numerator in ρ_q is a measure of the intensity of competition among these selected (but not all) unidirectional pairings of age classes. A little reflection shows that the competitive pairings among the remaining classes whose ages are q units apart appear in the numerator of ρ_{m-q} . As a result, the sum $\rho_q + \rho_{m-q}$ measures the total effect of competition among all classes that are q units apart (relative to within-class competition intensity).

We begin with two examples. First, we consider the case $m = 2$ known as Ebenman’s model [11, 18,19]. According to Theorem 3, the bifurcating positive equilibria are stable if

$$a_2 = \sum_{n=1}^2 p_n \partial_n^0 \sigma_n + \sum_{j=1}^2 p_j \partial_j^0 \sigma_{j+1} (-1) < 0$$

or equivalently

$$\rho_1 = \frac{\partial_1^0 \sigma_2 + s_1 \partial_2^0 \sigma_1}{\partial_1^0 \sigma_1 + s_1 \partial_2^0 \sigma_2} < 1.$$

The positive equilibria are unstable if this inequality is reversed. (This is the same result obtained in [7,11].) Thus, a stable (unstable) equilibrium bifurcation occurs when there is weak (strong) between-class competition in the sense that $\rho_1 < 1$ ($\rho_1 > 1$).

A similar result holds for the case $m = 3$. According to Theorem 3, the bifurcating positive equilibria are stable if

$$a_2 = \sum_{n=1}^3 p_n \partial_n^0 \sigma_n + \sum_{q=1}^2 \sum_{j=1}^3 p_j \partial_j^0 \sigma_{n+q} \left(-\frac{1}{2}\right) < 0$$

or equivalently

$$\rho_1 + \rho_2 = \frac{\partial_1^0 \sigma_2 + s_1 \partial_2^0 \sigma_3 + s_1 s_2 \partial_3^0 \sigma_1 + \partial_1^0 \sigma_3 + s_1 \partial_2^0 \sigma_1 + s_1 s_2 \partial_3^0 \sigma_2}{\partial_1^0 \sigma_1 + s_1 \partial_2^0 \sigma_2 + s_1 s_2 \partial_3^0 \sigma_3} < 2.$$

The bifurcating equilibria are unstable if this inequality is reversed. (This is the same result obtained in [10] (Theorem 4).) We again see that a stable (unstable) bifurcation occurs when there is weak (strong) between-class competition, as measured by these ratios and inequalities.

In general, from Equation (6) and the 2π -periodicity of cosine, we have

$$\begin{aligned} a_k &= \sum_{n=1}^m p_n \partial_n^0 \sigma_n + \sum_{q=1}^{m-1} \sum_{j=1}^m p_j \partial_j^0 \sigma_{j+q} \cos\left(\frac{2\pi}{m}(k-1)q\right) \\ &= \sum_{n=1}^m p_n \partial_n^0 \sigma_n + \sum_{q=1}^{m-1} \cos\left(\frac{2\pi}{m}[(k-1)q \bmod m]\right) \sum_{j=1}^m p_j \partial_j^0 \sigma_{j+q} \end{aligned}$$

for $k = 1, 2, \dots, m_{1/2} + 1$. We therefore can rewrite the stability criteria in Theorem 3(a) in terms of the competition ratios ρ_q as

$$1 + \sum_{q=1}^{m-1} \cos\left(\frac{2\pi}{m}[(k-1)q \bmod m]\right) \rho_q > 0 \quad \text{for } k = 2, \dots, m_{1/2} + 1. \tag{7}$$

The instability criteria in Theorem 3(a) mean that (at least) one of these inequalities is reversed.

Define

$$B_{k,q} \stackrel{\circ}{=} \cos\left(\frac{2\pi}{m}[(k-1)q \bmod m]\right).$$

Then,

$$B_{k,q} = B_{k,m-q}. \tag{8}$$

If m is odd, we see that

$$\begin{aligned} \sum_{q=1}^{m-1} B_{k,q} \rho_q &= \sum_{q=1}^{(m-1)/2} B_{k,q} \rho_q + \sum_{q=(m-1)/2+1}^{m-1} B_{k,q} \rho_q \\ &= \sum_{q=1}^{(m-1)/2} B_{k,q} \rho_q + \sum_{q=1}^{(m-1)/2} B_{k,m-q} \rho_{m-q} \\ &= \sum_{q=1}^{m_{1/2}} B_{k,q} (\rho_q + \rho_{m-q}) \end{aligned}$$

and the stability inequalities for odd m are

$$1 + \sum_{q=1}^{m_{1/2}} B_{k,q} (\rho_q + \rho_{m-q}) > 0, \quad k = 2, \dots, m_{1/2} + 1. \tag{9}$$

Similarly if m is even, we have

$$\begin{aligned} \sum_{q=1}^{m-1} B_{k,q} \rho_q &= \sum_{q=1}^{m/2-1} B_{k,q} \rho_q + B_{k,m/2} \rho_{m/2} + \sum_{q=m/2+1}^{m-1} B_{k,q} \rho_q \\ &= \sum_{q=1}^{m/2-1} B_{k,q} \rho_q + B_{k,m/2} \rho_{m/2} + \sum_{q=1}^{m/2-1} B_{k,m-q} \rho_{m-q} \\ &= B_{k,m/2} \rho_{m/2} + \sum_{q=1}^{m_{1/2}-1} B_{k,q} (\rho_q + \rho_{m-q}) \end{aligned}$$

and the stability inequalities for even m are

$$1 + B_{k,m_{1/2}}\rho_{m_{1/2}} + \sum_{q=1}^{m_{1/2}-1} B_{k,q}(\rho_q + \rho_{m-q}) > 0, \quad k = 2, \dots, m_{1/2} + 1. \quad (10)$$

Instability results if at least one inequality is reversed in Equations (9) and (10).

We can summarize these results with the following notation. For any matrix $P = (p_{nj})$, define $\cos(P) \doteq (\cos(p_{nj}))$. Let M be the $m_{1/2} \times m_{1/2}$ matrix whose entries are the products of the row and column indices, that is, $M = (nj)$. Note that, by the 2π -periodicity of cosine and by identity (8), we have

$$\cos\left(\frac{2\pi}{m}M\right) = \left(\cos\left(\frac{2\pi}{m}nj\right)\right) = \left(\cos\left(\frac{2\pi}{m}[nj] \bmod m\right)\right) = (B_{n+1,j}).$$

Define the $m_{1/2}$ -vectors

$$\hat{\mathbf{1}} \doteq \begin{pmatrix} 1 \\ 1 \\ \vdots \\ 1 \end{pmatrix} \in R_+^{m_{1/2}} \text{ and } \hat{\mathbf{v}} \doteq \begin{pmatrix} \rho_1 + \rho_{m-1} \\ \rho_2 + \rho_{m-2} \\ \vdots \\ \rho_{m_{1/2}} \end{pmatrix} \text{ for } m \text{ even and } \begin{pmatrix} \rho_1 + \rho_{m-1} \\ \rho_2 + \rho_{m-2} \\ \vdots \\ \rho_{m_{1/2}} + \rho_{m_{1/2}+1} \end{pmatrix} \text{ for } m \text{ odd.}$$

Rewriting Equations (9) and (10) and applying Theorem 3, we obtain the following result.

THEOREM 4 *Assume A1 and A3 hold. Then for $R_0 \gtrsim 1$, the bifurcating positive equilibria in Theorem 3 are (locally asymptotically) stable if*

$$\hat{\mathbf{1}} + \cos\left(\frac{2\pi}{m}M\right)\hat{\mathbf{v}} \in R_+^{m_{1/2}}. \quad (11)$$

The equilibria are unstable if

$$\hat{\mathbf{1}} + \cos\left(\frac{2\pi}{m}M\right)\hat{\mathbf{v}} \notin \bar{R}_+^{m_{1/2}}. \quad (12)$$

The components $\rho_q + \rho_{m-q}$ of the vector $\hat{\mathbf{v}}$ are measures of the total (relative) competition among age classes q units apart. While there are $m - 1$ ratios ρ_q , the stability and instability criteria in Theorem 4 involve only $m_{1/2}$ quantities. The $m_{1/2}$ inequalities that constitute the stability criteria (11) describe the interior of a polyhedron in the positive cone $R_+^{m_{1/2}}$ with a corner at the origin within which the vector $\hat{\mathbf{v}}$ must lie. By way of illustration, the stability criteria for dimensions 2–6 are given in Table 1.

For models with special features, the stability criteria for the bifurcating positive equilibria can often be simplified.

Example 1 Suppose $m \geq 3$ and suppose only newborns (members of the first juvenile class) affect vital rates. Moreover, suppose the between-class effects that newborns have on other age

Table 1. Criteria (11) for the stability of the bifurcating positive equilibria for $R_0 \gtrsim 1$.

m	The stability criteria (11)
2	$1 - \rho_1 > 0$
3	$1 - \frac{1}{2}(\rho_1 + \rho_2) > 0$
4	$1 - \rho_2 > 0$ $1 - (\rho_1 + \rho_3) + \rho_2 > 0$
5	$1 + \frac{\sqrt{5}-1}{4}(\rho_1 + \rho_4) - \frac{\sqrt{5}+1}{4}(\rho_2 + \rho_3) > 0$ $1 - \frac{\sqrt{5}+1}{4}(\rho_1 + \rho_4) + \frac{\sqrt{5}-1}{4}(\rho_2 + \rho_3) > 0$
6	$1 - \rho_3 + \frac{1}{2}(\rho_1 + \rho_5) - \frac{1}{2}(\rho_2 + \rho_4) > 0$ $1 + \rho_3 - \frac{1}{2}(\rho_1 + \rho_5) - \frac{1}{2}(\rho_2 + \rho_4) > 0$ $1 - \rho_3 - (\rho_1 + \rho_5) + (\rho_2 + \rho_4) > 0$

Note: The equilibria are unstable if (at least) one inequality is reversed.

classes are identical for all age classes. Then,

$$\sigma_1 = \sigma_1(x_1) \quad \text{and} \quad \sigma_n = \sigma_2(x_1) \quad \text{for } n = 2, 3, \dots, m$$

and the competition ratios are

$$\rho_q = \frac{\partial_1^0 \sigma_2}{\partial_1^0 \sigma_1} \quad \text{for all } q = 2, \dots, m - 1.$$

In this case, the criteria for stable bifurcating positive equilibria are

$$1 + \frac{\partial_1^0 \sigma_2}{\partial_1^0 \sigma_1} \sum_{q=1}^{m-1} \cos \left(\frac{2\pi}{m} [(k-1)q] \bmod m \right) > 0 \quad \text{for } k = 2, 3, \dots, m_{1/2} + 1.$$

From Equation (A4) in Appendix 2, we have

$$\sum_{q=1}^{m-1} \cos \left(\frac{2\pi}{m} [(k-1)q] \bmod m \right) + 1 = 0$$

for $k = 2, 3, \dots, m_{1/2} + 1$ and the stability criteria reduce to

$$\frac{\partial_1^0 \sigma_2}{\partial_1^0 \sigma_1} < 1.$$

The reverse inequality implies instability.

Example 2 The semelparous LPA model is the $m = 3$ dimensional semelparous Leslie model (1) and (2) with

$$\begin{aligned} \sigma_1(\hat{x}) &= 1, \\ \sigma_2(\hat{x}) &= \exp(-\beta_{23}x_3), \\ \sigma_3(\hat{x}) &= \exp(-\beta_{31}x_1 - \beta_{33}x_3) \end{aligned}$$

and $s_2 = 1$. The well-known LPA model is the basic model used in extensive experimental studies of nonlinear dynamics involving the species *Tribolium* (four beetles) [4,12]. The LPA model is

not semelparous, but in many of the key experiments, the protocol manipulated the adult death rate to nearly 100% and therefore gave the insects, in effect, a semelparous life history [3,12,16]. Therefore, one might reasonably take the semelparous LPA model as an approximate model for these experiments.

The semelparous LPA model is an example of a single-class hierarchical model in which between-class competition (possibly) occurs with the next older age class (modulo m):

$$\sigma_n(\hat{x}) = \sigma_n(x_n, x_{n+1})$$

for all $n = 1, 2, \dots, m$ (recall that subscript arithmetic is modulo m). For such models, all partial derivatives $\partial_j^0 \sigma_{j+q}$ in the stability criteria (7), and hence ρ_q vanish except when $q = m - 1$ and as a result the stability criteria reduce to

$$1 + \rho_{m-1} \cos\left(\frac{2\pi}{m}[(k-1)(m-1)] \bmod m\right) > 0 \quad \text{for } k = 2, \dots, m_{1/2} + 1$$

or

$$1 + \rho_{m-1} \cos\left(\frac{2\pi}{m}(k-1)\right) > 0 \quad \text{for } k = 2, \dots, m_{1/2} + 1.$$

These reduce further to the single inequality at $k = m_{1/2} + 1$ (where the cosine terms are most negative). We conclude that the bifurcating positive equilibria are stable for $R_0 \gtrsim 1$ if

$$\begin{aligned} 1 - \rho_{m-1} &> 0 \quad \text{for } m \text{ even,} \\ 1 + \rho_{m-1} \cos\left(\frac{m-1}{m}\pi\right) &> 0 \quad \text{for } m \text{ odd.} \end{aligned}$$

They are unstable if the inequality is reversed. In this example, the ρ_{m-1} measures the intensity of between-class competition, relative to the intensity of within-class competition.

As an example, for the semelparous LPA model ($m = 3$),

$$\rho_2 \doteq \frac{\sum_{j=1}^3 p_j \partial_j^0 \sigma_{j+2}}{\sum_{n=1}^3 p_n \partial_n^0 \sigma_n} = \frac{\partial_1^0 \sigma_3 + p_2 \partial_2^0 \sigma_1 + p_3 \partial_3^0 \sigma_2}{\partial_1^0 \sigma_1 + p_2 \partial_2^0 \sigma_2 + p_3 \partial_3^0 \sigma_3} = \frac{\beta_{31} + s_1 s_2 \beta_{23}}{s_1 s_2 \beta_{33}}$$

and the stability criterion is (recall $s_2 = 1$)

$$1 - \frac{1}{2} \frac{\beta_{31} + s_1 \beta_{23}}{s_1 \beta_{33}} > 0. \tag{13}$$

In the experimental studies of nonlinear dynamics in *Tribolium* [3,12,16], numerical estimates of the parameters were made from data and the inter-class competition parameter β_{23} was experimentally manipulated. Specifically, $\beta_{31} = 0.01731$, $\beta_{33} = 0.01310$, $s_1 = 0.8$ and β_{23} ranged from 0 to 1. For these numbers, ρ_2 ranges from 0.17414 to -37.994 and, as a result, the bifurcating positive equilibria are stable for $\beta_{23} = 0$ and unstable for $\beta_{23} = 1$. This model prediction is confirmed by the experimental outcomes reported in [3,12,16]. It is also interesting to note that for $\beta_{23} = 1$, the beetle cultures displayed synchronous oscillations in which the three life stages were non-overlapping. This is also a prediction of the semelparous LPA model [8]. The existence and stability of such synchronous cycles for general Leslie models (1) and (2) are the subject of Section 4.

The case $m = 4$ is studied in [10].

4. Synchronous cycles and the boundary of the positive cone

We see from Theorem 3 that the bifurcating positive equilibria of the semelparous Leslie map (1) and (2) assured by Theorem 2 can be either stable or unstable, even in the case of a right (super-critical) bifurcation. If the positive equilibria are unstable in the case of a right bifurcation, then for $R_0 \gtrsim 1$, both these and the extinction equilibria are unstable. In that case, a natural question to be asked is whether there is another bifurcating invariant set that is stable.

It was shown in [7] that, in addition to a branch of positive equilibria, there also bifurcates from the extinction equilibrium at $R_0 = 1$ a branch of single-class m -cycles. A single-class m -cycle of Equations (1) and (2) is a periodic cycle of period m in which exactly one class is present at each point in time:

$$\hat{x}(1) = \begin{pmatrix} x_1(1) \\ 0 \\ \vdots \\ 0 \end{pmatrix} \rightarrow \hat{x}(2) = \begin{pmatrix} 0 \\ x_2(2) \\ \vdots \\ 0 \end{pmatrix} \rightarrow \dots \rightarrow \hat{x}(m) = \begin{pmatrix} 0 \\ 0 \\ \vdots \\ x_m(m) \end{pmatrix} \rightarrow \hat{x}(1). \quad (14)$$

This is a dynamic in which the age classes are synchronized so that they never overlap.

A property of the map (1) and (2) is that it holds both the interior and the boundary ∂R_+^m of the positive cone forward invariant. With regard to the boundary, the *open* coordinate planes of all dimensions are visited sequentially, since both zero and positive entries propagate one class forward with each iteration. Each point on such an orbit has exactly k positive entries and $m - k$ zero entries for some $k \in \{1, 2, \dots, m - 1\}$. For this reason, we refer to an orbit on $\partial R_+^m \setminus \{\hat{0}\}$ as a *k-class synchronous orbit*. We refer to a periodic k -class synchronous orbit, of period p , as a *k-class p-cycle*. A single-class m -cycle is the same as a 1-class m -cycle. Note that the origin is not, by definition, a synchronous orbit or cycle.

A key to understanding the dichotomy between synchronous orbits (representing oscillations with temporally synchronized age cohorts with missing classes) and positive equilibria (representing steady-state age cohorts with all classes present) is a knowledge of the dynamics on the invariant boundary $\partial \bar{R}_+^m$. Using that information, a successful approach that has been used to establish the asymptotic dynamics on \bar{R}_+^m (and in particular whether the boundary $\partial \bar{R}_+^m$ is an attractor or a repeller) utilizes the theory of average Lyapunov functions [21,22,24].

Although it does not occur always, it is possible under some circumstances that k -class m -cycles, for $k > 1$, also bifurcate from the origin at $R_0 = 1$ [8,10]. It is often the case that one can show that the only asymptotic attractors on $\partial \bar{R}_+^m$ are synchronous cycles, at least near the bifurcation point $R_0 = 1$. This is true, for example, under monotonicity assumptions on the $\sigma_i(\hat{x})$ in dimension $m = 3$ [8] and, for hierarchical models, in dimension $m = 4$ [10]. Under this assumption, as well as the assumption

A4: In addition to A1, assume $\sigma_i(\hat{x})x_i$ is bounded for $\hat{x} \in \bar{R}_+^m$ and $i \in \{1, 2, \dots, m\}$,

we can apply [24, Theorem 4.1] to obtain criteria for $\partial \bar{R}_+^m$ to be an attractor or a repeller. A4 implies that the map (1) and (2) is dissipative in the sense that all orbits initiating in the closed cone \bar{R}_+^m enter and remain in the hypercube

$$\{\hat{x} : 0 \leq x_n \leq b\}, \quad b \triangleq \max_{i=1,2,\dots,m} \left\{ \sup_{\bar{R}_+^m} s_i \sigma_i(\hat{x}) x_i \right\}.$$

If we assume

A5: Every synchronous orbit of the semelparous Leslie model (1) and (2) approaches a synchronous cycle as $t \rightarrow +\infty$,

it follows that for every synchronous orbit we have

$$\lim_{t \rightarrow +\infty} \frac{1}{t} \sum_{j=0}^{t-1} \ln \left(R_0 \prod_{n=1}^m \sigma_n(x_1(j), x_2(j), \dots, x_m(j)) \right) = \frac{1}{p} \sum_{j=1}^p \ln \left(R_0 \prod_{n=1}^m \sigma_n(\hat{c}(j)) \right),$$

where $\hat{x}(t)$ approaches the cycle $\hat{c}(t)$ of period p . From [24, Theorem 4.1], we obtain the following result.

THEOREM 5 *Assume A3, A4 and A5 hold.*

(a) *The boundary ∂R_+^m of the positive cone is an attractor if*

$$\sum_{j=1}^p \ln \left(R_0 \prod_{n=1}^m \sigma_n(\hat{c}(j)) \right) < 0$$

for every synchronous periodic cycle $\hat{c}(j)$ on ∂R_+^m . Here p is the period of $\hat{c}(j)$.

(b) *The boundary ∂R_+^m of the positive cone is a repeller if*

$$\sum_{j=1}^p \ln \left(R_0 \prod_{n=1}^m \sigma_n(\hat{c}(j)) \right) > 0$$

for every synchronous periodic cycle $\hat{c}(j)$ on ∂R_+^m .

Since there exists a single-class m -cycle for $R_0 \gtrsim 1$, it is necessary for the fulfilment of either criterion in Theorem 5 that these inequalities hold for the single-class cycle. For $R_0 \gtrsim 1$, the single-class m -cycle $\hat{c}(t) = \text{col}(c_n(t))$ has the form (14) with entries [7]

$$c_n(n) = -\frac{P_n}{\sum_{n=1}^m P_n \partial_n^0 \sigma_n} \varepsilon + O(\varepsilon^2), \quad \varepsilon = R_0 - 1. \quad (15)$$

These expansions lead to lower order approximations of the sum appearing in the inequalities of Theorem 5 calculated for the single-class cycle:

$$\begin{aligned} \sum_{j=1}^m \ln \left(R_0 \prod_{n=1}^m \sigma_n(\hat{c}(j)) \right) &= \sum_{j=1}^m \left(1 + \sum_{n=1}^m \partial_j^0 \sigma_n \left(-\frac{P_j}{\sum_{n=1}^m P_n \partial_n^0 \sigma_n} \right) \right) \varepsilon + O(\varepsilon^2) \\ &= \left(m - \frac{\sum_{j=1}^m \sum_{n=1}^m P_j \partial_j^0 \sigma_n}{\sum_{n=1}^m P_n \partial_n^0 \sigma_n} \right) \varepsilon + O(\varepsilon^2) \\ &= \left(m - \frac{\sum_{q=0}^{m-1} \sum_{j=1}^m P_j \partial_j^0 \sigma_{j+q}}{\sum_{n=1}^m P_n \partial_n^0 \sigma_n} \right) \varepsilon + O(\varepsilon^2) \end{aligned}$$

or

$$\sum_{j=1}^m \ln \left(R_0 \prod_{n=1}^m \sigma_n(\hat{c}(j)) \right) = \left(m - 1 - \sum_{q=1}^{m-1} \rho_q \right) \varepsilon + O(\varepsilon^2). \quad (16)$$

For $R_0 \gtrsim 1$ (i.e. for $\varepsilon \gtrsim 0$), it is necessary for the attractor (repeller) criterion in Theorem 5 that the coefficient of ε be negative (positive). This condition becomes sufficient if all boundary orbits approach the single-class m -cycle.

COROLLARY 3 Assume A3 and A4 hold and that A5 holds $R_0 \gtrsim 1$. Then for $R_0 \gtrsim 1$, the boundary ∂R_+^m of the positive cone is an attractor if

$$\sum_{q=1}^{m-1} \rho_q > m - 1$$

and is a repeller if

$$\sum_{q=1}^{m-1} \rho_q < m - 1.$$

Ebenman’s juvenile–adult model, in which $m = 2$ and $\sigma_i(\hat{x})$ have the rational function (Beverton–Holt) form

$$\sigma_i(\hat{x}) = \frac{1}{1 + \sum_{n=1}^m \beta_{in} x_n}, \quad \beta_{in} \geq 0,$$

is an example to which Corollary 3 applies. This is because the one-dimensional composite map for orbits on the coordinate axes is a monotone map which has a globally attracting fixed point (corresponding to the single-class 2-cycle). More generally, this one-dimensional map is monotone, and Corollary 3 applies, under the assumption

A6: $\sigma_n(\hat{x})x_n$ is monotone increasing in the variable $x_n \geq 0$.

Under assumptions A4 and A6, the two-dimensional composite map for orbits on the boundary of the $m = 3$ dimensional cone is a monotone competitive map. The theory of monotone planar maps was applied to this case in [8] where it was found that A5 holds, namely, that all orbits on the boundary of the cone tend to one of two 3-cycles: either to the single-class 3-cycle (14) and (15) or to a 2-class 3-cycle,

$$\hat{c}(1) = \begin{pmatrix} c_1(1) \\ c_2(1) \\ 0 \end{pmatrix} \rightarrow \hat{c}(2) = \begin{pmatrix} 0 \\ c_2(2) \\ c_3(2) \end{pmatrix} \rightarrow \hat{c}(3) = \begin{pmatrix} c_1(3) \\ 0 \\ c_3(3) \end{pmatrix},$$

which exists when both $\rho_q > 1$ or when both $\rho_q < 1$ ($i = 1, 2$). For $\varepsilon = R_0 - 1 \gtrsim 0$, the 2-class 3-cycle has the form

$$\hat{c}(1) = -\frac{1}{\sum_{n=1}^3 p_n \partial_n^0 \sigma_n} \begin{pmatrix} p_1 \frac{1 - \rho_2}{1 - \rho_1 \rho_2} \\ p_2 \frac{1 - \rho_1}{1 - \rho_1 \rho_2} \\ 0 \end{pmatrix} \varepsilon + O(\varepsilon^2),$$

$$\hat{c}(2) = -\frac{1}{\sum_{n=1}^3 p_n \partial_n^0 \sigma_n} \begin{pmatrix} 0 \\ p_2 \frac{1 - \rho_2}{1 - \rho_1 \rho_2} \\ p_3 \frac{1 - \rho_1}{1 - \rho_1 \rho_2} \end{pmatrix} \varepsilon + O(\varepsilon^2),$$

$$\hat{c}(3) = -\frac{1}{\sum_{n=1}^3 p_n \partial_n^0 \sigma_n} \begin{pmatrix} p_1 \frac{1 - \rho_1}{1 - \rho_1 \rho_2} \\ 0 \\ p_3 \frac{1 - \rho_2}{1 - \rho_1 \rho_2} \end{pmatrix} \varepsilon + O(\varepsilon^2),$$

which permits the (rather tedious) calculation

$$\sum_{j=1}^3 \ln \left(R_0 \prod_{n=1}^3 \sigma_n(\hat{c}(j)) \right) = \frac{\rho_1 + \rho_2 - \rho_1^2 - \rho_2^2 + \rho_1 \rho_2 - 1}{\rho_1 \rho_2 - 1} \varepsilon + O(\varepsilon^2)$$

for the 2-class 3-cycle. The sign of this expression is, for $\varepsilon \gtrsim 0$, the sign of the coefficient of ε , whose numerator is negative. For the single-class 3-cycle, this expression is given by Equation (16):

$$\sum_{j=1}^3 \ln \left(R_0 \prod_{n=1}^3 \sigma_n(\hat{c}(j)) \right) = (2 - \rho_1 - \rho_2) \varepsilon + O(\varepsilon^2)$$

whose sign, to lowest order in $\varepsilon \gtrsim 0$, is the sign of $2 - \rho_1 - \rho_2$. Theorem 5, together with Theorem 4, leads to the following result (also see [8,11]).

THEOREM 6 *Assume A3, A4 and A6 hold. For $R_0 \gtrsim 1$, we have the following alternatives for the $m = 2$ and $m = 3$ dimensional semelparous Leslie model (1) and (2).*

If $m = 2$, the bifurcating positive equilibria are (locally asymptotically) stable and the boundary of the positive cone is a repeller if $\rho_1 < 1$. If $\rho_1 > 1$, the bifurcating positive equilibria are unstable and the boundary of the cone is an attractor.

If $m = 3$, the bifurcating positive equilibria are (locally asymptotically) stable and the boundary of the positive cone is a repeller if $\rho_1 + \rho_2 < 2$. If $\rho_1 + \rho_2 > 2$, the bifurcating positive equilibria are unstable and the boundary of the cone is an attractor.

This theorem describes a dynamic dichotomy, near the bifurcation occurring as R_0 increases through 1, between the boundary of the positive cone and a branch of positive equilibria. The two alternatives represent distinct dynamic consequences for a semelparous population modelled by Equations (1) and (2): equilibration with complete temporal overlap of all age classes or oscillations in which a number of age classes are missing in a synchronized manner. In the $m = 3$ dimensional case, the precise nature of the dynamics in the positive cone is not necessarily an approach to a periodic oscillation (e.g. the single-class 3-cycle can be unstable when the boundary of the cone is an attractor). The nature of the bifurcation in this case is that the bifurcating single-class 3-cycle and the bifurcating 2-class 3-cycle (when it exists) are embedded in a cycle chain consisting of heteroclinic boundary orbits connecting the three phases of the cycles [8]. The factor that determines which alternative holds is the strength of between-class competition relative to within-class competition as measured by the ratios ρ_q . High-intensity between-class competition destabilizes the equilibria and results in a dynamic movement towards the boundary of the positive cone, that is, in oscillations with missing age classes.

The dynamic dichotomy that occurs at bifurcation for dimensions $m = 2$ and 3 (Theorem 6) leads one to ask whether such a dichotomy occurs for higher dimensions $m \geq 4$. This remains an open question. In [10], a dynamic dichotomy was established for a special class of $m = 4$ dimensional semelparous Leslie models (1) and (2), namely, one-step hierarchical models in which between-class competition occurs from the next older class (see Example 2). As can be seen from that case, the complexity of the possible dynamics on the boundary of the positive cone greatly increases at higher dimensions. This fact, in addition to the complexity of the equilibrium stability criteria as given in Theorem 3, greatly increases the difficulty of analysing higher dimensional models.

Moreover, the numerical example shown in Figure 1 suggests that perhaps the dichotomy between the equilibria and the boundary of the cone as given in Theorem 6 does not always

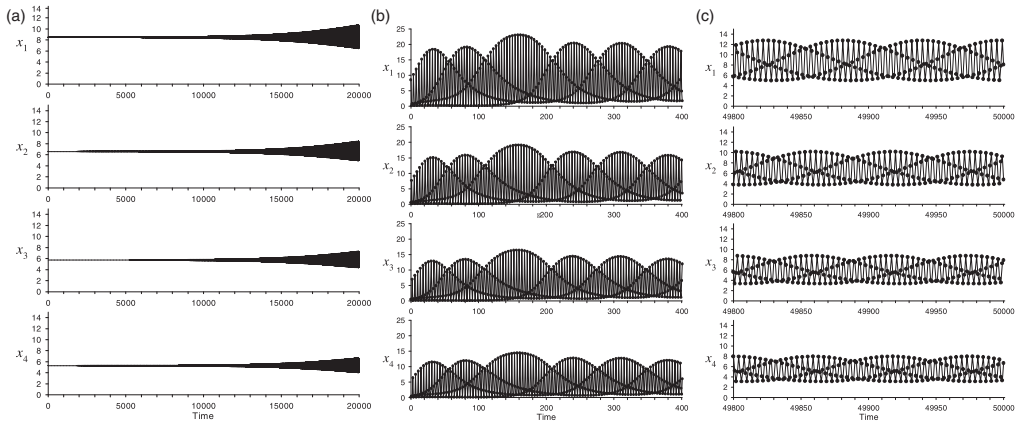


Figure 1. The components of two sample orbits plotted for the semelparous Leslie model (1) and (2) with nonlinear terms (17) and coefficients $\beta_{11} = \beta_{22} = \beta_{33} = 0.005, \beta_{44} = 0, \beta_{13} = 0.02, \beta_{12} = \beta_{23} = 0.01, \beta_{14} = \beta_{24} = \beta_{34} = 0$. The inherent parameters are $s_1 = s_2 = s_3 = 0.95$ and $s_4 = 1.6$ (which imply $R_0 = 1.3718$). (a) The orbit with initial condition $\hat{x} = \text{col}(8.5, 6.5870, 5.7393, 5.3002)$ near the equilibrium point $\text{col}(8.4804, 6.5870, 5.7393, 5.3002)$ moves away from the equilibrium. (b) The orbit with initial condition $\hat{x} = \text{col}(8.5, 0.5, 0.5, 0.5)$ near the boundary of the positive cone moves away from the boundary. (c) The oscillation approached by orbits in (a) and (b) after 50,000 time steps.

occur for dimensions $m \geq 4$. Consider the semelparous Leslie model (1) and (2) with $m = 4$ and nonlinearities

$$\sigma_n(\hat{x}) = \frac{1}{1 + \sum_{j=n}^4 \beta_{nj}x_j}, \quad n = 1, 2, 3, 4. \tag{17}$$

This is a hierarchical competition model in which competition between age classes is asymmetric. Individuals in an age class are adversely affected by competition only from individuals in older classes. For the coefficient values in the caption of Figure 1, a calculation shows that $\rho_2 = 1.2655 > 1$ and consequently the bifurcating positive equilibria are unstable for $R_0 \gtrsim 1$; see Table 1. For the numerical example shown in Figure 1, $R_0 = 1.3718$. Figure 1(a) shows a sample orbit that initiates very near the equilibrium, but which is repelled from it. Figure 1(b) shows a sample orbit that initiates near the boundary of the cone and is repelled from the boundary. Taken together, these sample orbits suggest that neither the equilibrium nor the boundary of the cone is an attractor, in contrast to the dynamic dichotomy in Theorem 6 that occurs for dimensions $m = 2$ and 3. Figure 1(c) shows the attractor of both orbits, which is an oscillation (with overlapping generations) that is suggestive of an invariant loop in phase space.

5. Concluding remarks

For the general semelparous Leslie model (1) and (2), it is known that the destabilization of the extinction equilibrium $\hat{x} = \hat{0}$ that occurs as R_0 increases through 1 results in the bifurcation of a branch of positive equilibria and a branch of single-class m -cycles [7]. For lower dimensional models ($m = 2$ and 3), it is also known that the principle of exchange of stability for transcritical bifurcations fails to hold for the semelparous models (1) and (2) [7,8]. This is due to the imprimitivity of the projection matrix. For these lower dimensional models, there is a dynamic dichotomy between the bifurcating positive equilibria and the boundary of the positive cone (on which the single-class m -cycle resides) that asserts either that the equilibria are unstable and the boundary is an attractor or the opposite [7,8]. Which of the two alternatives occurs depends on the relative intensity of between-class competition and within-class competition.

For higher dimensional models, this dichotomy is an open question. Part of this question concerns the stability or instability of the bifurcating equilibria. The main result of this paper, Theorem 3, establishes stability and instability criteria for the bifurcating positive equilibria and $R_0 \approx 1$ under general conditions and arbitrary dimension m . Left (or sub-critical) bifurcations always result in instability, as is expected. This occurs when positive feedback (Allee effects) in the dependence on survivorship and fecundity rates on population density occurs with sufficient strength. When negative density feedback predominates, the bifurcation is to the right (super-critical) and the criteria in Theorem 3 determine when the bifurcating equilibria are stable or unstable. While the number and details of these technical criteria, and hence their ecological interpretation, depend on the dimension m of the Leslie model, one general conclusion that can be drawn is that stability occurs when between-class competition is weak relative to within-class competition (Corollary 2). In the case when certain monotonicity conditions hold on the nonlinearities at least near the origin $\hat{x} = \hat{0}$, we expressed in Theorem 4 the stability and instability criteria in terms of certain ratios that directly measure the relative competition intensity between age classes of fixed distances apart compared to within-class competition intensity.

The stability/instability criteria for bifurcating equilibria established in this paper address only part of the dynamic consequences that can result when a right (super-critical) bifurcation occurs at $R_0 = 1$. If the bifurcating equilibria are unstable, a question that arises (especially since the extinction equilibrium is also unstable) is what the attractor of orbits might be. Based on the known results for $m = 2$ and 3, an attractor candidate in this case is the boundary of the positive cone (or synchronous cycles that lie on the boundary of the cone). In Section 4, we have given some criteria under which the boundary of the cone is in fact an attractor or a repeller. This question is not fully resolved for dimensions $m \geq 4$, however. While the dynamic dichotomy between the positive equilibria and the boundary of the positive cone has been established for models with specialized properties [10], the numerical example given in Section 4 suggests that perhaps the dichotomy does not hold in general.

Acknowledgements

J.M. Cushing was supported by NSF grant DMS 0917435. The authors thank an anonymous referee for valuable comments.

References

- [1] H. Behncke, *Periodical cicadas*, J. Math. Biol. 40 (2000), pp. 413–431.
- [2] M.G. Bulmer, *Periodical insects*, Am. Nat. 111(982) (1977), pp. 1099–1117.
- [3] R.F. Costantino, R.A. Desharnais, J.M. Cushing, and B. Dennis, *Chaotic dynamics in an insect population*, Science 275(January) (1997), pp. 389–391.
- [4] R.F. Costantino, R.A. Desharnais, J.M. Cushing, B. Dennis, S.M. Henson, and A.A. King, *The flour beetle Tribolium as an effective tool of discovery*, Adv. Ecol. Res. 37 (2005), pp. 101–141.
- [5] J.M. Cushing, *Periodic Kolmogorov systems*, SIAM J. Math. Anal. 13(5) (1982), pp. 811–827.
- [6] J.M. Cushing, *An Introduction to Structured Population Dynamics*, CBMS-NSF Regional Conference Series in Applied Mathematics Vol. 71, SIAM, Philadelphia, 1998.
- [7] J.M. Cushing, *Nonlinear semelparous Leslie models*, Math. Biosci. Eng. 3(1) (2006), pp. 17–36.
- [8] J.M. Cushing, *Three stage semelparous Leslie models*, J. Math. Biol. 59 (2009), pp. 75–104.
- [9] J.M. Cushing, *Matrix models and population dynamics*, in *Mathematical Biology*, M. Lewis, A.J. Chaplain, J.P. Keener, and P.K. Maini, eds., IAS/Park City Mathematics Series Vol. 14, American Mathematical Society, Providence, RI, 2009, pp. 47–150.
- [10] J.M. Cushing, *A dynamic dichotomy for a system of hierarchical difference equations*, J. Difference Equ. Appl. 18(1) (2012), pp. 1–26.
- [11] J.M. Cushing and J. Li, *On Ebenman's model for the dynamics of a population with competing juveniles and adults*, Bull. Math. Biol. 51(6) (1989), pp. 687–713.
- [12] J.M. Cushing, R.F. Costantino, B. Dennis, R.A. Desharnais, and S.M. Henson, *Chaos in Ecology: Experimental Nonlinear Dynamics*, Theoretical Ecology Series Vol. 1, Academic Press (Elsevier Science), New York, 2003.
- [13] N.V. Davydova, *Old and young: Can they coexist?* Ph.D. diss., University of Utrecht, The Netherlands, 2004.

- [14] N.V. Davydova, O. Diekmann, and S.A. van Gils, *Year class coexistence or competitive exclusion for strict biennials?* J. Math. Biol. 46 (2003), pp. 95–131.
- [15] N.V. Davydova, O. Diekmann, and S.A. van Gils, *On circulant populations. I. The algebra of semelparity*, Linear Algebra Appl. 398 (2005), pp. 185–243.
- [16] B. Dennis, R.A. Desharnais, J.M. Cushing, S.M. Henson, and R.F. Costantino, *Estimating chaos and complex dynamics in an insect population*, Ecol. Monogr. 71(2) (2001), pp. 277–303.
- [17] O. Diekmann, N.V. Davydova, and S. van Gils, *On a boom and bust year class cycle*, J. Difference Equ. Appl. 11 (2005), pp. 327–335.
- [18] B. Ebenman, *Niche difference between age classes and intraspecific competition in age-structured populations*, J. Theor. Biol. 124 (1987), pp. 25–33.
- [19] B. Ebenman, *Competition between age classes and population dynamics*, J. Theor. Biol. 131 (1988), pp. 389–400.
- [20] H. Keilhöfer, *Bifurcation Theory: An Introduction with Applications to PDEs*, Applied Mathematical Sciences Vol. 156, Springer, New York, 2004.
- [21] R. Kon, *Nonexistence of synchronous orbits and class coexistence in matrix population models*, SIAM J. Appl. Math. 66(2) (2005), pp. 616–626.
- [22] R. Kon, *Competitive exclusion between year-classes in a semelparous biennial population*, in *Mathematical Modeling of Biological Systems*, A. Deutsch, R. Bravodela Parra, R. de Boer, O. Diekmann, P. Jagers, E. Kisdi, M. Kretzschmar, P. Lansky, and H. Metz, eds., Vol. II, Birkhäuser, Boston, MA, 2008, pp. 79–90.
- [23] R. Kon, *Permanence induced by life-cycle resonances: The periodical cicada problem*, J. Biol. Dyn. 6(2) (2012), pp. 855–890.
- [24] R. Kon and Y. Iwasa, *Single-class orbits in nonlinear Leslie matrix models for semelparous populations*, J. Math. Biol. 55 (2007), pp. 781–802.
- [25] E. Mjølhus, A. Wikan, and T. Solberg, *On synchronization in semelparous populations*, J. Math. Biol. 50 (2005), pp. 1–21.
- [26] S.L. Robertson and J.M. Cushing, *A bifurcation analysis of stage-structured density dependent integrodifference equations*, J. Math. Anal. Appl. 388 (2012), pp. 490–499.
- [27] J.A.L. Silva and T.G. Hallam, *Effects of delay, truncations and density dependence in reproduction schedules on stability of nonlinear Leslie matrix models*, J. Math. Biol. 31 (1993), pp. 367–395.
- [28] A. Wikan, *Dynamic consequences of reproductive delay in Leslie matrix models with nonlinear survival probabilities*, Math. Biosci. 146 (1997), pp. 37–62.
- [29] A. Wikan and E. Mjølhus, *Overcompensatory recruitment and generation delay in discrete age-structured population models*, J. Math. Biol. 35 (1996), pp. 195–239.

Appendix 1. Proof of Theorem 3

The Jacobian of the map (1) and (2) is $J = L + M$, where

$$L = \begin{pmatrix} 0 & 0 & \cdots & 0 & R_0 p_m^{-1} \sigma_m(\hat{x}) \\ s_1 \sigma_1(\hat{x}) & 0 & \cdots & 0 & 0 \\ 0 & s_2 \sigma_2(\hat{x}) & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & s_{m-1} \sigma_{m-1}(\hat{x}) & 0 \end{pmatrix}, \tag{A1}$$

$$M = \begin{pmatrix} R_0 p_m^{-1} \partial_1 \sigma_m(\hat{x}) x_m & R_0 p_m^{-1} \partial_2 \sigma_m(\hat{x}) x_m & \cdots & R_0 p_m^{-1} \partial_m \sigma_m(\hat{x}) x_m \\ s_1 \partial_1 \sigma_1(\hat{x}) x_1 & s_1 \partial_2 \sigma_1(\hat{x}) x_1 & \cdots & s_1 \partial_m \sigma_1(\hat{x}) x_1 \\ \vdots & \vdots & & \vdots \\ s_{m-1} \partial_1 \sigma_{m-1}(\hat{x}) x_{m-1} & s_{m-1} \partial_2 \sigma_{m-1}(\hat{x}) x_{m-1} & \cdots & s_{m-1} \partial_m \sigma_{m-1}(\hat{x}) x_{m-1} \end{pmatrix} \tag{A2}$$

(note that $R_0 p_m^{-1} = s_m$). When evaluated at the positive equilibrium $\hat{x} = \hat{x}(\varepsilon)$ and $R_0 = 1 + \varepsilon$ in Theorem 2, the Jacobian $J(\varepsilon) = L(\varepsilon) + M(\varepsilon)$ is a function of ε . The eigenvalues of

$$J(0) = \begin{pmatrix} 0 & 0 & 0 & \cdots & 0 & p_m^{-1} \\ s_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & s_2 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & s_{m-1} & 0 \end{pmatrix}$$

are the roots of unity u_k (recall $p_m = \prod_{q=1}^{m-1} s_q$). To first order in ε , the m eigenvalues of $J(\varepsilon)$ are

$$\lambda_k(\varepsilon) = u_k + \lambda'_k(0)\varepsilon + O(\varepsilon^2).$$

Let $\hat{v}_k(\varepsilon)$ and $\hat{w}_k(\varepsilon)$ denote the right and left eigenvectors of $J(\varepsilon)$ associated with $\lambda_k(\varepsilon)$:

$$\begin{aligned} J(\varepsilon)\hat{v}_k(\varepsilon) &= \lambda_k(\varepsilon)\hat{v}_k(\varepsilon), \\ \hat{w}_k(\varepsilon)J(\varepsilon) &= \bar{\lambda}_k(\varepsilon)\hat{w}_k(\varepsilon). \end{aligned} \tag{A3}$$

We denote the standard inner product of two vectors $\hat{v} = \text{col}(v_n)$ and $\hat{w} = \text{row}(w_n)$ by

$$\langle \hat{w}, \hat{v} \rangle \triangleq \sum_{n=1}^m \bar{w}_n v_n,$$

where the bar in \bar{w}_n denotes complex conjugation.

LEMMA A.1 For $\varepsilon \approx 0$, we have the expansion

$$|\lambda_k(\varepsilon)| = 1 + \text{Re}(\bar{u}_k \lambda'_k(0))\varepsilon + O(\varepsilon^2).$$

Proof Note $|\lambda_k(0)| = |u_k| = 1$. Write $\lambda'_k(0) = \alpha_k + i\beta_k$. Then,

$$\begin{aligned} |\lambda_k(\varepsilon)|^2 &= \left| \cos\left(\frac{2\pi(k-1)}{m}\right) + i \sin\left(\frac{2\pi(k-1)}{m}\right) + (\alpha_k + i\beta_k)\varepsilon + O(\varepsilon^2) \right|^2 \\ &= \left[\cos\left(\frac{2\pi(k-1)}{m}\right) + \alpha_k\varepsilon + O(\varepsilon^2) \right]^2 + \left[\sin\left(\frac{2\pi(k-1)}{m}\right) + \beta_k\varepsilon + O(\varepsilon^2) \right]^2 \end{aligned}$$

and

$$\left. \frac{d|\lambda_k(\varepsilon)|}{d\varepsilon} \right|_{\varepsilon=0} = \alpha_k \cos\left(\frac{2\pi(k-1)}{m}\right) + \beta_k \sin\left(\frac{2\pi(k-1)}{m}\right).$$

From

$$\begin{aligned} \text{Re}(\bar{u}_k \lambda'_k(0)) &= \text{Re}\left(\left[\cos\left(\frac{2\pi(k-1)}{m}\right) - i \sin\left(\frac{2\pi(k-1)}{m}\right) \right] [\alpha_k + i\beta_k] \right) \\ &= \alpha_k \cos\left(\frac{2\pi(k-1)}{m}\right) + \beta_k \sin\left(\frac{2\pi(k-1)}{m}\right) \end{aligned}$$

follows

$$\left. \frac{d|\lambda_k(\varepsilon)|}{d\varepsilon} \right|_{\varepsilon=0} = \text{Re}(\bar{u}_k \lambda'_k(0)). \quad \blacksquare$$

In order to determine whether $|\lambda_k(\varepsilon)|$ is greater or less than 1 for $\varepsilon \approx 0$, we need to determine the sign of $\text{Re}(\bar{u}_k \lambda'_k(0))$. From an implicit differentiation of Equation (A3) with respect to ε , followed by an evaluation at $\varepsilon = 0$, we obtain

$$J(0)\hat{v}'_k(0) = u_k \hat{v}'_k(0) + \lambda'_k(0)\hat{v}_k(0) - J'(0)\hat{v}_k(0),$$

from which we obtain

$$\langle \hat{w}_k(0)J(0), \hat{v}'_k(0) \rangle = u_k \langle \hat{w}_k(0), \hat{v}'_k(0) \rangle + \lambda'_k(0) \langle \hat{w}_k(0), \hat{v}_k(0) \rangle - \langle \hat{w}_k(0), J'(0)\hat{v}_k(0) \rangle.$$

Since we also have

$$\langle \hat{w}_k(0)J(0), \hat{v}'_k(0) \rangle = \langle \bar{u}_k \hat{w}_k(0), \hat{v}'_k(0) \rangle = u_k \langle \hat{w}_k(0), \hat{v}'_k(0) \rangle,$$

we obtain

$$\begin{aligned} u_k \langle \hat{w}_k(0), \hat{v}'_k(0) \rangle &= u_k \langle \hat{w}_k(0), \hat{v}'_k(0) \rangle + \lambda'_k(0) \langle \hat{w}_k(0), \hat{v}_k(0) \rangle - \langle \hat{w}_k(0), J'(0)\hat{v}_k(0) \rangle, \\ 0 &= \lambda'_k(0) \langle \hat{w}_k(0), \hat{v}_k(0) \rangle - \langle \hat{w}_k(0), J'(0)\hat{v}_k(0) \rangle \end{aligned}$$

or

$$\lambda'_k(0) = \frac{\langle \hat{w}_k(0), J'(0)\hat{v}_k(0) \rangle}{\langle \hat{w}_k(0), \hat{v}_k(0) \rangle}.$$

In this formula, we need $\hat{v}_k(0)$ and $\hat{w}_k(0)$.

LEMMA A.2 *The right and left eigenvectors of $J(0)$ associated with eigenvalue u_k are*

$$\hat{v}_k(0) = \begin{pmatrix} p_1 \\ p_2 u_k^{-1} \\ p_3 u_k^{-2} \\ \vdots \\ p_m u_k^{-(m-1)} \end{pmatrix}, \quad \hat{w}_k(0) = (p_1^{-1} \quad p_2^{-1} \bar{u}_k \quad p_3^{-1} \bar{u}_k^2 \quad \cdots \quad p_m^{-1} \bar{u}_k^{m-1}).$$

Thus, $\langle \hat{w}_k(0), \hat{v}_k(0) \rangle = m$.

Proof That these are eigenvectors is straightforwardly verified by substitution into the equations

$$\begin{aligned} J(0)\hat{v}_k(0) &= u_k \hat{v}_k(0), \\ \hat{w}_k(0)J(0) &= \bar{u}_k \hat{w}_k(0) \end{aligned}$$

and recalling definition (3) of p_n . ■

The Jacobian evaluated at the equilibrium $\hat{x}(\varepsilon)$ and $R_0 = 1 + \varepsilon$ has the additive form $J(\varepsilon) = L(\varepsilon) + M(\varepsilon)$ where $L(\varepsilon)$ and $M(\varepsilon)$ are given by Equations (A1) and (A2). Therefore, from Lemma A.2, we have

$$\lambda'_k(0) = \frac{1}{m} \langle \hat{w}_k(0), L'(0)\hat{v}_k(0) \rangle + \frac{1}{m} \langle \hat{w}_k(0), M'(0)\hat{v}_k(0) \rangle.$$

LEMMA A.3 *$\langle \hat{w}_k(0), L'(0)\hat{v}_k(0) \rangle = 0$ and therefore*

$$\lambda'_k(0) = \frac{1}{m} \langle \hat{w}_k(0), M'(0)\hat{v}_k(0) \rangle.$$

Proof Recalling that $\sigma_n(\hat{0}) = 1$, the matrix $L'(0)$ is

$$\begin{pmatrix} 0 & 0 & \cdots & 0 & p_m^{-1} + p_m^{-1} \sum_{j=1}^m \partial_j^0 \sigma_m x'_j(0) \\ s_1 \sum_{j=1}^m \partial_j^0 \sigma_1 x'_j(0) & 0 & \cdots & 0 & 0 \\ 0 & s_2 \sum_{j=1}^m \partial_j^0 \sigma_2 x'_j(0) & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & s_{m-1} \sum_{j=1}^m \partial_j^0 \sigma_{m-1} x'_j(0) & 0 \end{pmatrix}$$

and, using $x'_j(0) = -a_1^{-1} p_j$, becomes

$$\begin{pmatrix} 0 & 0 & \cdots & 0 & p_m^{-1} - p_m^{-1} a_1^{-1} \sum_{j=1}^m p_j \partial_j^0 \sigma_m \\ -s_1 a_1^{-1} \sum_{j=1}^m p_j \partial_j^0 \sigma_1 & 0 & \cdots & 0 & 0 \\ 0 & -s_2 a_1^{-1} \sum_{j=1}^m p_j \partial_j^0 \sigma_2 & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & -s_{m-1} a_1^{-1} \sum_{j=1}^m p_j \partial_j^0 \sigma_{m-1} & 0 \end{pmatrix}.$$

This gives

$$L'(0)\hat{v}_k(0) = \begin{pmatrix} \left(p_m^{-1} - p_m^{-1} a_1^{-1} \sum_{j=1}^m p_j \partial_j^0 \sigma_m \right) p_m u_k^{-(m-1)} \\ \left(-s_1 a_1^{-1} \sum_{j=1}^m p_j \partial_j^0 \sigma_1 \right) p_1 \\ \left(-s_2 a_1^{-1} \sum_{j=1}^m p_j \partial_j^0 \sigma_2 \right) p_2 u_k^{-1} \\ \vdots \\ \left(-s_{m-1} a_1^{-1} \sum_{j=1}^m p_j \partial_j^0 \sigma_{m-1} \right) p_{m-1} u_k^{-(m-2)} \end{pmatrix}.$$

Recalling definition (3) of p_n , we have

$$L'(0)\hat{v}_k(0) = \begin{pmatrix} \left(1 - a_1^{-1} \sum_{j=1}^m p_j \partial_j^0 \sigma_m \right) p_1 u_k^{-(m-1)} \\ \left(-a_1^{-1} \sum_{j=1}^m p_j \partial_j^0 \sigma_1 \right) p_2 \\ \left(-a_1^{-1} \sum_{j=1}^m p_j \partial_j^0 \sigma_2 \right) p_3 u_k^{-1} \\ \vdots \\ \left(-a_1^{-1} \sum_{j=1}^m p_j \partial_j^0 \sigma_{m-1} \right) p_m u_k^{-(m-2)} \end{pmatrix}$$

and

$$\begin{aligned} \langle \hat{w}_k(0), L'(0)\hat{v}_k(0) \rangle &= p_1^{-1} \left(1 - a_1^{-1} \sum_{j=1}^m p_j \partial_j^0 \sigma_m \right) p_1 u_k^{-(m-1)} + p_2^{-1} u_k \left(-a_1^{-1} \sum_{j=1}^m p_j \partial_j^0 \sigma_1 \right) p_2 \\ &\quad + p_3^{-1} u_k^2 \left(-a_1^{-1} \sum_{j=1}^m p_j \partial_j^0 \sigma_2 \right) p_3 u_k^{-1} + \cdots + p_m^{-1} u_k^{m-1} \left(-a_1^{-1} \sum_{j=1}^m p_j \partial_j^0 \sigma_{m-1} \right) p_m u_k^{-(m-2)}. \end{aligned}$$

Note that $u_k^m = 1$ implies $u_k^{-(m-1)} = u_k$

$$\begin{aligned} \langle \hat{w}_k, L'(0)\hat{v}_k(0) \rangle &= \left(1 - a_1^{-1} \sum_{j=1}^m p_j \partial_j^0 \sigma_m \right) u_k + u_k \left(-a_1^{-1} \sum_{j=1}^m p_j \partial_j^0 \sigma_1 \right) \\ &\quad + u_k \left(-a_1^{-1} p_j \partial_j^0 \sigma_2 \right) + \cdots + u_k \left(-a_1^{-1} \sum_{j=1}^m p_j \partial_j^0 \sigma_{m-1} \right) \end{aligned}$$

and, from the definition of a_1 in A2,

$$\langle \hat{w}_k, L'(0)\hat{v}_k(0) \rangle = \left(1 - a_1^{-1} \sum_{n=1}^m \sum_{j=1}^m p_j \partial_j^0 \sigma_n \right) u_k = 0. \quad \blacksquare$$

The next lemma establishes a formula for $\lambda'_k(0)$ from the expression in Lemma A.3.

LEMMA A.4 For $\lambda'_k(0)$ in Lemma A.3, we have that

$$\langle \hat{w}_k(0), M'(0)\hat{v}_k(0) \rangle = -a_1^{-1}u_k \sum_{n=1}^m \sum_{j=1}^m p_j \partial_j \sigma_n^0 u_k^{n-j}$$

and hence

$$\lambda'_k(0) = -\frac{1}{m}a_1^{-1}u_k \sum_{n=1}^m \sum_{j=1}^m p_j \partial_j \sigma_n^0 u_k^{n-j}.$$

Proof From Equation (A2) evaluated at the equilibrium $\hat{x}(\varepsilon)$ and $R_0 = 1 + \varepsilon$, we calculate

$$M'(0) = \begin{pmatrix} p_m^{-1} \partial_1 \sigma_m^0 x'_m(0) & p_m^{-1} \partial_2 \sigma_m^0 x'_m(0) & \cdots & p_m^{-1} \partial_m \sigma_m^0 x'_m(0) \\ s_1 \partial_1 \sigma_1^0 x'_1(0) & s_1 \partial_2 \sigma_1^0 x'_1(0) & \cdots & s_1 \partial_m \sigma_1^0 x'_1(0) \\ \vdots & \vdots & \ddots & \vdots \\ s_{m-1} \partial_1 \sigma_{m-1}^0 x'_{m-1}(0) & s_{m-1} \partial_2 \sigma_{m-1}^0 x'_{m-1}(0) & \cdots & s_{m-1} \partial_m \sigma_{m-1}^0 x'_{m-1}(0) \end{pmatrix},$$

from which we can calculate

$$M'(0)\hat{v}_k(0) = \begin{pmatrix} -a_1^{-1} \sum_{j=1}^m p_j \partial_j \sigma_m^0 u_k^{-(j-1)} \\ -p_2 a_1^{-1} \sum_{j=1}^m p_j \partial_j \sigma_1^0 u_k^{-(j-1)} \\ -p_3 a_1^{-1} \sum_{j=1}^m p_j \partial_j \sigma_2^0 u_k^{-(j-1)} \\ \vdots \\ -p_m a_1^{-1} \sum_{j=1}^m p_j \partial_j \sigma_{m-1}^0 u_k^{-(j-1)} \end{pmatrix}$$

and

$$\begin{aligned} \langle \hat{w}_k(0), M'(0)\hat{v}_k(0) \rangle &= -a_1^{-1} \sum_{j=1}^m p_j \partial_j \sigma_m^0 u_k^{-(j-1)} - u_k a_1^{-1} \sum_{j=1}^m p_j \partial_j \sigma_1^0 u_k^{-(j-1)} \\ &\quad - u_k^2 a_1^{-1} \sum_{j=1}^m p_j \partial_j \sigma_2^0 u_k^{-(j-1)} - \cdots - u_k^{m-1} a_1^{-1} \sum_{j=1}^m p_j \partial_j \sigma_{m-1}^0 u_k^{-(j-1)} \\ &= -a_1^{-1} \sum_{j=1}^m p_j \partial_j \sigma_m^0 u_k^{1-j} u_k^m - a_1^{-1} \sum_{j=1}^m p_j \partial_j \sigma_1^0 u_k^{2-j} \\ &\quad - a_1^{-1} \sum_{j=1}^m p_j \partial_j \sigma_2^0 u_k^{3-j} - \cdots - a_1^{-1} \sum_{j=1}^m p_j \partial_j \sigma_{m-1}^0 u_k^{m-j}, \end{aligned}$$

which yields the formula in the lemma. ■

The following lemma establishes the proof of Theorem 3.

LEMMA A.5 Assume A1 and A2. All eigenvalues λ_k of the Jacobian evaluated at the bifurcating positive equilibria $\hat{x}(\varepsilon)$ in Theorem 2 satisfy $|\lambda_k(\varepsilon)| < 1$ for $|\varepsilon|$ small provided $a_k < 0$ for all

$$k = \begin{cases} 1, 2, \dots, \frac{m+2}{2} & \text{if } m \geq 2 \text{ is even,} \\ 1, 2, \dots, \frac{m+1}{2} & \text{if } m \geq 3 \text{ is odd.} \end{cases}$$

If $a_k > 0$ for some k , then $|\lambda_k(\varepsilon)| > 1$ for $|\varepsilon|$ small. It follows that the equilibria are unstable in the case of a left bifurcation, that is, when $a_1 > 0$.

Proof From Lemmas A.3 and A.4, we have, for each $k = 1, 2, \dots, m$, that

$$\lambda'_k(0) = -\frac{1}{m}a_1^{-1}u_k a_k,$$

and from Lemma A.1, it follows that

$$|\lambda_k(\varepsilon)| = 1 + \frac{1}{m}a_k(-a_1^{-1}\varepsilon) + O(\varepsilon^2).$$

By Theorem 2, positive equilibria correspond to $-a_1^{-1}\varepsilon \gtrsim 0$ and the assertions in the lemma follow. The index k needs to be only run over the indicated range, rather than from 2 to m , because the eigenvalues are in complex conjugate pairs of equal magnitude. ■

Appendix 2. A lemma

LEMMA A.6 For $m \geq 2$ and any integer k satisfying $1 \leq k < m$, we have that

$$\sum_{n=1}^m \cos \frac{2nk\pi}{m} = \sum_{n=1}^m \sin \frac{2nk\pi}{m} = 0.$$

Proof Treating

$$\sum_{n=1}^m e^{(2nk\pi/m)i} = \sum_{n=1}^m \cos \frac{2nk\pi}{m} + i \sum_{n=1}^m \sin \frac{2nk\pi}{m}$$

as a geometric series, we see that

$$\sum_{n=1}^m (e^{(2k\pi/m)i})^n = e^{(2k\pi/m)i} \frac{1 - (e^{(2k\pi/m)i})^m}{1 - e^{(2k\pi/m)i}} = e^{(2k\pi/m)i} \frac{1 - e^{2k\pi i}}{1 - e^{(2k\pi/m)i}} = 0,$$

from which the assertion follows. ■

Since cosine and sine are 2π -periodic, we also have

$$\sum_{q=1}^m \cos \left(\frac{2\pi}{m} [(k-1)q] \bmod m \right) = 0. \tag{A4}$$