Equilibrium Stability and the Geometry of Bifurcation Graphs for a Class of Nonlinear Leslie Models

J. M. Cushing

Abstract For nonlinear scalar difference equations that arise in population dynamics the geometry of the graph obtained by plotting the population growth rate as a function of inherent fertility leads to information about the number of positive equilibria and about the local stability of positive equilibria. Specifically, equilibria on decreasing segments of this graph are always unstable. Equilibria on increasing segments are stable in two circumstances: when the equilibrium is sufficiently close either to 0 or to a critical point on the graph. These geometric criteria are shown to hold for a class of nonlinear Leslie models in which (age-specific) survival rates are population density independent and fertilities are dependent on a weighted total population size. Examples are given to show how this geometric method can be used to identity strong Allee and hysteresis effects in these models.

Keywords Leslie matrix models · Bifurcation · Stability · Allee effects · Hysteresis

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1 Nonlinear Leslie Matrix Equations

Difference equations arise as models of population dynamics by means of a straightforward accounting of the individuals present at time $t+1$, the total of which consists of new individuals who were not present at time t plus those who were present at time t and survived to time $t+1$. If no immigration or emigration occurs, the former are newborns, so that the population at time $t+1$ consists simply of newborns plus survivors. If $\hat{x}(t)$ is demographic m-dimensional column vector of population densities as categorized by a classification scheme such as age, size, life history stage,

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disease classifications, etc., then

$$\hat{x}(t+1) = F\hat{x}(t) + T\hat{x}(t)$$

where $F\hat{x}(t)$ is the vector of newborns and $T\hat{x}(t)$ the vector of survivors. Here $F = \left[f_{ij}\right]$ is an $m \times m$ non-negative matrix of class specific fertilities f_{ij} and $T = \left[s_{ij}\right]$ is an $m \times m$ non-negative matrix of survival and between class transition probabilities s_{ij}, which if dependent on population density become functions of $\hat{x}(t)$ and create a nonlinear difference equation

$$\hat{x}(t+1) = F\left(\hat{x}(t)\right)\hat{x}(t) + T\left(\hat{x}(t)\right)\hat{x}(t). \tag{1}$$

In the non-structured population case $m = 1$, we have a scalar difference equation

$$x(t+1) = f\left(x(t)\right)x(t) + s\left(x(t)\right)x(t).$$

Denoting the inherent (or intrinsic) fertility by b (i.e. fertility in the absence of density effects), we re-write the scalar equation as

$$x(t+1) = b\beta\left(x(t)\right)x(t) + s\left(x(t)\right)x(t)$$

where $\beta(0) = 1$. Besides the extinction equilibrium $x = 0$, we are interested in positive equilibria, which are roots of the algebraic equation

$$1 = b\beta(x) + s(x)$$

or

$$b = \frac{1 - s(x)}{\beta(x)}. \tag{2}$$

To have a feasible population model, we require $\beta(x) > 0$ and $0 \leq s(x) < 1$ on some interval of positive x values. We assume these inequalities hold for $x \in I$ where I is an open interval containing $x = 0$. In applications I is often a half line, as is the case when β and/or s have one of the commonly used forms

$$\frac{1}{1+cx} \text{ or } \exp(-cx), \quad c > 0.$$

The graph, G, of $b = b(x)$ as a function of x defined by (2), together with the horizontal line $x = 0$, plotted in the positive quadrant geometrically displays the existence of relevant equilibria for the population model. From this graph the number of equilibria for any value of b can be determined as well as any bifurcation points where that number changes. The following facts are straightforwardly derived from the linearization principle, provided β and s are twice continuously differentiable on I. See [9].

1. The extinction equilibrium loses stability as b increases through the critical value $b_0 := 1 - s(0) > 0$.
2. A positive equilibrium $x = x_e$ corresponding to $b = b_e$ is unstable if the point (b_e, x_e) lies on a decreasing segment of the graph G.
3. A positive equilibrium $x = x_e$ corresponding to $b = b_e$ is stable if the point (b_e, x_e) lies on a increasing segment of the graph G provided $x_e \approx 0$ or x_e is near a critical point of $b(x)$, i.e. a point for which $b'(x_e) = 0$.

Thus, by simply graphing $b(x)$ given by (2) one can not only determine the existence and number of positive equilibria, but also learn a considerable amount about their local stability properties.

Here we will extend these conclusions to a class of matrix models (1) when $m > 1$. Specifically, we consider Leslie age-structured models under two assumptions: that only fertility is density dependent and that the density dependence is by means of a weighted total population size

$$w(t) = \hat{w}^{\tau} \hat{x}(t)$$

where $\hat{w} \in R_+^m \backslash \{\hat{0}\}$. Here R_+^m denotes the non-negative cone in Euclidean space R^m and the superscript τ denotes the vector transpose. Thus, in (1) we have

$$F(w) = \begin{pmatrix} 0 \cdots 0 & f_n(w) & \cdots & f_m(w) \\ 0 \cdots 0 & 0 & \cdots & 0 \\ 0 \cdots 0 & 0 & \cdots & 0 \\ \vdots \quad \vdots & \vdots & & \vdots \\ 0 \cdots 0 & 0 & \cdots & 0 \end{pmatrix}, \quad T = \begin{pmatrix} 0 & 0 & \cdots & 0 & 0 \\ s_1 & 0 & \cdots & 0 & 0 \\ 0 & s_2 & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & s_{m-1} & s_m \end{pmatrix} \quad (3)$$

where n is the first adult (reproducing) age class and $0 < s_i \leq 1$ for $i = 1, ..., m-1$ and $0 \leq s_m < 1$. If $s_m = 0$ then $F(w) + T$ is a standard Leslie age-structured projection matrix, designed so that no individual lives past age class m. If $s_m > 0$ then the matrix is an extended Leslie matrix in which no maximal age is specified and the m-age class consists of all individuals older than age m.

In summary, we consider the nonlinear Leslie matrix equation

$$\hat{x}(t+1) = F(w(t))\,\hat{x}(t) + T\hat{x}(t) \quad (4)$$

with $F(w)$ and T given by (3). We assume

A1: $f_i(w) \geq 0$ are twice continuously differentiable functions of $w \in I$.

In order that n is the youngest and m is the oldest fertile age class we make the following assumption:

A2: $f_n(w) > 0$ and $f_m(w) > 0$ on I.

Under this assumption $F(w) + T$ is non-negative and irreducible for $w \in I$. Finally, we will use the inherent fertility of the youngest fertility class as a bifurcation parameter.

A3: Let λ denote the inherent fertility of the youngest adult class n and write

$$f_n(w) = \lambda\beta(w) \quad \text{where} \quad \beta(0) = 1.$$

In the $m = 1$ dimensional case discussed above, λ is the inherent fertility rate b.

2 Equilibria

By Perron–Frobenius theory $F(w) + T$ has a simple, dominant eigenvalue $r(w) > 0$ which possesses a positive eigenvector (i.e. an eigenvector in the interior $int\left(R_+^m\right)$ of the positive cone R_+^m in R^m) and no other eigenvalue has a nonnegative eigenvector (i.e. no other eigenvector in $R_+^m \backslash \{\hat{0}\}$). The equilibrium equation

$$\hat{x} = (F(w) + T)\,\hat{x} \tag{5}$$

has, of course, the solution $\hat{x} = \hat{0}$ (the extinction equilibrium). If $\hat{x} \in R_+^m \backslash \{\hat{0}\}$ is a solution of (5), then by Perron–Frobenius theory $r(w) = 1$ and $\hat{x}$ is in fact a positive vector, i.e. $\hat{x} \in int\left(R_+^m\right)$. Thus, *the only non-negative equilibria of the nonlinear Leslie model* (4) *are positive equilibria.*

Suppose $\hat{x} \in int\left(R_+^m\right)$ solves the equilibrium equation (5). Since $r(w) = 1$ it follows from well-known theorems [4, 12] that the net reproduction number $R_0(w)$ of $F(w) + T$ also equals 1. While there is no analytic formula for $r(w)$, there is a formula for $R_0(w)$ for Leslie matrices [5, 6], namely

$$R_0(w) = p_n\lambda\beta(w) + \sum_{i=n+1}^{m-1} p_i f_i(w) + p_m \frac{1}{1 - s_m} f_m(w) \tag{6}$$

where

$$p_1 = 1, \quad p_i = \prod\nolimits_{j=1}^{i-1} s_j$$

is the probability a newborn lives to reach age class i. Thus, we conclude that to each positive equilibrium $\hat{x}_e \in int\left(R_+^m\right)$ of the nonlinear Leslie equation (4) there corresponds a positive solution $w_e = \hat{w}^\tau \hat{x}_e > 0$ of the equation

$$p_n\lambda\beta(w) + \sum_{i=n+1}^{m-1} p_i f_i(w) + p_m \frac{1}{1 - s_m} f_m(w) = 1 \tag{7}$$

which we can re-write as

$$\lambda = \frac{1}{p_n \beta(w)} \left(1 - \sum_{i=n+1}^{m-1} p_i f_i(w) - p_m \frac{1}{1 - s_m} f_m(w) \right). \tag{8}$$

Conversely, suppose $w_e > 0$ solves this equation. Then $R_0(w_e) = 1$ which in turn implies $r(w_e) = 1$ [4, 12]. By Perron–Frobenius theory, the eigen-space of $F(w_e) + T$ associated with 1 is spanned by a positive eigenvector $\hat{v} \in int\left(R_+^m\right)$. There is, then, a unique positive eigenvector $\hat{x}_e$ of $F(w_e) + T$ such that $\hat{w}^\tau \hat{x}_e = w_e$, namely, $\hat{x}_e = \left(w_e / \hat{w}^\tau \hat{v}\right) \hat{v}$, which is therefore a unique positive equilibrium of (5).

In conclusion, we have shown that *there is a one-one correspondence between the positive equilibria of the nonlinear Leslie matrix equation* (3)–(4) *and positive solutions* w *of* (7), *or equivalently of* (8). This allows us to study the existence of positive equilibria by investigating the graph G of $\lambda = \lambda(w)$, as defined by (8), in the (λ, w)-plane, as we did in the $m = 1$ case above. To be biologically meaningful, λ must be positive and so we are interested in the graph of G only in the positive quadrant of the (λ, w)-plane.

3 Equilibrium Stability

The Jacobian of (4) evaluated at the extinction equilibrium $\hat{x} = \hat{0}$ is (the non-negative and irreducible matrix) $F(\hat{0}) + T$. The extinction equilibrium is locally asymptotically stable (LAS) if the dominant eigenvalue $r(\hat{0}) < 1$ and unstable if $r(\hat{0}) > 1$. It follows, then, from well-known theorems [4, 12] that the extinction equilibrium is stable if $R_0(\hat{0}) < 1$ and unstable if $R_0(\hat{0}) > 1$. Using formula (6) we conclude by the linearization principle [11] that the extinction equilibrium is LAS if $\lambda < \lambda_0$ and unstable if $\lambda > \lambda_0$ where

$$\lambda_0 := \frac{1}{p_n} \left(1 - \sum_{i=n+1}^{m-1} p_i f_i(0) + p_m \frac{1}{1 - s_m} f_m(0) \right). \tag{9}$$

If $\lambda_0 \leq 0$ then the extinction equilibrium is unstable for all biologically meaningful values of $\lambda > 0$ and the population is not threatened by extinction. Therefore, in so far as a study of extinction versus survival is concerned, we are interested in the case when $\lambda_0 > 0$. We have proved part (a) of the following Theorem.

Theorem 1 *Assume A1, A2, and A3 and that* $\lambda_0 > 0$.
(a) The extinction equilibrium of the nonlinear Leslie matrix equation (4) is LAS if $\lambda < \lambda_0$ *and unstable if* $\lambda > \lambda_0$.
(b) A positive equilibrium $\hat{x}_e \in int\left(R_+^m\right)$ *of (4) is unstable if the point* $(\lambda, w_e) = \left(\lambda, \hat{w}^\tau \hat{x}_e\right)$ *lies on a strictly decreasing segment of the graph G, i.e. if* $\lambda'(w_e) < 0$.

(c) A positive equilibrium $\hat{x}_e \in int\left(R_+^m\right)$ of (4) is LAS if the point $(\lambda, w_e) = \left(\lambda, \hat{w}^\tau \hat{x}_e\right)$ lies on a strictly increasing segment of the graph G, i.e. $\lambda'(w_e) > 0$, and is either near the bifurcation point $(\lambda_0, 0)$ or near a critical point (λ_c, w_c) on G, i.e. a point where $\lambda'(w_c) = 0$.

Proof We have only to prove (b) and (c) From (6) we calculate

$$R_0'(w) = p_n \lambda \beta'(w) + \sum_{i=n+1}^{m-1} p_i f_i'(w) + p_m \frac{1}{1-s_m} f_m'(w). \tag{10}$$

At a positive equilibrium point (λ, w_e), with λ given by (8), we have

$$\begin{aligned} R_0'(w_e) = {} & \frac{1}{\beta(w_e)}\left(1 - \sum_{i=n+1}^{m-1} p_i f_i(w_e) - p_m \frac{1}{1-s_m} f_m(w_e)\right)\beta'(w_e) \\ & + \sum_{i=n+1}^{m-1} p_i f_i'(w_e) + p_m \frac{1}{1-s_m} f_m'(w_e). \end{aligned}$$

From the definition (8) of $\lambda = \lambda(w)$ we calculate

$$\begin{aligned} \lambda'(w) = -\frac{1}{p_n \beta(w)} & \left[\frac{1}{\beta(w)}\left(1 - \sum_{i=n+1}^{m-1} p_i f_i(w) - p_m \frac{1}{1-s_m} f_m(w)\right)\beta'(w)\right. \\ & \left. + \sum_{i=n+1}^{m-1} p_i f_i'(w) + p_m \frac{1}{1-s_m} f_m'(w)\right]. \end{aligned}$$

Thus, we find that

$$\lambda'(w_e) = -\frac{1}{p_n \beta(w_e)} R_0'(w_e). \tag{11}$$

and that, when nonzero, $\lambda'(w_e)$ and $R_0'(w_e)$ have opposite signs. (This is related to general results concerning $r(w)$ and $R_0(w)$ in [7].)

(b) If $\lambda'(w_e) < 0$ then $R_0'(w_e) > 0$ and hence by Theorem 1 in [13] the positive equilibrium $\hat{x}_e$ is unstable.

(c) If $\lambda'(w_e) > 0$ then $R_0'(w_e) < 0$ then, by Theorem 3 in [13] the positive equilibrium $\hat{x}_e = \mathrm{col}(x_i)$ is LAS provided $\left|F'(w_e)\hat{x}_e\right|$ is sufficiently small. From the equilibrium equation (5) it is easily seen that any positive equilibrium has the form

$$\hat{x}_e = \begin{pmatrix} 1 \\ p_1 \\ \vdots \\ p_{m-1} \\ p_m \frac{1}{1-s_m} \end{pmatrix} x_1$$

and hence (using the vector norm $\left|\hat{x}\right| = \Sigma_{i=1}^{m} |x_i|$) we find that $\left|F'(w_e)\,\hat{x}_e\right| = \left|R_0'(w_e)\right| x_1$. Thus, $\left|F'(w_e)\,\hat{x}_e\right|$ is small if $x_1 \approx 0$, which is true if the equilibrium is near the bifurcation point. However, $\left|R_0'(w_e)\right| x_1$ is also small if the equilibrium point (λ, w_e) lies near a point (λ_c, u_c) where $R_0'(w_c) = 0$, i.e. by (11) where $\lambda'(w_c) = 0$. ■

The graph G connects to the point $(\lambda, w) = (\lambda_0, 0)$ since this point satisfies equation (8), i.e. this point is a transcritical bifurcation point where the branches of extinction and positive equilibria intersect. By Theorem 1 the bifurcating positive equilibria near this bifurcation point are LAS (respectively, unstable) if the bifurcation is forward (respectively, backward), i.e. if the graph of G is increasing (respectively, decreasing) at $(\lambda_0, 0)$. That is to say, near the bifurcation point, the bifurcating positive equilibria are stable (respectively, unstable) if $\lambda'(0) > 0$ (respectively, $\lambda'(0) < 0$) or equivalently $R_0'(0) < 0$ (respectively $R_0'(0) > 0$). From

$$R_0'(0) = p_n \lambda \beta'(0) + \sum_{i=n+1}^{m-1} p_i f_i'(0) + p_m \frac{1}{1 - s_m} f_m'(0)$$

we see that a forward bifurcation of stable positive equilibria occurs if all density effects are negative (at low population levels $w \approx 0$), i.e. if $\beta'(0) \leq 0$, $f_i'(0) \leq 0$ and not all equal 0. The density effects used in most population models are in fact negative effects, i.e. $\beta'(w) \leq 0$, $f_i'(w) \leq 0$ and not all equal to 0 for all values of $w > 0$. By (10) this implies $R_0'(w) < 0$ and, by (11), $\lambda'(w) > 0$ for all population levels $w \geq 0$. Thus, there are no critical points nor decreasing segments on the graph G. As is well known, the stability of the bifurcating positive equilibria is not necessarily maintained along the entire graph G. Positive equilibrium destabilization can occur and result in periodic orbits, invariant loops, and cascades to chaos.

Positive density effects at low population levels are called *component Allee effects* [3]. If present and if they are of sufficient magnitude so as to give $R_0'(0) > 0$, then component Allee effects result in the backward bifurcation of positive equilibria from the extinction equilibrium $(\lambda_0, 0)$. Backward bifurcations, when coupled with negative density effects at high population levels, generally lead to a multiple attractor scenario called a *strong Allee effect* [8]. The importance of strong Allee effects in population dynamics has been emphasized since the early work of W. C. Allee [1]; see for example [3, 10]. For the nonlinear Leslie models (4) considered here, the geometry of the graph G, as a straightforward plotting exercise, can easily detect strong Allee effects (and other tipping points and hysteresis effects). We give an example in the next section.

4 An Application

Consider (4) with $m = 4$ and $n = 2$, i.e. a Leslie matrix model with four age classes, the first of which consists of juveniles:

$$F(w) = \begin{pmatrix} 0 & f_2(w) & f_3(w) & f_4(w) \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix}, \quad T = \begin{pmatrix} 0 & 0 & 0 & 0 \\ s_1 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 \\ 0 & 0 & s_3 & 0 \end{pmatrix}. \tag{12}$$

We consider density terms $f_i(w)$ in which two factors $\exp(-cw)$ and $\exp\left(1 - e^{-dw}\right)$ are present. The first is of the famous Ricker-type used to model negative density effects and the second, which is increasing in w, is one often used to model component Allee effects [3, 10]. We take

$$f_i(w) = b_i \exp(-c_i w) \exp\left(1 - e^{-d_i w}\right) \tag{13}$$

for $c_i \geq 0$ and $d_i \geq 0$. A rationale for this model is that fertility $f_i(w)$ is the product of a per capita birth rate times the probability that a newborn survives to the next census. In this model, the birth rates are negatively affected by increased population density w while newborn survival is positively affected by increased population density (for example, because of herding protection of newborns from predators [3, 10]).

The bifurcation parameter is $\lambda = b_2$ and

$$\beta(w) = \exp(-c_2 w) \exp\left(1 - e^{-d_2 w}\right).$$

The graph G in the (λ, w)-plane, is that of $\lambda = \lambda(w)$ given by (8), i.e.

$$\lambda(w) = \frac{1}{s_1 \beta(w)} \left(1 - s_1 s_2 f_3(w) - s_1 s_2 s_3 f_4(w)\right). \tag{14}$$

The bifurcation point $\lambda_0 = \lambda(0)$, which we assume is positive, is given by (9)

$$\lambda_0 = \frac{1 - s_1 s_2 b_3 - s_1 s_2 s_3 b_4}{s_1} > 0.$$

The direction of bifurcation is determined by the sign of

$$\lambda'(0) = c_2 \lambda_0 + b_3 c_3 s_2 + b_4 c_4 s_2 s_3 - \lambda_0 d_2 - b_3 s_2 d_3 - b_4 s_2 s_3 d_4.$$

Thus, we see that in the absence of component Allee effects, i.e. when all $d_i = 0$, the bifurcation is forward since $\lambda'(0) > 0$ and the graph of G is increasing at the bifurcation point $(\lambda, w) = (\lambda_0, 0)$. If, on the other hand, component Allee effects d_i are sufficiently large so that

$$\lambda_0 d_2 + b_3 s_2 d_3 + b_4 s_2 s_3 d_4 > c_2 \lambda_0 + b_3 c_3 s_2 + b_4 c_4 s_2 s_3$$

i.e., so that $\lambda'(0) < 0$, then the bifurcation is backward.

Figure 1a shows an example of the graph G when component Allee effects are absent. By Theorem 1 we know the positive equilibria are LAS at least near the

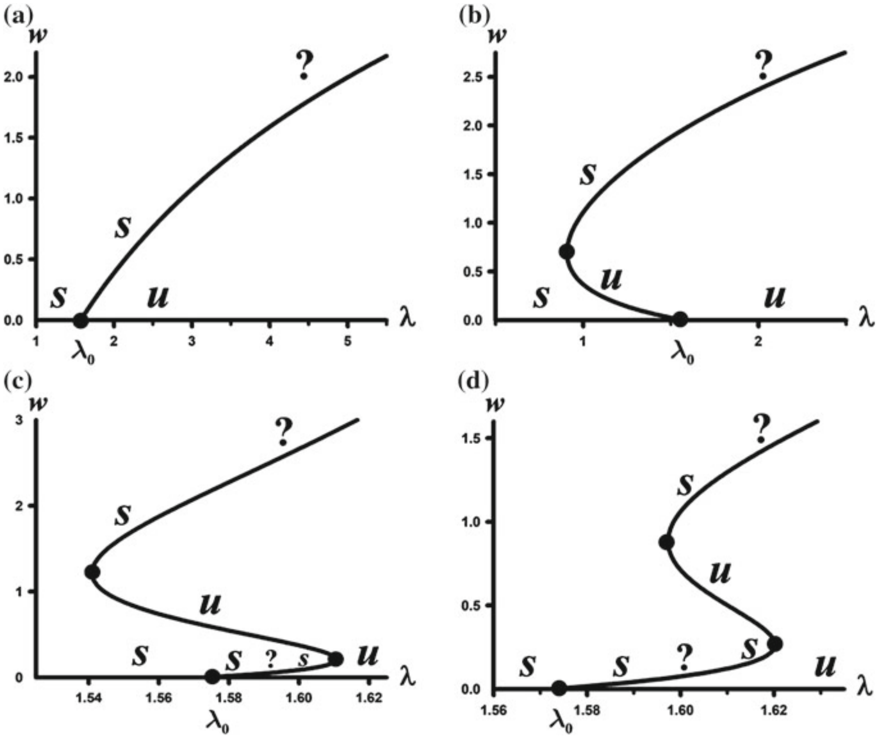

Fig. 1 In all plots of the graph G defined by (14)–(13) used parameter values $b_2 = b_3 = 1/4$, $s_1 = 1/2$, $s_2 = s_3 = 9/10$. **a Forward bifurcation:** $c_1 = 1/2$, $c_2 = 1/2$, $c_3 = 1/2$, $d_1 = 0$, $d_2 = 0$, $d_3 = 0$; **b Backward bifurcation and strong Allee effect:** $c_1 = 1/2$, $c_2 = 1/2$, $c_3 = 1/2$, $d_1 = 2$, $d_2 = 2$, $d_3 = 2$; **c Forward bifurcation and strong Allee effect:** $c_1 = 0$, $c_2 = 1/5$, $c_3 = 9/2$, $d_1 = 1/100$, $d_2 = 2$, $d_3 = 1/5$; **d Hysteresis:** $c_1 = 0$, $c_2 = 1/3$, $c_3 = 9/2$, $d_1 = 1/100$, $d_2 = 2$, $d_3 = 1/5$. The letters u stands for unstable equilibria of the nonlinear matrix model (4)–(12). The letter s stands for LAS equilibria, but only in neighborhoods of critical (bifurcation) points, indicated by solid circles, as guaranteed by Theorem 1. Outside such neighborhoods, equilibrium stability is not assured, as indicated by the question marks

bifurcation point. Figure 1b shows an example when the bifurcation is backward. In this case, Theorem 1 tells us that the positive equilibria corresponding to points (λ, w) on the increasing segment of G are LAS at least near the critical point (a saddle node bifurcation point). This is an example of a backward bifurcation producing a strong Allee effect, i.e. an interval of parameter values $\lambda < \lambda_0$ for which there exists both a stable positive equilibrium and a stable extinction equilibrium (and hence survival is initial condition dependent). Figure 1c shows an interesting case when a strong Allee effect occurs in an example when the bifurcation is forward. Finally, Fig. 1d shows a case of hysteresis and multiple stable positive equilibria, which illustrates the complicated geometry that can arise in a nonlinear Leslie model (4) when component Allee effects are present in each of the fertility terms.

5 Some Concluding Remarks

We have considered only Leslie matrix models in this paper. The geometric analysis of equilibria and their stability properties, as given in Theorem 1, are straightforwardly extendable to any model in which the transition matrix T is density independent and has spectral radius less than 1 and the fertility matrix depends on a single total weighted population size w provided there is only one newborn class (i.e. all but one row of F is a row of zeroes). This is because for such matrices there is an explicit formula for R_0 [4, 5, 12]. An example is an Usher, or standard population size structured, matrix [2, 5, 6]. It is an open question, however, whether this method can be successfully used when the transition matrix T also depends on w. Other open problems involve the construction of geometric methods for matrix models in which F and T have other types of nonlinear dependencies, for example, a dependency on more than one weighted population size. Examples in [13] suggest that this will not be, in general, straightforward.

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