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NONLINEAR SEMELPAROUS LESLIE MODELS

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Abstract. In this paper we consider the bifurcations that occur at the trivial equilibrium of a general class of nonlinear Leslie matrix models for the dynamics of a structured population in which only the oldest class is reproductive. Using the inherent net reproductive number n as a parameter, we show that a global branch of positive equilibria bifurcates from the trivial equilibrium at $n = 1$ despite the fact that the bifurcation is nongeneric. The bifurcation can be either supercritical or subcritical, but unlike the case of a generic transcritical bifurcation in iteroparous models, the stability of the bifurcating positive equilibria is not determined by the direction of bifurcation. In addition we show that a branch of single-class cycles also bifurcates from the trivial equilibrium at $n = 1$. In the case of two population classes, either the bifurcating equilibria or the bifurcating cycles are stable (but not both) depending on the relative strengths of the inter- and intra-class competition. Strong inter-class competition leads to stable cycles in which the two population classes are temporally separated. In the case of three or more classes the bifurcating cycles often lie on a bifurcating invariant loop whose structure is that of a cycle chain consisting of the different phases of a periodic cycle connected by heteroclinic orbits. Under certain circumstances, these bifurcating loops are attractors.

1. **Introduction.**

Since their introduction by Lewis [18] and Leslie [19, 20] matrix models have found extensive use in theoretical and applied studies of the dynamics of biological populations structured by means of physiological classes [2]. These dynamic models have the form

$$\hat{x}(t+1) = P(\hat{x}(t))\hat{x}(t) \tag{1}$$

where P is an $m \times m$ projection matrix that defines, by iteration, a sequence of class distribution vectors $\hat{x}(t) = \mathrm{col}(x_i(t)) \in R^m$, $t = 0, 1, 2, \ldots$. Lewis and Leslie were primarily interested in classifications based on chronological age, in which case

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the projection matrix takes the form (assuming age classes of equal length)

$$P(\hat{x}) = F(\hat{x}) + T(\hat{x})$$

$$F(\hat{x}) = \begin{pmatrix} f_1(\hat{x}) & f_2(\hat{x}) & \cdots & f_m(\hat{x}) \\ 0 & 0 & \cdots & 0 \\ \vdots & \vdots & & \vdots \\ 0 & 0 & \cdots & 0 \end{pmatrix}, \quad T(\hat{x}) = \begin{pmatrix} 0 & \cdots & 0 & 0 \\ \tau_1(\hat{x}) & \cdots & 0 & 0 \\ \vdots & & \vdots & \vdots \\ 0 & \cdots & \tau_{m-1}(\hat{x}) & 0 \end{pmatrix}$$

where the fertility matrix F contains the numbers f_i of newborns (per unit time) produced by an individual of age i, and the transition matrix T contains the fractions τ_i of individuals of age $i-1$ that survive to age i. As indicated by the notation, the fertility and survivorship rates can be functions of densities in any of the age classes. For example, sometimes we write $f_i(x_1, x_2, \ldots, x_m)$ in place of $f_i(\hat{x})$.

The trivial (or extinction) equilibrium $\hat{x} = \hat{0}$ is locally asymptotically stable (LAS) if all eigenvalues of the Jacobian matrix evaluated at $\hat{x} = \hat{0}$, which equals

$$P\left(\hat{0}\right) = \begin{pmatrix} f_1\left(\hat{0}\right) & \cdots & f_{m-1}\left(\hat{0}\right) & f_m\left(\hat{0}\right) \\ \tau_1\left(\hat{0}\right) & \cdots & 0 & 0 \\ \vdots & & \vdots & \vdots \\ 0 & \cdots & \tau_{m-1}\left(\hat{0}\right) & 0 \end{pmatrix},$$

are less than one in magnitude. This is true if and only if the inherent net reproductive number $n \triangleq f_1\left(\hat{0}\right) + \sum_{i=2}^{m} f_i\left(\hat{0}\right) \prod_{j=1}^{i-1} \tau_j\left(\hat{0}\right)$ is less than one [9]. If $n > 1$ then $\hat{x} = \hat{0}$ is unstable. Under quite general conditions, a branch B of nontrivial equilibria bifurcates from $\hat{x} = \hat{0}$ at $n = 1$. This branch contains a subbranch P of positive equilibrium that bifurcates from $\hat{x} = \hat{0}$ at $n = 1$. The branch B exhibits a typical exchange of stability with the trivial equilibrium $\hat{x} = \hat{0}$. It bifurcates supercritically (i.e., the positive equilibria from P near the bifurcation point correspond to $n > 1$) if density effects are deleterious. It bifurcates subcritically (i.e., the positive equilibria from P near the bifurcation point correspond to $n < 1$) if Allee effects are in play. See [4] for the details of a general bifurcation theory for population matrix models.

If $f_i = 0$ for $i = 1, 2, \ldots, m-1$, we have what might be considered a general model of a semelparous population (in which a mature individual reproduces only once, after which it dies). Such models fall outside the purview of the general bifurcation theorem described above. The reason for this is that as n increases through 1 all of the eigenvalues of the Jacobian $P\left(\hat{0}\right)$ simultaneously leave the complex unit circle (at the mth roots of unity). This is a nongeneric situation in bifurcation theory, and these models need special consideration.

We consider a nonlinear Leslie matrix model of the form

$$\hat{x}(t+1) = P(\hat{x})\hat{x}(t) \tag{2}$$

$$P(\hat{x}) = \begin{pmatrix} 0 & \cdots & 0 & bf(\hat{x}) \\ (1-\mu_1)\, g_1(\hat{x}) & \cdots & 0 & 0 \\ \vdots & & \vdots & \vdots \\ 0 & \cdots & (1-\mu_{m-1})\, g_{m-1}(\hat{x}) & 0 \end{pmatrix}.$$

Here we have normalized f and g_i so that $f\left(\hat{0}\right) = g_i\left(\hat{0}\right) = 1$ and the inherent net reproductive number is $n = b\prod_{i=1}^{m-1}(1-\mu_i)$.Thus, $P(\hat{x}) = n\Phi(\hat{x}) + T(\hat{x})$ where

$F(\hat{x}) = n\Phi(\hat{x})$ and

$$\Phi(\hat{x}) \triangleq \begin{pmatrix} 0 & \cdots & 0 & \frac{1}{\prod_{i=1}^{m-1}(1-\mu_i)} f(\hat{x}) \\ 0 & \cdots & 0 & 0 \\ \vdots & & \vdots & \vdots \\ 0 & \cdots & 0 & 0 \end{pmatrix}$$

$$T(\hat{x}) = \begin{pmatrix} 0 & \cdots & 0 & 0 \\ (1-\mu_1)\, g_1(\hat{x}) & \cdots & 0 & 0 \\ \vdots & & \vdots & \vdots \\ 0 & \cdots & (1-\mu_{m-1})\, g_{m-1}(\hat{x}) & 0 \end{pmatrix}.$$

Let $R_+^m = \{\hat{x} = \mathrm{col}(x_i) \in R^m : x_i \geq 0\}$ denote the nonnegative cone in R^m and $\mathring{R}_+^m$ denote the positive cone in R^m (the interior of R_+^m):

A1: Assume $b > 0, \quad 0 \leq \mu_i < 1, \quad m \geq 2$ and that for an open neighborhood Ω of $\hat{0} \in R^m$ there is a positive integer s such that $g_i, f \in C^s\left(\Omega \to R^1\right)$. Assume $g_i(\hat{0}) = f(\hat{0}) = 1$ and that $g_i\left(\Omega \cap R_+^m\right)$ and $f\left(\Omega \cap R_+^m\right) \subset R_+^1 \backslash \{\hat{0}\}$.

In section 2 we prove that a global branch of positive equilibria bifurcates from the trivial equilibrium $\hat{x} = \hat{0}$ at $n = 1$. In addition, we prove in section 3 that a branch of periodic cycles of period m (m-cycles) also bifurcates from the trivial solution at $n = 1$. The stability of the positive equilibria on the bifurcating branch is not necessarily determined by the direction of bifurcation (as it is for models that have a generic transcritical bifurcation at $n = 1$ [4]). We give some stability results in section 4.

2. **Equilibria.**

The equations for an equilibrium solution $\hat{x} = \mathrm{col}\,(x_i) \in R^m$ of the nonlinear Leslie model (2), when written in component form, are

$$x_1 = n\frac{1}{\prod_{i=1}^{m-1}(1-\mu_i)} f\,(\hat{x})\, x_m, \quad x_{i+1} = (1-\mu_i)\, g_i\,(\hat{x})\, x_i, \quad i = 1, \ldots, m-1. \tag{3}$$

We refer to an equilibrium lying in $R^m \backslash \{\hat{0}\}$ as a nontrivial equilibrium. The following lemma is obvious from A1 and equations (3).

LEMMA 2.1. *Assume A1. If $\hat{x}$ is a nontrivial equilibrium of (2) then $x_i \neq 0$ for all $i = 1, 2, \ldots, m$. Also, if $\hat{x} \in R_+^m$ is a nontrivial equilibrium of (2), then $\hat{x} \in \mathring{R}_+^m$.*

If $\hat{x} \in R^m \backslash \{\hat{0}\}$ is a nontrivial equilibrium, then by multiplying the equilibrium equations together and canceling the common factor of $\Pi_{i=1}^m x_i$ (which is nonzero by Lemma 2.1), we obtain the following result.

LEMMA 2.2. *Assume A1. If $\hat{x}$ is a nontrivial equilibrium of (2), then*

$$nf\,(\hat{x}) \prod\nolimits_{i=1}^{m-1} g_i\,(\hat{x}) = 1.$$

The biological interpretation of this lemma is that if a population is at a nonnegative nontrivial (hence positive) equilibrium, then the net reproductive number (not to be confused with the inherent net reproductive number n) equals one; that is, when the population is at equilibrium, a newborn exactly replaces itself over the course of its lifetime.

Denote differentiation with respect to x_i by ∂_i and denote differentiation followed by evaluation at $\hat{x} = \hat{0}$ by ∂_i^0. We make the following assumption:

$$\text{A2:}\quad 0 \neq d \triangleq \partial_1^0 f + \sum_{i=2}^{m} \partial_i^0 f \prod_{j=1}^{i-1} (1-\mu_j) + \sum_{k=1}^{m-1} \left(\partial_1^0 g_k + \sum_{i=2}^{m} \partial_i g_k^0 \prod_{j=1}^{i-1} (1-\mu_j) \right).$$

A density regulation effect in the fecundity term f, or a survivorship term g_k, means that the term is decreasing in a variable x_i; that is $\partial_i^0 f < 0$ or $\partial_i g_k^0 < 0$. The opposite inequality (e.g., $\partial_i^0 f > 0$ or $\partial_i g_k^0 > 0$) means there is an Allee effect in the term (with respect to x_i). Thus, $d < 0$ reflects the case when density regulation effects predominate at low population densities, while $d > 0$ means that Allee effects predominate at low densities. A strong case of density regulation at low densities occurs when all inequalities $\partial_i^0 f \leq 0$, $\partial_i^0 g_k \leq 0$ hold, with at least one inequality being strict. To the contrary, a strong Allee effect occurs at low densities if all the inequalities $\partial_i^0 f \geq 0$, $\partial_i^0 g_k \geq 0$ hold, with at least one inequality being strict. Mixed cases can obviously occur, in which there is a regulation effect with respect to the density in one class and an Allee effect with respect to the density in another class.

We could prove the following theorem by using the general parameterization Theorem 1.2.5 in [4]. However, it is just as easy to give a straightforward proof that has the advantage of establishing the existence of positive equilibria as a function of the inherent net reproductive n.

THEOREM 2.1. *Assume A1 and A2 hold for the nonlinear, semelparous Leslie model (2). There exists a (locally unique) branch of nontrivial equilibria that (transcritically) bifurcates from the trivial solution at $n = 1$. The equilibria are C^s functions of n in an open neighborhood of $n = 1$. For $s \geq 2$ in A1, the equilibria have the form*

$$x_1 = -\frac{1}{d}(n-1) + O\left(|n-1|^2\right), \quad x_i = \left(-\frac{1}{d} \prod_{j=1}^{i-1} (1-\mu_j) \right)(n-1) + O\left(|n-1|^2\right)$$

for $|n-1|$ small.

Note that when $d < 0$ the bifurcation is *supercritical* in the sense that the positive equilibria exist near bifurcation for $n > 1$. This case occurs in the most common modeling situation when density effects are deleterious, that is, when all partial derivatives $\partial_i^0 f$ and $\partial_i g_k^0$ are nonpositive and at least one is negative. When $d > 0$ the bifurcation is *subcritical*, which means the positive equilibria exist near bifurcation for $n < 1$. This case requires some of the partial derivatives to be positive, which means some density effects are advantageous (as in Allee effects).

Proof. By Lemmas 2.1 and 2.2, the equilibrium equations (3) are equivalent to the equations

$$n f(\hat{x}) \textstyle\prod_{i=1}^{m-1} g_i(\hat{x}) - 1 = 0 \tag{4}$$

$$x_{i+1} - (1-\mu_i)\, g_i(\hat{x})\, x_i = 0, \quad i = 1, \ldots, m-1. \tag{5}$$

The Jacobian of the left-hand sides of the $m-1$ equations (5) with respect to $x_2, \ldots, x_m$, when evaluated at $\hat{x} = \hat{0}$, equals the nonsingular (triangular) matrix

$$\begin{pmatrix} -1 & 0 & \cdots & 0 & 0 \\ 1-\mu_2 & -1 & \cdots & 0 & 0 \\ 0 & 1-\mu_3 & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & 1-\mu_{m-1} & -1 \end{pmatrix}.$$

By the implicit function theorem, we can (uniquely) solve equations (5) for $x_2, \ldots, x_m$ in terms of x_1. We obtain solutions $x_i = x_i(x_1)$ of equations (5), for $i = 2, \ldots, m$, that satisfy

$$x_i \in C^s\left((-\varepsilon, \varepsilon) \to R^1\right), \ x_i(0) = 0$$

for some $\varepsilon > 0$.

A substitution of $x_i = x_i(x_1)$ into equations (5), followed by an implicit differentiation with respect to x_1 and an evaluation at $x_1 = 0$, yields

$$\partial_1 x_i(0) = \textstyle\prod_{j=1}^{i-1}(1-\mu_j) > 0, \quad i = 2, 3, \ldots, m.$$

Thus (for ε smaller if necessary) each function $x_i(x_1)$ is increasing on the interval $(-\varepsilon, \varepsilon)$.

The remaining equilibrium equation (4) reduces to the equation

$$k(n, x_1) = 0$$

to be solved for $x_1 = x_1(n)$, $x_1(1) = 0$, where

$$k(n, x_1) \triangleq nf(x_1, x_2(x_1), \ldots, x_m(x_1)) \textstyle\prod_{i=1}^{m-1} g_i(x_1, x_2(x_1), \ldots, x_m(x_1)) - 1.$$

By A1 we have $k(1, 0) = 0$, and by A2 we have that $\partial_1 k$, evaluated at $n = 1$ and $x_1 = 0$, equals $d \neq 0$. The implicit function theorem implies the (locally unique) existence of a C^s solution $x_1 = x_1(n)$ satisfying $x_1(1) = 0$.

An implicit differentiation of $k(n, x_1(n)) = 0$ with respect to n (followed by an evaluation at $n = 1$) shows that

$$\left.\frac{dx_1}{dn}\right|_{n=1} = -\frac{1}{d}.$$

A substitution of the solutions

$$x_1 = x_1(n), \quad x_i = x_i(x_1(n)), \quad i = 2, 3, \ldots m$$

into equations (5), followed by an implicit differentiation and evaluation at $n = 1$, shows that

$$\left.\frac{dx_i}{dn}\right|_{n=1} = -\frac{1}{d}\prod_{j=1}^{i-1}(1-\mu_j).$$

□

The next theorem establishes the global existence of the bifurcating equilibrium branch established by Theorem 2.1. The theorem is analogous to Theorem 1.2.7 in [4], which, however, does not apply to the nonlinear Leslie model (2), because the projection matrix P is not primitive.

Theorem 2.2. *Consider the nonlinear, semelparous Leslie model (2). Assume A1 holds with $s = 1$ and an open set Ω that contains R_+^m. There exists a continuum $\mathbb{C}$ of pairs $(n, \hat{x}) \in R_+^1 \times R_+^m$ which has the following properties:*

a. $\hat{x}$ is a nontrivial equilibrium of (2) corresponding to n.

b. The closure of $\mathbb{C}$ *contains the bifurcation point* $(n,\hat{x}) = \left(1,\hat{0}\right)$.
c. $\mathbb{C}$ *is unbounded and* $n > 0$ *for all pairs* $(n,\hat{x}) \in \mathbb{C}$.

Proof. We can write the equilibrium equations of (2) as

$$\hat{x} = nL\hat{x} + \hat{h}(n,\hat{x})$$

where $L = \left(I - T(\hat{0})\right)^{-1}\Phi(\hat{0})$ or

$$L = \begin{pmatrix} 0 & 0 & \cdots & 0 & \frac{1}{\prod_{i=1}^{m-1}(1-\mu_i)} \\ 0 & 0 & \cdots & 0 & \frac{1}{\prod_{i=1}^{m-2}(1-\mu_i)} \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & 0 & 1 \end{pmatrix}$$

and $\hat{h} \in C^2\left(R_+^1 \times \Omega \to R^m\right)$ is higher order near the origin; that is, $|\hat{h}(n,\hat{x})| = o(|\hat{x}|)$ near $\hat{x} = \hat{0}$ uniformly on finite intervals for n. Characteristic values are reciprocals of nonzero eigenvalues. The only characteristic value of L is 1, and it is algebraically simple. It follows that there exists a continuum $\mathbb{C}$ of pairs $(n,\hat{x}) \in R \times R^m$ that has properties a and b in Theorem 2.2 and that connects to the boundary of $R\times\Omega$ (Theorem 1.40 in [23] or Theorem B.1.1 in [4]). In this conclusion ∞ is considered part of the boundary of $R \times \Omega$, and stating that $\mathbb{C}$ connects to ∞ means $\mathbb{C}$ is unbounded in $R \times \Omega$. (There also exists a continuum of nonpositive equilibrium in which we have no interest.)

To finish the proof, we need to show that $\mathbb{C} \subset R_+^1 \times R_+^m$. Near the bifurcation point, the continuum $\mathbb{C}$ coincides with the branch of equilibria in Theorem 2.1. Therefore, near the bifurcation point the equilibria from $\mathbb{C}$ are positive. There can be no pair $(n,\hat{x}) \in \mathbb{C}$ for which the nontrivial equilibrium $\hat{x}^*$ lies on the boundary of the nonnegative cone R_+^m, because the existence of such a pair would contradict Lemma 2.1. Moreover, $n > 0$ for all pairs $(n,\hat{x}) \in \mathbb{C}$ since equilibrium equation (4) shows there can be no nontrivial equilibrium when $n = 0$.

Since Ω contains R_+^m, the set inclusion $\mathbb{C} \subset R_+^1 \times R_+^m$ implies that $\mathbb{C}$ connects to ∞. □

$\mathbb{C}$ is unbounded and $n > 0$ for all pairs $(n,\hat{x}) \in \mathbb{C}$ means that either the range of positive equilibria is unbounded, that is

$$\Lambda \triangleq \{|\hat{x}| : (n,\hat{x}) \in \mathbb{C}\} \subset R_+^1$$

is unbounded, or the spectrum

$$S \triangleq \{n : (n,\hat{x}) \in \mathbb{C}\} \subset R_+^1$$

is unbounded. The interval S contains the bifurcation value 1 in its closure and Λ contains 0 in its closure. If S is unbounded, then we know that the nonlinear Leslie model (2) has at least one positive equilibrium for all values of $n > 1$. (Positive equilibria might also exist for values of $n < 1$. For example, this is true if $d > 0$ in Theorem 2.1.)

We can sometimes deduce properties of the intervals Λ and S from equation (4). For example, suppose in A1 that $R_+^m \subset \Omega$ and

$$g_i,\ f : R_+^m \to (0,1]. \tag{6}$$

From (4) we see that $n \in S$ implies $n > 1$. Suppose in addition that the condition

$$\lim_{|\hat{x}|\to+\infty} f(\hat{x})\prod_{i=1}^{m-1} g_i(\hat{x}) = 0 \tag{7}$$

holds (as is usually the case in specific models). Then if S were bounded, Λ would have to be unbounded and this limit condition together with (4) would lead to a contradiction. Thus, the two conditions (6) and (7) on f and g_i imply S is unbounded and hence $S = (1, +\infty)$. This means that under these conditions there will exist at least one positive equilibrium of (2) for every $n > 1$.

3. **Single-Class Cycles.** Theorems 2.1 and 2.2 tell us that despite the degeneracy of the bifurcation that occurs at $n = 1$, it is still true that a positive branch of equilibria bifurcates from the trivial equilibrium. This degeneracy suggests, however, the possibility that other kinds of invariant sets might also bifurcate from $\hat{x} = \hat{0}$ at $n = 1$. In this section we show that a branch of cycles also bifurcates from $\hat{x} = \hat{0}$ at $n = 1$.

A vector $\hat{x} \in R_+^m$ in which all components, save one, equal 0 represents a class distribution in which individuals are present in one and only one class. According to the model equations (2), a single-class vector is mapped to a single-class vector, and therefore a single-class initial vector $\hat{x}_0$ produces a *single-class orbit.* This is to say that the nonnegative coordinate axes are invariant (and are in fact visited sequentially by a single-class orbit). Thus, the $m-1$ fold composite of the map defined by (2) is a one dimensional map of each nonnegative coordinate axis into itself.

For example, the orbit emanating from an initial distribution with only newborns has the form

$$\operatorname{col}(\alpha_1, 0, \ldots, 0) \to \operatorname{col}(0, \alpha_2(\alpha_1), \ldots, 0) \to \cdots \to \operatorname{col}(0, 0, \ldots, \alpha_m(\alpha_1)) \to \cdots \quad (8)$$

where the $\alpha_i(x)$ are defined recursively as follows:

$$\alpha_i(x) \triangleq \left(\prod_{j=1}^{i-1} (1 - \mu_j)\, \bar{g}_j(x) \right) x, \quad i = 2, \ldots, m$$

with

$$\bar{g}_1(x) \triangleq g_1(x, 0, \ldots, 0)$$
$$\bar{g}_i(x) \triangleq g_i(0, \ldots, \alpha_i(x), \ldots 0) \prod_{j=1}^{i-1} \bar{g}_j(x), \quad i = 2, \ldots, m.$$

(In the expression $g_i(0, \ldots, \alpha_i(x), \ldots 0)$, the term $\alpha_i(x)$ occupies the ith position in the argument list for g_i.) Note that

$$\alpha_i(0) = 0, \quad \bar{g}_i(0) = 1, \quad \partial^0_{\alpha_1} \alpha_i = \prod_{j=1}^{i-1} (1 - \mu_j)$$

After m steps

$$\operatorname{col}(\alpha_1, 0, \ldots, 0) \to \operatorname{col}(bf(0, \ldots 0, \alpha_m(\alpha_1))\, \alpha_m(\alpha_1), 0, \ldots, 0),$$

and we see that the dynamics on the coordinate axis are described by the one dimensional map $x_{t+1} = bf(0, \ldots, \alpha_m(x_t))\, \alpha_m(x_t)$ or

$$x_{t+1} = nF(x_t)\, x_t, \quad F(x) \triangleq f(0, \ldots, 0, \alpha_m(x)) \prod_{j=1}^{m-1} \bar{g}_j(x). \quad (9)$$

From A1 follow $F \in C^s(\Omega \to R^1)$, $F(\Omega \cap R_+^1) \subset R_+^1 \backslash \{\hat{0}\}$, $F(0) = 1$. An equilibrium $x = \alpha_1$ of the map (9) corresponds to a single-class m-cycle (consisting of the vectors (8)) of the nonlinear Leslie model (2).

We can apply to the map (9) the same analytic methods we used to study the bifurcation of equilibria of the matrix model (2). This application results in local and global bifurcation results analogous to those in Theorems 2.1 and 2.2.

Theorem 3.1. *Consider the nonlinear Leslie model (2).*

i. Assume A1 holds with $s = 1$ *and an open set* Ω *that contains* R_+^m*. There exists a continuum of nonnegative single-class m-cycles (2) that bifurcates from the trivial equilibrium at* $n = 1$*. More specifically, there exists a continuum of pairs* $(n, \alpha_1) \in R_+^1 \times R_+^1$ *that has the following properties:*

a. The single-class vector $col(\alpha_1, 0, \ldots, 0)$ *yields a single-class m-cycle (8) of (2) corresponding to* n*.*

b. The closure of the continuum contains the bifurcation point $(n, \alpha_1) = (1, 0)$*.*

c. The continuum is unbounded and $n > 0$ *for all pairs* (n, α_1) *on the continuum.*

ii. Assume A1 with $s = 2$ *and A2 hold. If* $\partial_x^0 F \neq 0$*, then the single-class m-cycles near the bifurcation point have the form (8) with*

$$\alpha_1(n) = -\frac{1}{\partial_x^0 F}(n-1) + O\left(|n-1|^2\right)$$

$$\alpha_i(n) = -\frac{\prod_{j=1}^{i-1}(1-\mu_j)}{\partial_x^0 F}(n-1) + O\left(|n-1|^2\right)$$

for $|n-1|$ *small.*

The direction of bifurcation of the bifurcating nonnegative m-cycles (that is, whether they exist for $n > 1$ or $n < 1$) depends on the sign of $\partial_x^0 F$. A calculation shows for $m > 2$ that

$$\partial_x^0 F = \partial_m^0 f \prod_{i=1}^{m-1}(1-\mu_i) + (m-1)\partial_1^0 g_1 + \sum_{j=2}^{m-1}(m-j)\partial_j^0 g_j \prod_{i=1}^{j-1}(1-\mu_i)$$

and for $m = 2$ that

$$\partial_x^0 F = (1-\mu_1)\,\partial_2^0 f + \partial_1^0 g_1.$$

Because of the degeneracy of the bifurcation at the trivial equilibrium, invariant sets other than the positive equilibria and the nonnegative single-class m-cycles described in Theorems 2.1, 2.2, and 3.1 might also bifurcate at $n = 1$. For example, in some cases the m-cycles might be embedded in a bifurcating invariant loop. We consider examples of these possibilities in the next section.

For an extensive study of single-class cycles and semelparity in Leslie matrix models with certain types of nonlinearities, see [11, 12, 13].

4. **Some Stability Results.** The Jacobian of the nonlinear Leslie model (2) evaluated at the trivial equilibrium $\hat{x} = \hat{0}$ is

$$\begin{pmatrix} 0 & \cdots & 0 & b \\ 1-\mu_1 & \cdots & 0 & 0 \\ \vdots & & \vdots & \vdots \\ 0 & \cdots & 1-\mu_{m-1} & 0 \end{pmatrix}.$$

The dominant eigenvalue of this nonnegative, irreducible matrix (called the inherent growth rate and often denote by R_0 or r in the literature) is less than one if $n < 1$ and greater than one if $n > 1$ [4, 9]. It follows by the linearization principle [14] that the trivial equilibrium loses stability at the bifurcation point $n = 1$; that is, $\hat{x} = \hat{0}$ is locally asymptotically stable (LAS) for $n < 1$ and is unstable for $n > 1$. In fact it follows from Theorem 3 in [16] that the model (2) is uniformly persistent (permanent) with respect to the origin for $n > 1$. This means all orbits in the nonnegative cone (with the exception of the trivial equilibrium) are asymptotically bounded away from the origin by a positive constant.

For a generic transcritical bifurcation of equilibria, such as occurs at $n = 1$ (Theorem 2.1), an exchange of stability occurs between the intersecting branches. For example, typically the positive equilibria that supercritically bifurcate at $n = 1$ would obtain the stability lost by the trivial equilibrium. We will see, however, that this is not always the case for the nongeneric bifurcation that occurs at $n = 1$ for the model (2).

In this section we take a closer look at the nonlinear Leslie model (2) with $m = 2$ and 3 and obtain some results concerning the stability of the positive equilibria. Equation (2) with $m = 2$ is a model that describes the dynamics of a population that consists of an immature, nonreproductive stage whose duration equals that of the reproductively mature stage. In this case we will give a complete account of the bifurcations and their stabilities near $n = 1$. The case $m = 3$ describes the dynamics of a population with an immature stage whose duration is twice as long as that of the mature stage. We will consider a restricted case of (2) with $m = 3$ and find that the bifurcation possibilities at $n = 1$ have complexities not present in the $m = 2$ case.

With $m = 2$ the nonlinear Leslie model (2) is

$$\begin{pmatrix} x_1(t+1) \\ x_2(t+1) \end{pmatrix} = \begin{pmatrix} 0 & \frac{n}{1-\mu} f(x_1(t), x_2(t)) \\ (1-\mu)\, g(x_1(t), x_2(t)) & 0 \end{pmatrix} \begin{pmatrix} x_1(t) \\ x_2(t) \end{pmatrix}. \tag{10}$$

Here we have dropped unnecessary subscripts from μ and g and have let $b = n/(1-\mu)$. From Theorem 2.1 the bifurcating equilibria have the expansions

$$x_1(\varepsilon) = -\frac{1}{\delta_1 + \delta_2}\varepsilon + O\left(\varepsilon^2\right), \quad x_2(\varepsilon) = -\frac{1-\mu}{\delta_1 + \delta_2}\varepsilon + O\left(\varepsilon^2\right), \quad n = 1 + \varepsilon$$

where we have additively decomposed $d = \delta_1 + \delta_2 \neq 0$ with $\delta_1 \triangleq (1-\mu)\,\partial_2^0 f + \partial_1^0 g$ and $\delta_2 \triangleq (1-\mu)\,\partial_2^0 g + \partial_1^0 f$. Substituting these expansions into the Jacobian

$$J(x_1, x_2) = \begin{pmatrix} \frac{n}{1-\mu} x_2 \partial_1 f & \frac{n}{1-\mu}\left(x_2 \partial_2 f + f\right) \\ (1-\mu)\left(x_1 \partial_1 g + g\right) & (1-\mu)\, x_1 \partial_2 g \end{pmatrix},$$

we obtain $J(x_1(\varepsilon), x_2(\varepsilon)) = J_0 + J_1 \varepsilon + O\left(\varepsilon^2\right)$ where

$$J_0 = \begin{pmatrix} 0 & \frac{1}{1-\mu} \\ 1-\mu & 0 \end{pmatrix}$$

$$J_1 = \begin{pmatrix} -\frac{1}{\delta_1+\delta_2}\partial_1^0 f & \frac{1 - \frac{1}{\delta_1+\delta_2}\left(\partial_1^0 f + 2(1-\mu)\partial_2^0 f\right)}{1-\mu} \\ -\frac{(1-\mu)\left(2\partial_1^0 g + (1-\mu)\partial_2^0 g\right)}{\delta_1+\delta_2} & -\frac{(1-\mu)\partial_2^0 g}{\delta_1+\delta_2} \end{pmatrix}.$$

The eigenvalues of the Jacobian $J(x_1(\varepsilon), x_2(\varepsilon))$ have the expansions

$$\lambda_1 = 1 - \frac{1}{2}\varepsilon + O\left(\varepsilon^2\right), \quad \lambda_2 = -1 + \frac{1}{2}\frac{\delta_1 - \delta_2}{\delta_1 + \delta_2}\varepsilon + O\left(\varepsilon^2\right).$$

The equilibria lying on the bifurcating branch are LAS near the bifurcation point $n = 1$ if both $|\lambda_i| < 1$ for $|\varepsilon|$ small; they are unstable if either $|\lambda_1| > 1$ or $|\lambda_2| > 1$ or both.

Before summarizing the stability possibilities for the bifurcating equilibrium branch, we consider the stability of the bifurcating single-class 2-cycles given by Theorem 3.1. Under the assumption $\delta_1 \neq 0$, the single-class 2-cycles that bifurcate at $n = 1$ have the form

$$\begin{pmatrix} \alpha_1(\varepsilon) \\ 0 \end{pmatrix} \to \begin{pmatrix} 0 \\ \alpha_2(\varepsilon) \end{pmatrix}$$

$$\alpha_1(\varepsilon) = -\frac{1}{\delta_1}\varepsilon + O\left(\varepsilon^2\right), \quad \alpha_2(\varepsilon) = -\frac{1-\mu}{\delta_1}\varepsilon + O\left(\varepsilon^2\right), \quad n = 1+\varepsilon.$$

The stability of these cycles can be determined by eigenvalues of the Jacobian of the composite map. This Jacobian is the product $J\left(\alpha_1(\varepsilon), 0\right) J\left(0, \alpha_2(\varepsilon)\right)$, which turns out to be a lower triangular matrix. The eigenvalues (diagonal terms) μ_1 and μ_2 of this matrix have expansions

$$\mu_1 = 1 + \frac{\delta_1 - \delta_2}{\delta_1}\varepsilon + O(\varepsilon^2), \quad \mu_2 = 1 - \varepsilon + O(\varepsilon^2).$$

The single-class 2-cycles lying on the bifurcating branch are LAS near the bifurcation point $n = 1$ if both $|\mu_i| < 1$ for $|\varepsilon|$ small; they are unstable if either $|\mu_1| > 1$ or $|\mu_2| > 1$ or both.

We are interested in the existence and stability of nonnegative equilibria and cycles. We say the branch of equilibria (or 2-cycles) bifurcates *supercritically* at $n = 1$ if the equilibria (or 2-cycles) are nonnegative for $n > 1$ and near 1. The branch bifurcates *subcritically* at $n = 1$ if the equilibria (or 2-cycles) are nonnegative for $n < 1$ and near 1. We say the bifurcating branch is *stable* (or *unstable*) if the nonnegative equilibria (or 2-cycles) lying on it are LAS (or unstable) for n near 1.

The following theorem summarizes these findings. It is a generalization of the results in [7].

THEOREM 4.1. *Consider the nonlinear Leslie model (10) and assume A1 with* $s = 2$ *and A2 hold. Assume* $\delta_1 + \delta_2 \neq 0$ *and* $\delta_1 \neq 0$ *where* $\delta_1 \triangleq (1-\mu)\,\partial_2^0 f + \partial_1^0 g$ *and* $\delta_2 \triangleq (1-\mu)\,\partial_2^0 g + \partial_1^0 f$. *Let* $\mathbb{C}_e$ *and* $\mathbb{C}_2$ *denote the bifurcating branches of equilibria and single-class 2-cycles guaranteed by Theorems 2.1 and 3.1.*

a. If $\delta_1 + \delta_2 < 0$, $\delta_1 < 0$, *then* $\mathbb{C}_e$ *and* $\mathbb{C}_2$ *bifurcate supercritically. If* $\delta_1 - \delta_2 < 0$, *then* $\mathbb{C}_e$ *is stable and* $\mathbb{C}_2$ *is unstable. If* $\delta_1 - \delta_2 > 0$, *then* $\mathbb{C}_e$ *is unstable and* $\mathbb{C}_2$ *is stable.*

b. If $\delta_1 + \delta_2 > 0$, $\delta_1 < 0$, *then* $\mathbb{C}_e$ *bifurcates subcritically and is* ~~*stable*~~ unstable, *and* $\mathbb{C}_2$ *bifurcates supercritically and is unstable.*

c. If $\delta_1 + \delta_2 < 0$, $\delta_1 > 0$, *then* $\mathbb{C}_e$ *bifurcates supercritically and is unstable, and* $\mathbb{C}_2$ *bifurcates subcritically and is* ~~*stable*~~ unstable.

d. If $\delta_1 + \delta_2 > 0$, $\delta_1 > 0$, *then* $\mathbb{C}_e$ *and* $\mathbb{C}_2$ *bifurcate subcritically. If* $\delta_1 - \delta_2$ ~~< 0,~~ is nonzero *then* $\mathbb{C}_e$ *is* ~~*stable*~~ unstable *and* $\mathbb{C}_2$ *is unstable.* ~~*If* $\delta_1 - \delta_2 > 0$, *then* $\mathbb{C}_e$ *is unstable and* $\mathbb{C}_2$ *is stable.*~~

Notice that the stability of the bifurcating equilibrium (or 2-cycles) is not determined only by the direction of bifurcation, as it is in the case of a generic transcritical bifurcations [4]. Also notice that in all cases one of the branches $\mathbb{C}_e$ or $\mathbb{C}_2$ is stable, but not both.

We next consider the case $m = 3$ for a class of models with certain restricted types of interclass interactions. Specifically, in the nonlinear Leslie model (2) with $m = 3$, we suppose that the density effects on survivorship and on fertility have the forms

$$f = f\left(x_1, x_3\right), \quad g_i = g_i\left(x_i, x_{i+1}\right) \text{ for } i = 1 \text{ and } 2. \tag{11}$$

Thus, density effects on fertility and survivorship of each class are due to population densities in its own class and that of the predecessor class. This kind of model is motivated by an example, called the LPA model, that has found extensive use in experimental numerous studies of the nonlinear dynamics of insect populations [6, 10].

From Theorem 2.1, for $\varepsilon = n-1$ small, the bifurcating positive equilibria are

$$x_1(\varepsilon) = -\frac{1}{d}\varepsilon + O\left(\varepsilon^2\right), \quad x_2(\varepsilon) = -\frac{(1-\mu_1)}{d}\varepsilon + O\left(\varepsilon^2\right)$$
$$x_3(\varepsilon) = -\frac{(1-\mu_1)(1-\mu_2)}{d}\varepsilon + O\left(\varepsilon^2\right)$$

where

$$d = \partial_1^0 f + \partial_1^0 g_1 + \left(\partial_2 g_1^0 + \partial_2 g_2^0\right)(1-\mu_1) + \left(\partial_3^0 f + \partial_3 g_2^0\right)(1-\mu_1)(1-\mu_2). \quad (12)$$

The Jacobian

$$J(x_1, x_2, x_3) = \begin{pmatrix} \frac{nx_3\partial_1 f}{(1-\mu_1)(1-\mu_2)} & 0 & \frac{n(f+x_3\partial_3 f)}{(1-\mu_1)(1-\mu_2)} \\ (1-\mu_1)(g_1 + x_1\partial_1 g_1) & (1-\mu_1)x_1\partial_2 g_1 & 0 \\ 0 & (1-\mu_2)(g_2+x_2\partial_2 g_2) & (1-\mu_2)x_2\partial_3 g_2 \end{pmatrix}$$

evaluated at the positive equilibria has the expansion $J(x_1(\varepsilon), x_2(\varepsilon), x_3(\varepsilon)) = J_0 + J_1\varepsilon + O\left(\varepsilon^2\right)$ where

$$J_0 = \begin{pmatrix} 0 & 0 & \frac{1}{(1-\mu_1)(1-\mu_2)} \\ 1-\mu_1 & 0 & 0 \\ 0 & 1-\mu_2 & 0 \end{pmatrix}$$

has eigenvalues equal to the cube roots of unity: 1 and $\left(-1 \pm i\sqrt{3}\right)/2$. The eigenvalue of $J(x_1(\varepsilon), x_2(\varepsilon), x_3(\varepsilon))$ that equals 1 when $\varepsilon = 0$ has an expansion

$$\lambda = 1 + \lambda_1\varepsilon + O\left(\varepsilon^2\right), \quad \lambda_1 = \frac{wJ_1v}{wv}$$

where v and w are right and left eigenvectors of J_0 associated with the eigenvalue 1. A straightforward calculation of these eigenvectors and the matrix J_1 shows that $\lambda_1 = -1/3$, and hence the eigenvalue $\lambda = 1 - \varepsilon/3 + O\left(\varepsilon^2\right)$ has magnitude less than one for $\varepsilon > 0$ small and greater than one for $\varepsilon < 0$ small. This means that the positive equilibria are unstable if $d > 0$ (when they correspond to $\varepsilon = n-1 < 0$, i.e., a subcritical bifurcation).

If $d < 0$, however, stability is determined by the complex (conjugate) eigenvalues of the Jacobian $J(x_1(\varepsilon), x_2(\varepsilon), x_3(\varepsilon))$ that equal $\left(-1 \pm i\sqrt{3}\right)/2$ when $\varepsilon = 0$.

To determine whether the two complex conjugate eigenvalues are inside or outside the unit circle in the complex plane we could carry out ε-expansions to first order for these eigenvalues, as we did for the real eigenvalue. An easier calculation determines their magnitude, as follows. Since the determinant of the Jacobian equals the product of the three eigenvalues, we have $\det J(x_1(\varepsilon), x_2(\varepsilon), x_3(\varepsilon)) = \left(1 - \varepsilon/3 + O\left(\varepsilon^2\right)\right) r^2$ where r is the magnitude of the complex conjugate eigenvalues. A calculation shows $\det J(x_1(\varepsilon), x_2(\varepsilon), x_3(\varepsilon)) = 1 + \Delta\varepsilon + O\left(\varepsilon^2\right)$ where

$$\Delta \triangleq -\left(\partial_1^0 g_1 + (1-\mu_1)\partial_2 g_2^0 + (1-\mu_1)(1-\mu_2)\partial_3^0 f\right) d^{-1}.$$

Thus

$$r^2 = \frac{1 + \Delta\varepsilon + O\left(\varepsilon^2\right)}{1 - \frac{1}{3}\varepsilon + O\left(\varepsilon^2\right)} = 1 + \rho\varepsilon + O\left(\varepsilon^2\right), \quad \rho \triangleq \Delta + \frac{1}{3},$$

and we find that when $d < 0$ the positive equilibria are stable for $\varepsilon = n-1 > 0$ small provided $\rho < 0$ (corresponding to a supercritical bifurcation). If $\rho > 0$ the positive equilibria are unstable for $\varepsilon = n-1 < 0$ small (subcritical bifurcation). A calculation shows

$$\rho = \frac{1}{3}\frac{\partial_1^0 f - 2\partial_1^0 g_1 + \left(\partial_2 g_1^0 - 2\partial_2 g_2^0\right)(1-\mu_1) + \left(\partial_3 g_2^0 - 2\partial_3^0 f\right)(1-\mu_1)(1-\mu_2)}{d}.$$

THEOREM 4.2. *Consider the nonlinear Leslie model (2)* ~~*with*~~ with (11) and $m = 3$. *Assume A1 with* $s = 2$ *and A2 hold and that* $d \neq 0$ *(see (12)).*

a. If $d < 0$*, then the positive equilibria in Theorem 2.1 bifurcate supercritically at* $n = 1$*, and they are LAS if* $\rho < 0$ *and unstable if* $\rho > 0$*.*

b. If $d > 0$*, then the positive equilibria in Theorem 2.1 bifurcate subcritically at* $n = 1$*, and they are unstable.*

In the case when $m = 3$, a branch of single-class 3-cycles also bifurcates from the origin at $n = 1$ (Theorem 3.1). The map defined by the equations (2) not only holds the coordinate axes invariant, but also holds the coordinate planes invariant (visiting them consecutively). When $m = 3$ orbits lying in the coordinate planes consist of vectors in which one class is empty and two classes are nonempty:

$$\operatorname{col}(\alpha_1, \beta_1, 0) \to \operatorname{col}(0, \alpha_2, \beta_2, 0) \to \operatorname{col}(\beta_3, 0, \alpha_3) \to \operatorname{col}(\alpha_4, \beta_4, 0).$$

A study of the dynamics of these orbits therefore reduces to the study of planar maps defined by the second composite map. Under the assumptions (11) it turns out that one component of these planar maps uncouples; that is, the equations describing the dynamics on coordinate planes have the form

$$y(t+1) = nh_1(y(t), z(t))\, y(t) \tag{13}$$

$$z(t+1) = nh_2(z(t))\, z(t). \tag{14}$$

One approach to these equations is first to analyze the uncoupled (one-dimensional) equation for z and then analyze the equation for y as a nonautonomous, one-dimensional equation (treating z as known). For example, if the equation for z has a globally attracting equilibrium z_e, then the equation for y is asymptotically autonomous and theorems are available that relate the dynamics of y to those of the one-dimensional, autonomous "limit equation" [17]

$$w(t+1) = nh_1(w(t), z_e)\, w(t). \tag{15}$$

From a knowledge of the dynamics in each coordinate plane one can gain some understanding of the dynamics of the single-class 3-cycles that bifurcate from the origin at $n = 1$. Of course, in application to population dynamics we are interested only in the nonnegative quadrants of the coordinate planes.

One possibility is that the bifurcating 3-cycles are embedded within an invariant loop that bifurcates at $n = 1$. Indeed, one excepts an invariant loop bifurcation to occur when a conjugate pair of eigenvalues crosses the unit circle, as is the case when $m = 3$ at $n = 1$ in the nonlinear Leslie model (2). The invariant loop bifurcation theorem [15, 21, 24] does not apply to this problem, however, because the bifurcation is degenerate. (It is degenerate for two reasons: because an eigenvalue also leaves the unit circle at 1 at $n = 1$ and because the conjugate pair leaves at a cube root of unity.)

To illustrate the case of a bifurcating invariant loop, we further specialize the functions f and g_i. Let

$$f = \frac{1}{1 + c_{11}x_1 + c_{13}x_3}, \quad g_1 = \frac{1}{1 + c_{21}x_1 + c_{22}x_2}, \quad g_2 = \frac{1}{1 + c_{32}x_2 + c_{33}x_3} \tag{16}$$

where all $c_{ij} \geq 0$. These types of density terms are common in ecological models (the earliest example in structured population models seems to appear in [20]). In Theorem 4.2,

$$d = -\left(c_{11} + c_{21} + (c_{22} + c_{32})(1 - \mu_1) + (c_{13} + c_{33})(1 - \mu_1)(1 - \mu_2)\right) < 0$$

if at least one $c_{ij} > 0$. The bifurcating positive equilibria are LAS if

$$\rho = \frac{c_{11} - 2c_{21} + (c_{22} - 2c_{32})(1-\mu_1) + (c_{33} - 2c_{13})(1-\mu_1)(1-\mu_2)}{c_{11} + c_{21} + (c_{22} + c_{32})(1-\mu_1) + (c_{13} + c_{33})(1-\mu_1)(1-\mu_2)} < 0$$

and unstable if the opposite inequality holds.

Consider first the dynamics in the nonnegative quadrant of the $(y, z) = (x_1, x_2)$ plane. A calculation of two composites of the map shows that

$$h_2(z) = \frac{1-\mu_1}{1-\mu_1 + (nc_{21} + c_{32}(1-\mu_1) + c_{13}(1-\mu_1)(1-\mu_2))z}$$

in the uncoupled equation (14) for $z = x_2$. This difference equation (sometimes called a discrete logistic equation [22] or a Beverton-Holt equation [1]) defines a monotone map. If $n > 1$, there exists a unique positive equilibrium $x_2 = \alpha_2$ that is globally asymptotically stable (for positive initial conditions), namely,

$$\alpha_2 = \frac{1}{1-\mu_1}\frac{n-1}{nc_{21} + c_{32}(1-\mu_1) + c_{13}(1-\mu_1)(1-\mu_2)}.$$

The limit equation (15) is also a discrete logistic equation. Since for all $w > 0$

$$\begin{aligned} nh_1(w, \alpha_2) &< nh_1(0, \alpha_2) \\ &= 1 + \left(1 - \frac{c_{11} + c_{22}(1-\mu_1) + c_{33}(1-\mu_1)(1-\mu_2)}{c_{21} + c_{32}(1-\mu_1) + c_{13}(1-\mu_1)(1-\mu_2)}\right)\varepsilon + O\left(\varepsilon^2\right) \end{aligned}$$

where $\varepsilon = n - 1$. If

$$\sigma \triangleq \frac{c_{11} + c_{22}(1-\mu_1) + c_{33}(1-\mu_1)(1-\mu_2)}{c_{21} + c_{32}(1-\mu_1) + c_{13}(1-\mu_1)(1-\mu_2)} > 1, \tag{17}$$

then $h_1(w, \alpha_2) < 1$ for all $w > 0$ provided $\varepsilon > 0$ is small. It follows that $\lim_{t\to+\infty} w(t) = 0$. By Theorem 4 in [3] (also see [5]) it follows that all orbits in the nonnegative plane satisfy $\lim_{t\to+\infty} \mathrm{col}(y(t), z(t)) = \lim_{t\to+\infty} \mathrm{col}(x_1(t), x_2(t))$ $= \mathrm{col}(0, \alpha_2)$. As a result, all orbits of the composite map in the (x_1, x_2)-plane tend to an equilibrium on the x_2-axis:

$$\lim_{t\to+\infty} \mathrm{col}(x_1(t), x_2(t), 0) = \mathrm{col}(0, \alpha_2, 0).$$

Analogous arguments and calculations show that the dynamics of the composite map in the other two coordinate planes also equilibrate to an axis equilibrium under the same assumption (17); namely,

$$\begin{aligned} \lim_{t\to+\infty} \mathrm{col}(0, x_2(t), x_3(t), 0) &= \mathrm{col}(0, 0, \alpha_3) \\ \lim_{t\to+\infty} \mathrm{col}(x_1(t), 0, x_3(t)) &= \mathrm{col}(\alpha_1, 0, 0). \end{aligned}$$

where

$$\begin{aligned} \alpha_1 &= \frac{n-1}{c_{21} + c_{32}(1-\mu_1) + c_{13}(1-\mu_1)(1-\mu_2)} \\ \alpha_3 &= (1-\mu_1)(1-\mu_2)\frac{n-1}{n(c_{21} + c_{32}(1-\mu_1)) + c_{13}(1-\mu_1)(1-\mu_2)}. \end{aligned}$$

In the (x_1, x_2)-plane the equilibrium $\mathrm{col}(0, \alpha_2)$ is LAS and globally attracting in the nonnegative quadrant. The equilibrium $\mathrm{col}(\alpha_1, 0)$ is a saddle whose stable manifold lies on the x_1-axis. Thus, the unstable manifold of $\mathrm{col}(\alpha_1, 0)$ lying in the nonnegative quadrant must tend asymptotically to the equilibrium $\mathrm{col}(0, \alpha_2)$ and thereby forms a heteroclinic connection between these two equilibria. See Figure

1a. Similar heteroclinic connections between the equilibria exist in the other two coordinate planes, all of which together form an invariant loop consisting of the three equilibria and the heteroclinic connectors. These invariant loops bifurcate from the origin at $n = 1$ and can be stable or unstable (see Fig. 1).

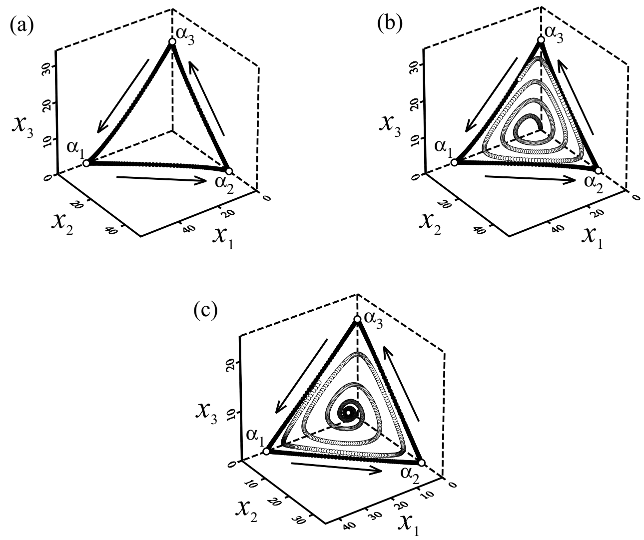

FIGURE 1. (a) The two-fold composite of the map defined by the nonlinear Leslie model (2) with $m = 3$ maps the nonnegative quadrant of each coordinate plane into itself. For the case (16), all orbits in each nonnegative quadrant tend to an axis equilibria (open circles) when $n > 1$ and $\sigma > 1$. Moreover, there exist heteroclinic orbits connecting these equilibria, forming an invariant loop of the composite map. The invariant loop is shown for parameter values $c_{11} = c_{21} = c_{22} = c_{32} = 0$, $c_{33} = 0.01$, $c_{13} = 0.004$ and $n = 1.1$, $\mu_1 = 0.25$, $\mu_2 = 0.25$. The equilibria are located at $\alpha_1 = 44.44$, $\alpha_2 = 33.33$, $\alpha_3 = 25.00$, and $\sigma = 5/2 > 2$. (b) The orbit of the composite with initial conditions $x_1(0) = x_2(0) = x_3(0) = 1$ approaches the invariant loop in (a) in a counterclockwise manner. (c) With c_{13} changed to $c_{13} = 0.006$, the invariant loop becomes unstable. With initial conditions $x_1(0) = 15$, $x_2(0) = 0.01$, $x_3(0) = 10$ near the invariant loop, the orbit approaches the positive equilibrium in counterclockwise manner. The equilibria are located at $\alpha_1 = 35.56$, $\alpha_2 = 26.67$, $\alpha_3 = 20.00$, and $\sigma = 5/3 < 2$.

With respect to the original map, the three composite map equilibria correspond to the three phases of a single-class 3-cycle:

$$\text{col}\,(\alpha_1, 0, 0) \to \text{col}\,(0, \alpha_2, 0) \to \text{col}\,(0, 0, \alpha_3) \to \text{col}\,(\alpha_1, 0, 0) \to \cdots .$$

We have shown that there exists an invariant loop consisting of (the phases of) the single-class 3-cycle and connecting heteroclinic orbits that lie in the coordinate planes (see Fig. 2).

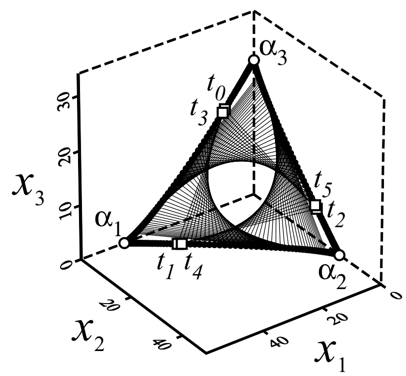

Figure 2. The invariant loop shown in Figure 1a for the composite map corresponds to an invariant loop of the original nonlinear Leslie model on which there resides a single-class 3-cycle connected by heteroclinic orbits. Lines connecting successive orbit points (such the six open squares) show the motion of a heteroclinic orbit as it moves consecutively from one coordinate plane to the next in its approach to the single-class 3-cycle.

Algebraic manipulations show that $\rho < 0 \Longleftrightarrow \sigma < 2$ and $\rho > 0 \Longleftrightarrow \sigma > 2$. We summarize these results in the following theorem.

Theorem 4.3. *Consider the nonlinear Leslie model (2) with* $m = 3$ *and nonlinearities (16) with at least one of the nonnegative coefficients* c_{ij} *being positive.*

a. If the coefficients c_{ij} *satisfy* $1 < \sigma$, *then a branch of positive equilibria and a branch of invariant loops (lying in the coordinate planes) both supercritically bifurcate at* $n = 1$. *The invariant loops are made up of a single-class 3-cycle whose three phases are connected by heteroclinic orbits.*

b. If $\sigma < 2$, *then the bifurcating positive equilibria are LAS (for* $n-1 > 0$ *small). If* $\sigma > 2$, *then the bifurcating positive equilibria are unstable (for* $n - 1 > 0$ *small).*

We conjecture that if $\sigma > 2$ in Theorem 4.3, then the bifurcating invariant loops are stable (attractors) and if $\sigma < 2$ they are unstable (not attractors). See Figure 3 and 4 for example illustrations.

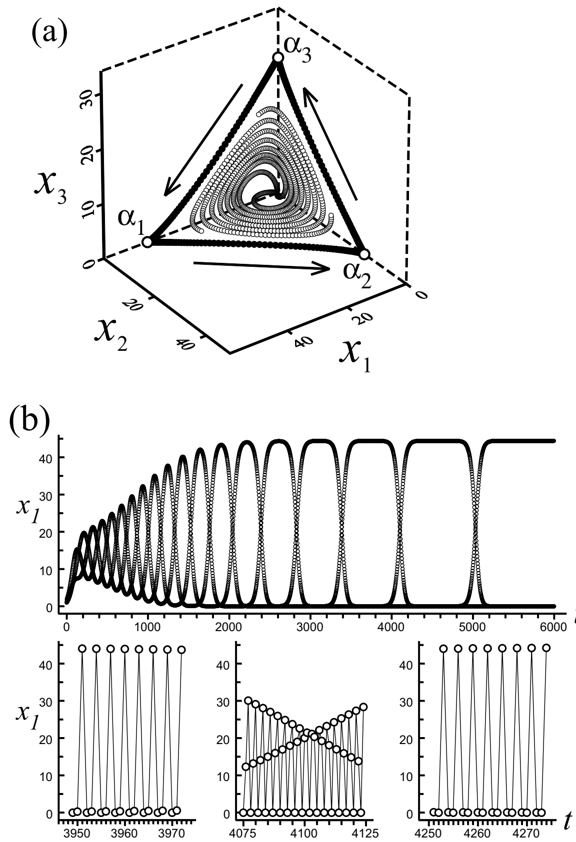

FIGURE 3. (a) The invariant loop shown in Figure 2 is an attractor. The orbit with initial conditions $x_1 = x_2 = x_3 = 1$ winds outward and approaches the loop asymptotically. Note the three "strands" of the orbits, which are visited sequentially in time. (b) The time series of the component x_1 of the orbit in (a) shows episodes of increasing length during which it has nearly a periodic oscillation of period three. These oscillations are due to fly-bys of the three phases of the single-class 3-cycle, which is a saddle cycle, as the orbit approaches the invariant loop. Each fly-by results in a phase shift of the (nearly period three) oscillation, as demonstrated by the lower row of graphs in (b).

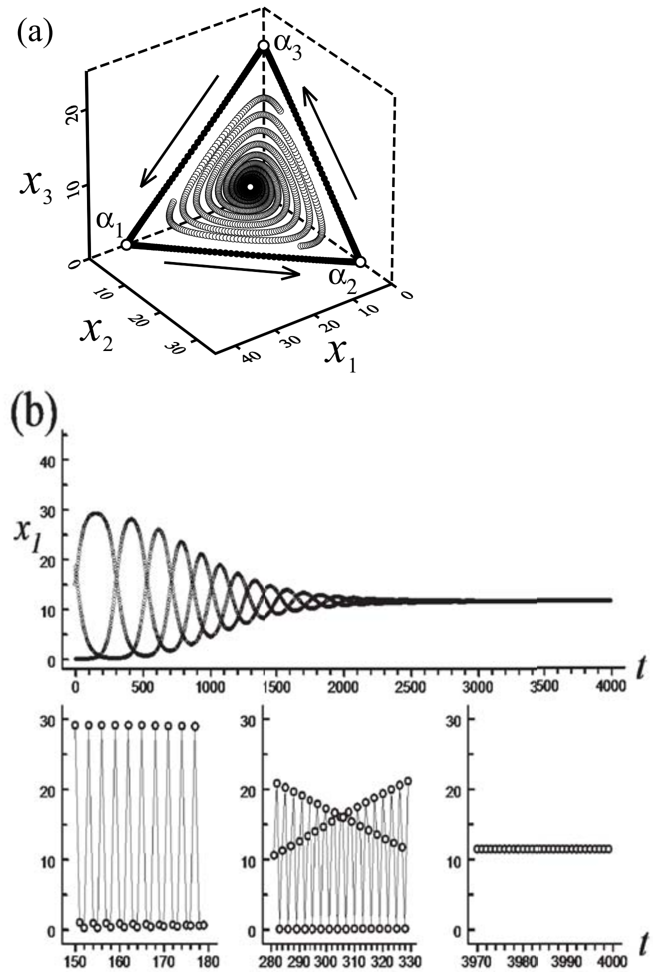

FIGURE 4. (a) The invariant loop in Figure 1c is unstable. The orbit with initial conditions $x_1 = 15$, $x_2 = 0.01$, $x_3 = 10$ near the loop spiral inward to the positive equilibrium $x_1 = 11.53$, $x_2 = 8.644$, 6.111, which is LAS. (b) Time series segments of the x_1 component show transients that are episodes of a near (single-class) 3-cycle followed ultimately by equilibration.

5. **Concluding Remarks.** The nonlinear Leslie model (2) describes a semelparous population whose individuals reproduce and die after an extended juvenile stage in which they pass through $m - 1$ nonreproductive stages. A nongeneric bifurcation at the trivial equilibrium $\hat{x} = \hat{0}$ occurs in this model at $n = 1$, where n is the inherent net reproductive number. The typical scenario for nonlinear matrix models is a transcritical bifurcation of the trivial equilibrium with a branch of nontrivial equilibria in which an exchange of stability occurs from the trivial equilibrium to a

branch of positive equilibria [4]. This typical case is the result of a single eigenvalue of the Jacobian at the trivial solution leaving the unit circle in the complex plane at 1 as n increases through 1.

The destabilization of $\hat{x} = \hat{0}$ at $n = 1$ for the model (2), however, leads to a nongeneric situation in which all m eigenvalues of the Jacobian simultaneously leave the unit circle at $n = 1$ (at the m roots of unity). We proved in this paper that, nonetheless, a branch of positive equilibria bifurcations from $\hat{x} = \hat{0}$ at $n = 1$ (Theorems 2.1 and 2.2). However, an exchange of stability between $\hat{x} = \hat{0}$ and the bifurcating positive equilibria might or might not occur. We showed that a branch of m-cycles also bifurcates from $\hat{x} = \hat{0}$ at $n = 1$ (Theorem 3.1). These single-class cycles have the special form in which only one class is nonempty at any time, and thus the generations are temporally separated. A study of the $m = 2$ and $m = 3$ class cases illustrates several possibilities for the nongeneric bifurcation at $n = 1$.

In the case $m = 2$ of a single juvenile class, we showed that either the bifurcating branch of positive equilibrium is stable or the branch of bifurcating single-class 2-cycles is stable, but not both (Theorem 4.1). Stability is determined by two quantities δ_1 and δ_2 given in Theorem 4.1. The bifurcating positive equilibria are stable (and the 2-cycles unstable) if $\delta_2 > \delta_1$. The bifurcating 2-cycles are stable (and the positive equilibria are unstable) if $\delta_2 < \delta_1$. This result can be interpreted as follows. If interclass competition, as measured by δ_1, is not too intense, then the equilibrium is stable and the population will equilibrate with overlapping generations. If, on the other hand, interclass competition is too intense, then the population will approach a period two oscillation with the generations separated. (These results are similar to those in [7] and [8].)

In the case $m = 3$ of two juvenile classes, the bifurcation possibilities at $n = 1$ are more complicated. A condition sufficient for the supercritical and stable bifurcation of the positive equilibria appears in Theorem 4.2. The special case studied in Theorem 4.3 shows, however, that the bifurcating positive equilibria are not always stable. Instead, it is possible that the bifurcating branch of single-class 3-cycles are embedded in a bifurcating invariant loop that is stable. This leads to an attracting state in which the population wanders near one phase of the 3-cycle to another, spending increasing periods of time in each episode. This dynamic occurs when interclass competition is sufficiently intense as measured by the quantity σ in Theorem 4.3. (For another example of this phenomenon, but with stronger exponential or Ricker nonlinearities, see [5].)

Another type of bifurcation can occur in the $m = 3$ case that is not covered by Theorem 4.3. The condition $\sigma > 1$ in this theorem implies that the bifurcating single-class 3-cycle is stable within the invariant coordinate planes. The heteroclinic orbits connecting the phases of the 3-cycle form the bifurcating invariant loop. On the other hand, if $\sigma < 1$, then it is possible that there exists positive equilibria of the composite map lying in the positive coordinate planes, equilibria that correspond to a *two*-class 3-cycle of the nonlinear Leslie model. In the example shown in Figure 5, the phases of this 3-cycle are heteroclinically connected to phases of the single-class 3-cycle to form a bifurcating invariant loop in which both cycles are embedded. In this example, however, the invariant loop is unstable in the three-dimensional phase space (where orbits approach the stable positive equilibrium).

An open problem is to prove, under appropriate conditions, the stability of the bifurcating invariant loop in the case $m = 3$ considered in section 4. Also awaiting further study are what undoubtedly are more complicated and elaborate invariant loops composed of cycles lying on the invariant coordinate subspaces when $m > 3$.

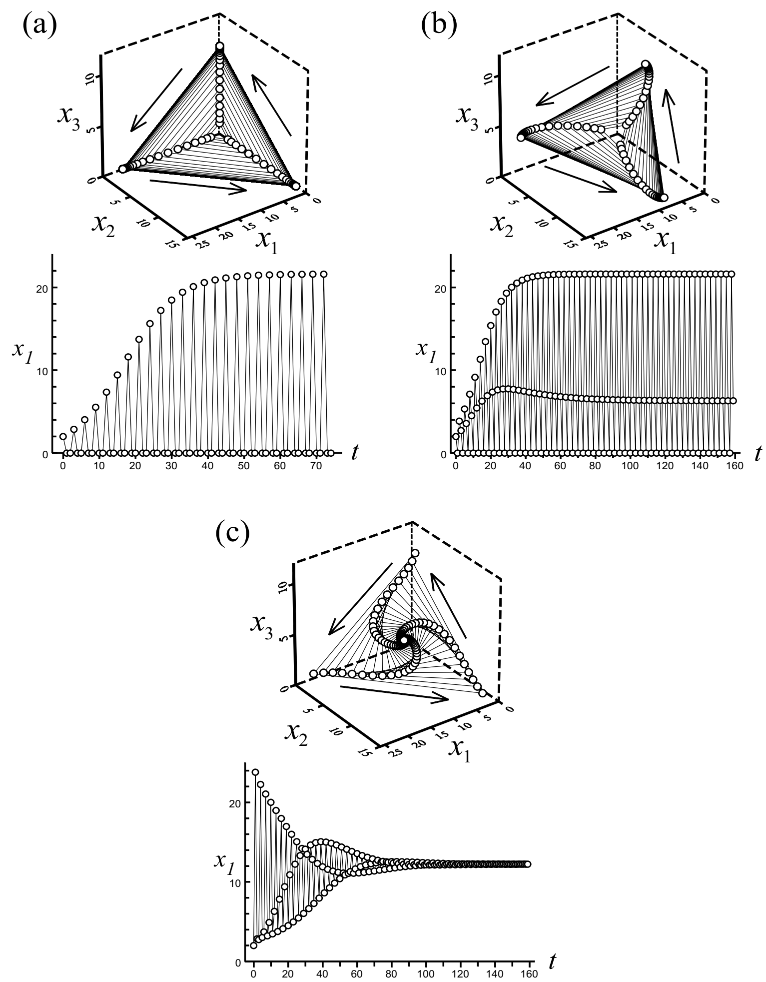

FIGURE 5. For the parameter values $c_{11} = c_{13} = c_{32} = c_{33} = c_{21} = 0.01$, $c_{22} = 0$, $\mu_1 = \mu_2 = 0.25$, $n = 1.5$ in the nonlinear Leslie model (2) with $m = 3$ and (16), the quantity $\sigma = 0.9189 < 1$. Theorem 4.3 implies the positive equilibrium is LAS (for $n-1 > 0$ sufficiently small). There exists a bifurcating invariant loop lying in the coordinate planes that contains a single-class 3-cycle (on the coordinate axes) and a two class 3-cycle (in the positive quadrant of the coordinate planes). (a) The single-class 3-cycle is stable within the coordinate axes, as is illustrated by the orbit with initial conditions $x_1 = 2$, $x_2 = 0$, $x_3 = 0$. (b) The two class 3-cycle is stable within the coordinate axes, as is illustrated by the orbit with initial conditions $x_1 = 2$, $x_2 = 2$, $x_3 = 0$. (c) The invariant loop

is unstable in three-dimensional phase space, as is illustrated by the orbit with initial conditions $x_1 = 2$, $x_2 = 2$, $x_3 = 10$, which approaches the positive equilibrium.

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