

Backward Bifurcations and Strong Allee Effects in Matrix Models for the Dynamics of Structured Populations

J. M. Cushing¹

*Department of Mathematics, 617 N Santa Rita, University of Arizona, Tucson, AZ 85721, USA;
Interdisciplinary Program in Applied Mathematics, University of Arizona, Tucson, AZ 85721, USA*

Abstract: In nonlinear matrix models, strong Allee effects typically arise when the fundamental bifurcation of positive equilibria from the extinction equilibrium at $r = 1$ (or $R_0 = 1$) is backward. This occurs when positive feedback (component Allee) effects are dominant at low densities and negative feedback effects are dominant at high densities. This scenario allows population survival when r (or equivalently R_0) is *less* than 1, provided population densities are sufficiently high. For $r > 1$ (or equivalently $R_0 > 1$) the extinction equilibrium is unstable and a strong Allee effect cannot occur. We give criteria sufficient for a strong Allee effect to occur in a general nonlinear matrix model. An juvenile-adult example model illustrates the criteria as well as some other possible phenomena concerning strong Allee effects (such as positive cycles instead of equilibria).

Keywords: Allee effects, structured population dynamics, equilibrium, bifurcation, backward bifurcation, stability

1 Introduction

The majority of nonlinear population dynamic models appearing in the literature are based on negative feedback effects caused by increased population density. That is to say, they are based on negative correlations between increased population density and (per capita) model components that describe vital parameters relating to individual fitness (fertility, survivorship, growth rates, metabolic rates, etc.). Although interest in positive correlations between increased density and fitness arose as early as the 1930's in the work of W. C. Allee [1, 2, 3], little theoretical or applied studies of such effects appeared in the literature until the end of last century. A seminal paper of Dennis [18] describes the early history of Allee effects and introduces some basic models in which fertility (specifically, the probability of finding mates) is the mechanism responsible for the positive feedback effects. In his work Allee described many other biological and environmental causes responsible for such positive feedback effects. The recent book by Courchamp et al. [5] also describes many mechanism for Allee effects that have now been well documented by ecologists. This book and its large bibliography demonstrate the exponential growth in interest in Allee effects that has occurred during the last couple of decades. This interest has been spurred by concerns about endangered species, conservation management, sustainability, species extinction, and biological diversity. Positive feedback effects, due to increases of low level densities, on parameters relating to individual fitness – called *component Allee effects* – can, if sufficiently “strong”, lead to a threshold population density below which a population will go extinct. It is argued that this threshold can be significantly higher than that at which random events dominate extinction events and therefore provide a deterministic mechanism for extinction [5, 18].

¹Corresponding author. Email: cushing@math.arizona.edu

We say that a population dynamic model has a *strong Allee effect* if there exist both a positive and an extinction attractor. The typical case involves equilibria, i.e., an extinction equilibrium and a positive equilibrium, both of which are stable. (However, we give an example in Section 4 in which a strong Allee effect occurs with a stable positive 2-cycle in place of a stable positive equilibrium.) In this paper, strong Allee effects are considered from the point of view of bifurcation theory and their relation to a backward bifurcation is explored. Because strong Allee effects concern extinction, the stability or instability of an extinction equilibrium in a model is of fundamental interest. The stability of the extinction equilibrium is, of course, governed by the parameter values in the model. In general, convenient parameters for such an investigation are the inherent population growth rate r and the inherent net reproductive number R_0 . These quantities (defined for matrix models in Section 2) are combinations of model parameters related to various vital rates (birth, death, growth, maturation, etc.). The extinction equilibrium is stable if $r < 1$ (equivalently $R_0 < 1$) and is unstable if $r > 1$ (equivalently $R_0 > 1$). Therefore, in general, a strong Allee effect cannot occur if $r > 1$ (or equivalently if $R_0 > 1$).

In this paper, a bifurcation theoretic approach is taken to study strong Allee effects in nonlinear matrix models for the discrete time dynamics of structured populations [4, 12, 14]. Theorem 3 in Section 3 gives criteria sufficient to guarantee that a strong Allee effect occurs in a nonlinear matrix model for values of $r < 1$ (or $R_0 < 1$). Key to this approach are the fundamental bifurcation Theorems 1 and 2 in Section 2. These theorems describe how the destabilization of the extinction equilibrium at $r = 1$ ($R_0 = 1$) results in the bifurcation, from the extinction equilibrium, of a continuum of positive (survival) equilibria and how, at least near bifurcation, the stability of these bifurcating positive equilibria depends on the direction of bifurcation. Forward bifurcating positive equilibria (which correspond to $r \gtrsim 1$ or $R_0 \gtrsim 1$) are stable while backward bifurcating equilibria (which correspond to $r \lesssim 1$ or $R_0 \lesssim 1$) are unstable. As will be seen in Section 2, backward bifurcations occur when the positive feedbacks, arising from the model's component Allee effects at low densities, are sufficiently large in magnitude (relative to any negative feedback effects due to increased low level density). It will turn out that this low density phenomenon, when coupled with dominant negative feedbacks at high population levels, can lead to strong Allee effects. Mathematically, this occurs because the backward bifurcating continuum "folds over" or "turns around" at a saddle-node bifurcation (sometimes called a blue-sky or tangent bifurcation) and creates multiple positive (survival) equilibria, which in turn can, if they are stable, create a strong Allee effect.

We focus on strong Allee effects involving a stable extinction equilibrium in the presence of a stable positive (survival) equilibrium, as opposed to other kinds of positive attractors. However, the example given in Section 4 not only demonstrates the theorems of Section 3, but also provides an example of a strong Allee effect associated with a stable positive cycle rather than a stable positive equilibrium.

2 A fundamental bifurcation theorem for matrix models

Let $x = \text{col}(x_i)$ denote a column vector in n -dimensional Euclidean space R^n and let

$$R_+^n = \{x : x_i > 0 \text{ for all } i\}, \quad \text{cl}(R_+^n) = \{x : x_i \geq 0 \text{ for all } i\}, \quad \partial R_+^n = \text{cl}(R_+^n) \setminus R_+^n.$$

Let Ω be an open set in R^n such that $cl(R_+^n) \subset \Omega$. We denote the spectral radius of a $n \times n$ matrix M by $\rho[M]$ and use the norm

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

on R^n .

The vector x represents a distribution of population densities in n -classes which we wish to follow in time. The discrete time dynamics are described by the equation

$$x' = P(x)x \tag{1}$$

where $P(x) = (p_{ij}(x))$ is an $n \times n$ matrix and the prime “ ’ ” denotes the distribution vector at the next time step [21]. We assume

A1: $p_{ij}(x) \in C^2(\Omega, [0, +\infty))$ and $P(x)$ is primitive for all $x \in \Omega$.

Under A1, we know from Perron-Frobenius theory that for each $x \in \Omega$ the matrix $P(x)$

- (a) has a positive, simple, strictly dominant eigenvalue (namely, $\rho[P(x)]$) which has an associated positive eigenvector and
 - (b) no other eigenvalue of $P(x)$ has a nonnegative eigenvector.
- (2)

In order to introduce a bifurcation parameter into (1) we write

$$P(x) = r\bar{P}(x) \quad \text{where} \quad \rho[\bar{P}(0)] = 1.$$

Note that (a) and (b) are also true for the normalized projection matrix $\bar{P}(x)$. The quantity $r = \rho[P(0)]$, which is the strictly dominant eigenvalue of $P(0)$, is the *inherent population growth rate*. We re-write (1) as

$$x' = r\bar{P}(x)x. \tag{3}$$

An equilibrium (fixed point) $x \in R^n$ of (3) satisfies the algebraic equation

$$x = r\bar{P}(x)x \tag{4}$$

and, following [25], we refer to $(r, x) \in R \times R^n$ as an *equilibrium pair*. If a solution of (4) lies in R_+^n we say it is a *positive equilibrium*, in which case we say $(r, x) \in R \times R_+^n$ is a *positive equilibrium pair*.

Write the equilibrium equation (4) as

$$x = r\bar{P}(0)x + h(r, x) \tag{5}$$

where

$$|h(r, x)| = O(|x|^2) \quad \text{near } x = 0 \text{ uniformly for } r \text{ on finite intervals.}$$

The Rabinowitz Alternative from nonlinear functional analysis (Theorems 1.3 and 1.40 in [25]) guarantees the existence of a *(maximal) continuum C of equilibrium pairs* of (5) that bifurcates from $(r, x) = (1, 0)$ (i.e., a closed and connected set of equilibrium pairs that contains $(1, 0)$) for which $C \setminus \{(1, 0)\}$ lies in $R_+ \times R_+^n$ (i.e. consists positive equilibrium pairs) near $(r, x) = (1, 0)$ and which either (i) meets infinity (i.e. is unbounded) in $R \times \Omega$ or (ii) meets $(\hat{r}, 0)$ where $\hat{r} \neq 1$ is a real characteristic value of $\bar{P}(0)$.² Also see [20]. For a proof of the following result, see Appendix A.

² A characteristic value of a matrix is the reciprocal of a real nonzero eigenvalue.

Theorem 1 Under assumption A1, the matrix equation (4) has an unbounded continuum \mathcal{C} of equilibrium pairs that bifurcates from $(r, x) = (1, 0)$ and for which $\mathcal{C} \setminus \{(1, 0)\} \subset R_+ \times R_+^n$.

This theorem says, under assumption A1, that the matrix equation (4) has an unbounded continuum of positive solution pairs that bifurcates from $(r, x) = (1, 0)$. Let

$$\Sigma_r \doteq \{r : (r, x) \in \mathcal{C} \setminus \{(1, 0)\}\} \subset R_+$$

denote the *spectrum* of \mathcal{C} , i.e., the set of r values corresponding to positive equilibria from the continuum \mathcal{C} . Let the *range* of \mathcal{C} be denoted by

$$\Xi \doteq \{x : (r, x) \in \mathcal{C} \setminus \{(1, 0)\}\} \subset R_+^n.$$

The range Ξ is the set of positive equilibria associated with the continuum \mathcal{C} . Since \mathcal{C} is a continuum, the closures $cl(\Sigma_r)$ and $cl(\Xi)$ of Σ_r and Ξ in R_+^1 and R_+^n respectively are continua. Moreover, it follows from Theorem 1 that $1 \in cl(\Sigma_r)$ and either the spectrum or the range (or both) are unbounded.

The bifurcation occurring at $(r, x) = (1, 0)$ in Theorem 1 is said to be *forward* (or supercritical or to-the-right) if $r > 1$ for those equilibrium pairs $(r, x) \in \mathcal{C}$ in a neighborhood of $(1, 0)$. If, on the other hand, $r < 1$ for equilibrium pairs $(r, x) \in \mathcal{C}$ in a neighborhood of $(1, 0)$, then the bifurcation is said to be *backward* (or subcritical or to-the-left).

The next theorem shows that the stability of the equilibria lying on the bifurcating continuum \mathcal{C} near the bifurcation point $(1, 0)$ is determined by the direction of bifurcation, which in turn is determined by sign the quantity

$$\bar{\kappa} \doteq -\frac{w\bar{D}v}{wv} \text{ where } \bar{D} \doteq (\nabla^0 \bar{p}_{ij}v) \text{ at } r = 1. \quad (6)$$

Here $v > 0$ and $w > 0$ are the right and left eigenvectors associated with eigenvalue 1 of $\bar{P}(0)$ and $\nabla^0 \bar{p}_{ij}$ is the gradient of $\bar{p}_{ij}(x)$ with respect to x evaluated at $x = 0$ (written as a row vector). Since \bar{p}_{ij} is a scalar multiple r of p_{ij} , the sign of $\bar{\kappa}$ is the same as the sign of

$$\kappa \doteq -\frac{wDv}{wv} \text{ where } D \doteq (\nabla^0 p_{ij}v). \quad (7)$$

Theorem 2 [12, 14] Assume A1. Near the point $(r, x) = (1, 0)$ we have the following two alternatives.

(a) $\kappa < 0$ implies the bifurcation of \mathcal{C} is backward and the positive equilibria $x \in \Xi$ from the continuum \mathcal{C} are unstable for $r \lesssim 1$.

(b) $\kappa > 0$ implies the bifurcation of \mathcal{C} forward and the positive equilibria $x \in \Xi$ from the continuum \mathcal{C} are (locally asymptotically) stable for $r \gtrsim 1$.

Note 1. If all partial derivatives of entries in the projection matrix satisfy $\partial_k^0 p_{ij}(0) \leq 0$ and are not all equal 0, then $\kappa > 0$ and the bifurcation is forward and hence stable. This is a useful observation since in applications one can often observe this criterion by inspection and avoid the calculation of κ or any linearized stability analysis.

For $\kappa < 0$ to hold, at least one derivative $\partial_k^0 p_{ij}(0)$ must be positive. That is to say, at least one component in the projection matrix must have a positive feedback relationship with increased

density in some demographic class, i.e. a component Allee effect. Such component Allee effects do not necessarily lead to a backward bifurcation, however. To do so, their magnitudes must be sufficiently large so as to dominate any negative derivatives appearing in κ and make κ negative. This would certainly be true, for example if all partial derivatives satisfy $\partial_{\kappa}^0 p_{ij}(0) \geq 0$ and are not all equal 0, that is to say, if there are no low density negative feedback components at all (and at least one component Allee effect is present).

Note 2. Given the generality of Theorems 1 and 2 (and their analogous counterparts for other types of population models, such as models based on ordinary and partial differential, integral, integro-differential, integro-difference, etc.), they can together be referred to as a Fundamental Bifurcation Theorem for nonlinear population dynamics.

3 Strong Allee effects from backward bifurcations

In this section we consider the matrix equation (3) when it has a backward bifurcation at $(r, x) = (1, 0)$. Therefore, we assume

A2: $\kappa < 0$ where κ is given by (7).

Under this assumption the matrix equation (3) has, by Theorem 2, a backward bifurcation at $r = 1$ and consequently has unstable positive equilibria for $r \gtrsim 1$. Recall that the extinction equilibrium $x = 0$ is stable when $r < 1$. In addition, we make the following assumption.

A3: (a) there exists an $x_+ \in R_+^n$ such that $x_+ = \bar{P}(x_+)x_+$
 (b) $\rho[J(x_+)] < 1$.

Another way of stating A3 is that (a) there exists a positive equilibrium $x_+ \in R_+^n$ of the matrix equation (1) with $r = 1$ and (b) this positive equilibrium is (locally asymptotically) stable by linearization.

Theorem 3 *Under the assumptions A1, A2 and A3 the matrix equation (3) has a strong Allee effect at least for $r \gtrsim 1$.*

For a proof of this theorem see Appendix B.

Note 3. For the case $n = 1$ of one dimensional maps, Theorem 3 provides criteria that are sufficient for the occurrence of a strong Allee effect involving a stable positive and extinction equilibria. These criteria, which are sufficient (but not necessary) for a strong Allee effect by our definition, are the same criteria used in [23] to define a strong Allee effect in a one dimensional map.

One way to guarantee A3(a) holds is to show two things: that the bifurcation is backward (for example by calculating κ or $\bar{\kappa}$) and that the spectrum Σ_r is unbounded in R_+ . From these facts it follows that $1 \in \Sigma_r$, which implies in turn that A3(a) holds.

In applications, one can often show the spectrum Σ_r is unbounded by an investigation of the equilibrium equation

$$x = r\bar{P}(x)x$$

which, of course, is satisfied by all pairs $(r, x) \in \mathcal{C}$. For example, consider the following assumption.

A4: There exists a real valued function $m(r)$, defined for $r \geq 1$ and bounded on bounded subintervals, such that for every equilibrium pair $(r, x) \in \mathcal{C}$ the inequality

$$|x| \leq m(r) \tag{8}$$

holds.

Under the a priori bound (8) the spectrum Σ_r is unbounded (because a bounded spectrum would imply a bounded range, which would contradict the fact that the continuum \mathcal{C} is unbounded).

Corollary 1 *Suppose A1 and A4 hold. The spectrum Σ_r is unbounded and hence $cl(\Sigma_r)$ is an interval of the form $[r^{\min}, +\infty)$ for $0 < r^{\min} \leq 1$.*

If the spectrum is unbounded and a backward bifurcation occurs, then $r^{\min} < 1$. It follows that $1 \in \Sigma_r$, which implies there is a positive equilibrium corresponding to $r = 1$.

Corollary 2 *If A1, A2 and A4 hold, then $1 \in \Sigma_r$ and A3(a) holds.*

Note 4. It is, of course, possible that A3(a) holds but A3(b) fails to hold. We will see an example of this possibility in Section 4.

Note 5. We have assume that the projection matrix $P(x)$ in the matrix equation (1) has the form

$$r\bar{P}(x) \text{ where } \rho[\bar{P}(0)] = 1.$$

This normalization implies the coefficient r is the spectral radius of the projection matrix at $x = 0$ and is therefore the inherent population growth rate. This normalization is convenient for theoretical purposes, but in applications it is unlikely possible to write the normalization explicitly since formulas for r are not in general available. Instead, it is often more convenient to use the inherent net reproductive number R_0 as the bifurcation parameter, which as it turns out can be substituted for r in the theorems above. The quantity R_0 is defined as follows.

In models of populations closed to immigration/emigration, the projection matrix can be additively decomposed

$$P(x) = F(x) + T(x)$$

where $F(x)$ is a nonnegative matrix consisting of class-specific fecundities (that is to say, the distribution newborns at the next time step is $F(x)x$). The transition matrix $T(x)$ describes how surviving individuals move between classes. Specifically, the ij^{th} entry in $T(x)$ is the fraction of j -class individuals that survive (a unit of time) and move to class i . The transition matrix $T(x)$ is therefore nonnegative, has entries that are less than or equal to 1 and column sums less than or equal to 1. The inherent net reproductive number is defined to be

$$R_0 \doteq \rho \left[F(0) (I - T(0))^{-1} \right]$$

(where I is the $n \times n$ identity matrix). If $\rho(T(0)) < 1$ (which means the expected life time of an individual is finite), then it is known that r and R_0 satisfy one of the following [17, 14, 22]:

$$0 < R_0 < r < 1 \text{ or } r = R_0 = 1 \text{ or } 1 < r < R_0.$$

The equilibrium equation $x = P(x)x$ and be replaced by

$$\begin{aligned} x &= (F(x) + T(x))x \\ x &= (F(0) + T(0))x + O(|x|^2) \end{aligned}$$

and, if we normalize the fertility matrix so that $F(0) = R_0 \bar{F}(0)$ where $\bar{F}(0) = I$, by

$$x = R_0 (I - T(0))^{-1} \bar{F}(0) + O(|x|^2)$$

and equation that can be analyzed by the Rabinowitz Alternatives using R_0 as the bifurcation parameter. For these reasons,

r can be replaced by R_0 in assumption A4, Theorems 1-3, and Corollaries 1 and 2. The spectrum Σ_{R_0} of R_0 values from the continuum C of positive equilibrium pairs (R_0, x) replaces that of the spectrum of r values.

The advantage of using R_0 as the bifurcation parameter is that it is often the case that explicit formulas in terms of the entries in the projection matrix P are available for R_0 , but not for r [12, 14]. We will use this fact in the next section.

4 An Example

The 2×2 projection matrix

$$P(x) = \begin{pmatrix} 0 & b\beta(x_2) \\ s_1\sigma(x_2) & s_2 \end{pmatrix} \quad (9)$$

in the matrix model (1) describes a population classified into juveniles x_1 and adults x_2 . It assumes that the density effects occur in juvenile survival $s_1\sigma(x_2)$ and adult fecundity $b\beta(x_2)$ and depend only on adult density x_2 . Adult survivorship s_2 is assumed density independent.

We assume that increased adult density x_2 , at all levels, has a negative effect on juvenile survival so that $\sigma(x_2)$ is a decreasing function of x_2 . On the other hand, we assume that increased adult density x_2 , at least at low densities, has a *positive* effect on adult fecundity so that $\beta(x_2)$ is an increasing function of $x_2 \gtrsim 0$. Under this assumption $b\beta(x_2)$ entails a component Allee effect.

Specifically, we assume the entries in the projection matrix (9) satisfy the following conditions:

$$\begin{aligned} 0 < s_1 \leq 1, 0 < s_2 < 1, \sigma, \beta \in \mathcal{C}^2(\Omega \rightarrow R_+^1) \text{ on an open interval } \Omega \supset \text{cl}(R_+^1). \\ \sigma : R_+^1 \rightarrow (0, 1], \sigma(0) = 1, \sigma'(x) < 0 \text{ and } \beta : R_+^1 \rightarrow R_+^1, \beta(0) = 1, \beta'(0) > 0. \\ \beta(x) \text{ and } \sigma(x)x \text{ are bounded for } x \geq 0. \end{aligned} \quad (10)$$

We apply Theorem 3 using the inherent net reproductive number in place of r (see Note 5)

$$R_0 \doteq b \frac{s_1}{1 - s_2}.$$

To do this we need to investigate the assumptions A2 and A3 required for that theorem.

Right and left eigenvectors v and w associated with eigenvalue 1 of $P(0)$ when $R_0 = 1$, i.e. of the matrix

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

are

$$v = \begin{pmatrix} 1 \\ \frac{s_1}{1-s_2} \end{pmatrix} \text{ and } w = \begin{pmatrix} \frac{1-s_2}{2-s_2} & \frac{1}{s_1} \frac{1-s_2}{2-s_2} \end{pmatrix}.$$

These are chosen so that $wv = 1$ and hence $\kappa \doteq -wDv$ where

$$D \doteq (\nabla^0 p_{ij} v) = \begin{pmatrix} 0 & \beta'(0) \\ \frac{s_1^2}{1-s_2} \sigma'(0) & 0 \end{pmatrix}.$$

Consequently

$$\kappa = -\frac{s_1}{2-s_2} (\sigma'(0) + \beta'(0)).$$

Assumption A2 holds and a backward bifurcation occurs if

$$\sigma'(0) + \beta'(0) > 0. \quad (11)$$

This inequality is interpreted as meaning that the positive feedback effect of adult density on adult fecundity, as measured by $\beta'(0) > 0$, outweighs its negative effect on juvenile survival, as measured by $\sigma'(0) < 0$.

To investigate A3(a) we re-write the equilibrium equations

$$\begin{aligned} x_1 &= b\beta(x_2)x_2 \\ x_2 &= s_1\sigma(x_2)x_1 + s_2x_2 \end{aligned}$$

equivalently as

$$x_1 = R_0 \frac{1-s_2}{s_1} \beta(x_2)x_2 \quad (12a)$$

$$x_2 = R_0\sigma(x_2)\beta(x_2)x_2. \quad (12b)$$

For any positive solution of these equations we have, by (10) and (12b), the bound $|x_2| \leq k_1 R_0$ for some constant $k_1 > 0$. From (12a) we obtain, for some constant $k_2 > 0$ such that $0 \leq \beta(x) \leq k_2$, the bound

$$|x_1| \leq R_0 \frac{1-s_2}{s_1} k_2 |x_2| \leq \frac{1-s_2}{s_1} k_1 k_2 R_0^2$$

and hence the bound

$$|x| = |x_1| + |x_2| \leq \frac{1-s_2}{s_1} k_1 k_2 R_0^2 + k_1 R_0 \doteq m(R_0).$$

The requirement A4 (with R_0 replacing r , as in Note 5) is satisfied. Corollaries 1 and 2 imply that A3(a) holds, i.e. that there exists a positive equilibrium $x^+ = \text{col}(x_1^+, x_2^+)$ with $R_0 = 1$.

Since the product $\sigma(x_2)\beta(x_2)$ equals 1 and has a positive derivative at $x_2 = 0$ and since it also equals 1 when evaluated at a positive $x_2 = x_2^+ > 0$, it follows that the equation $\sigma(x_2)\beta(x_2) = 1$ has a (at least one) positive root x_2^+ at which $\sigma(x_2)\beta(x_2)$ is nonincreasing. We assume something slightly stronger, namely, that there is a positive root of $\sigma(x_2)\beta(x_2) = 1$ at which $\sigma(x_2)\beta(x_2)$ strictly decreasing, i.e.

$$\left. \frac{d}{dx} (\sigma(x)\beta(x)) \right|_{x=x_2^+} < 0. \quad (13)$$

Finally we need to consider assumption A3(b), namely the requirement that the positive equilibrium

$$x^+ = \begin{pmatrix} \frac{1-s_2}{s_1} \beta(x_2^+) x_2^+ \\ x_2^+ \end{pmatrix}$$

is stable by linearization. The Jacobian matrix, evaluated at this equilibrium, is

$$J(x^+) = \begin{pmatrix} 0 & \frac{1-s_2}{s_1} [\beta(x_2^+) + \beta'(x_2^+) x_2^+] \\ s_1 \sigma(x_2^+) & (1-s_2) \sigma'(x_2^+) \beta(x_2^+) x_2^+ + s_2 \end{pmatrix}.$$

Note that x_2^+ , as a root of $\sigma(x)\beta(x) = 1$, does not depend on s_2 and that the eigenvalues of $J(x^+)$ are $\lambda_1 = 1$ and $\lambda_2 = 0$ when $s_2 = 1$. Define $\varepsilon \doteq 1 - s_2 > 0$ and treat the eigenvalues $\lambda_i = \lambda_i(\varepsilon)$ of $J(x^+)$ as functions of $\varepsilon \approx 0$. By continuity $|\lambda_2(\varepsilon)| < 1$ for $\varepsilon \approx 0$. To determine the magnitude of $\lambda_1(\varepsilon)$ for $\varepsilon \gtrsim 0$ we calculate the derivative

$$\lambda_1'(0) = x_2^+ \left. \frac{d}{dx} (\sigma(x)\beta(x)) \right|_{x=x_2^+}$$

which, by (13), is negative. It follows that $0 < \lambda_1(\varepsilon) < 1$, and hence A3(b) holds, for $\varepsilon \gtrsim 0$.

From Theorem 3 we get the following result.

Theorem 4 *Consider the juvenile-adult matrix model (1) with projection matrix (9) under the smoothness assumptions (10) on β and σ . Assume the backward bifurcation condition (11) and the inequality (13) hold. Then for $s_2 \lesssim 1$ the juvenile-adult model has a strong Allee effect when $R_0 = bs_1(1-s_2)^{-1} \lesssim 1$.*

We illustrate Theorem 4 with a specific example. This example will also illustrate other features of an Allee effect that can occur when created by a backward bifurcation. Take

$$\sigma(x_2) \doteq \frac{1}{1+cx_2}, \quad \beta(x_2) \doteq \frac{1+ax_2}{1+cx_2} \text{ with } a > 2c > 0. \quad (14)$$

These functions satisfy the conditions required in (10) with Ω taken to be the interval $-1/c < x_2 < +\infty$. The backward bifurcation criterion (11)

$$\sigma'(0) + \beta'(0) = a - 2c > 0$$

is satisfied.

What remains to be verified for the application of Theorem 4 is that the inequality (13) holds at a positive root of the equation $\sigma(x_2)\beta(x_2) = 1$, i.e. of the equation

$$\frac{1+ax_2}{(1+cx_2)^2} = 1.$$

This equation has roots $x_2 = 0$ and

$$x_2^+ = \frac{a-2c}{c^2} > 0.$$

A calculation shows

$$\left. \frac{d(\sigma(x)\beta(x))}{dx} \right|_{x=x_2^+} = -\frac{c^2(a-2c)}{(a-c)^2} < 0$$

and hence inequality (13) does hold. Theorem 4 implies a strong Allee effect occurs in this example if $s_2 \lesssim 1$ and $R_0 \lesssim 1$.

For this example, we can in fact carry out further analysis. For positive equilibria, we can cancel x_2 from the equilibrium equation (12b) and arrive at the equations

$$x_1 = R_0 \frac{1 - s_2}{s_1} \beta(x_2) x_2 \quad (15a)$$

$$1 = R_0 \sigma(x_2) \beta(x_2) \quad (15b)$$

for positive equilibria. In the specific case (14), we can easily solve the second equation

$$R_0 \frac{1 + ax_2}{(1 + cx_2)^2} = 1 \quad (16)$$

for positive solutions

$$0 < x_2^+ = \frac{(aR_0 - 2c) + \sqrt{(aR_0 - 2c)^2 + 4c^2(R_0 - 1)}}{2c^2} \text{ for } R_0^{\min} \leq R_0 < +\infty$$

$$0 < x_2^- = \frac{(aR_0 - 2c) - \sqrt{(aR_0 - 2c)^2 + 4c^2(R_0 - 1)}}{2c^2} \text{ for } R_0^{\min} \leq R_0 < 1$$

where

$$R_0^{\min} \doteq 4c \frac{a - c}{a^2} > 0.$$

Note that

$$x_2^- < x_2^+ \quad \text{for } R_0^{\min} < R_0 < 1$$

$$x_2^+ = x_2^- = x_m \quad \text{for } R_0 = R_0^{\min}.$$

where we have defined

$$x_m \doteq \frac{a - 2c}{ca} > 0.$$

Together with

$$x_1^\pm = R_0 \frac{1 - s_2}{s_1} \frac{1 + ax_2^\pm}{1 + cx_2^\pm} x_2^\pm$$

obtained from equilibrium equation (15a), these two roots define two positive equilibria

$$x^\pm = \begin{pmatrix} x_1^\pm \\ x_2^\pm \end{pmatrix}.$$

The spectrum is Σ_{R_0} is the half line $R_0^{\min} \leq R_0 < +\infty$ and there exist two positive equilibria x^\pm for $R_0^{\min} < R_0 < 1$ and one positive equilibrium x^+ for $1 \leq R_0 < +\infty$. At $R_0 = 1$ we have the (unique) positive equilibrium

$$x^+ = \begin{pmatrix} \frac{1 - s_2}{s_1} \frac{(a - 2c)(ac^2 + 1)}{c(a - c)} \\ \frac{a - 2c}{c^2} \end{pmatrix}.$$

Having accounted for all positive equilibria in this example, we turn our attention to their stability properties. The Jacobian of the map $x' = P(x)x$ with projection matrix (9), when evaluated at an equilibrium pair (R_0, x^\pm) is

$$J^\pm = \left(\begin{array}{cc} 0 & \frac{1-s_2}{s_1} \frac{1+2ax_2+cax_2^2}{1+ax_2} \\ \frac{s_1}{1+cx_2} & \frac{s_2+c(2s_2-1)x_2}{1+cx_2} \end{array} \right) \Big|_{x_2=x_2^\pm}$$

In calculating this Jacobian we made use of the equations (15). Stability by linearization is determined by the absolute value of the eigenvalues of J^\pm . The characteristic quadratic for J^\pm is

$$q(\lambda) \doteq \lambda^2 - \text{tr} J^\pm \lambda + \det J^\pm$$

where

$$\begin{aligned} \det J^\pm &= -(1-s_2) \frac{1+2ax_2+cax_2^2}{(1+ax_2)(1+cx_2)} \Big|_{x_2=x_2^\pm} < 0 \\ \text{tr} J^\pm &= \frac{s_2+c(2s_2-1)x_2}{1+cx_2} \Big|_{x_2=x_2^\pm}. \end{aligned}$$

The quadratic $q(\lambda)$ defines a concave upward parabola with a vertical intercept at $\det J^\pm < 0$. It follows that $q(\lambda)$ has two real roots

$$\lambda_- < 0 < \lambda_+.$$

Simple geometric observations imply that

$$\begin{aligned} 0 < \lambda_+ < 1 &\text{ if and only if } q(1) = 1 - \text{tr} J^\pm + \det J^\pm > 0 \\ -1 < \lambda_- < 0 &\text{ if and only if } q(-1) = 1 + \text{tr} J^\pm + \det J^\pm > 0 \end{aligned}$$

A calculation shows

$$q(1) = (1-s_2) \frac{2c-a+cax_2}{(1+ax_2)(1+cx_2)} x_2 \Big|_{x_2=x_2^\pm}$$

and therefore

$$q(1) > 0 \text{ if and only if } x_2^\pm > \frac{a-2c}{ca} = x_m.$$

Since $x_2^- < x_m$ we conclude that *the equilibrium x^- is unstable* (for all $R_0^{\min} < R_0 < 1$). Since $x_2^+ > x_m$ it follows that the stability (by linearization) of the equilibrium x^+ depends on λ_- . Specifically

$$x^+ \text{ stable if } q(-1) > 0 \tag{17a}$$

$$x^+ \text{ unstable if } q(-1) < 0 \tag{17b}$$

where

$$q(-1) = \frac{2s_2 - (1-3s_2)ax_2^+}{1+ax_2^+}.$$

Using these stability/instability criteria, we distinguish three cases.

Case 1. If $s_2 \geq 1/3$ then the inequality (17a) holds and x^+ is (locally asymptotically) stable for all $R_0 > R_0^{\min}$. We conclude that *there is a strong Allee effect for all R_0 satisfying $R_0^{\min} < R_0 < 1$.*

Suppose $s_2 < 1/3$. Since $q(-1) = 0$ if and only if

$$x_2^+ = \frac{2s_2}{a(1-3s_2)}$$

we see that

$$\begin{aligned} x^+ \text{ is stable if } x_2^+ < x^* \\ x^+ \text{ is unstable if } x_2^+ > x^*. \end{aligned}$$

where

$$x^* \doteq \frac{2s_2}{a(1-3s_2)}.$$

The equilibrium x^+ with component $x_2^+ = x^*$ occurs for, and only for, $R_0 = R_0^*$ where

$$R_0^* \doteq \frac{1}{1-3s_2} \frac{(a+2cs_2-3as_2)^2}{(1-s_2)a^2}.$$

We conclude

$$\begin{aligned} x^+ \text{ is stable if } R_0^{\min} < R_0 < R_0^* \\ x^+ \text{ is unstable if } R_0^* < R_0 \end{aligned}$$

Case 2. Suppose

$$s_2 < \frac{1}{3} \quad \text{and} \quad \frac{a}{c} < 1 + \sqrt{\frac{1-s_2}{1-3s_2}}.$$

Some algebra shows that in this case $R_0^* > 1$. We again conclude that *there is a strong Allee effect for all R_0 satisfying $R_0^{\min} < R_0 < 1$.*

Note that

$$2 < 1 + \sqrt{\frac{1-s_2}{1-3s_2}}$$

so that this inequality is compatible with $\frac{a}{c} > 2$.

Case 3. Suppose

$$s_2 < \frac{1}{3} \quad \text{and} \quad \frac{a}{c} > 1 + \sqrt{\frac{1-s_2}{1-3s_2}}.$$

Some algebra shows that in this case $R_0^* < 1$. We conclude that for R_0 satisfying $R_0^{\min} < R_0 < R_0^*$ *there is a strong Allee effect.*

In Cases 2 and 3 the positive equilibrium's loss of stability as R_0 increases through R_0^* is the result of the eigenvalue λ_- decreasing through -1 . This suggests a period doubling bifurcation of (stable) periodic 2-cycles. We will not formally prove that here, but the numerical simulation evidence (for example in Figures 2 and 3) corroborate this expectation. In Case 3 this means that *a strong Allee effect holds for R_0 throughout the interval $R_0^{\min} < R_0 < 1$, but that it involves a positive equilibrium on the subinterval $R_0^{\min} < R_0 < R_0^*$ and a stable 2-cycle on the subinterval $R_0^* < R_0 < 1$.*

The three scenarios represented by Cases 1-3 are illustrated in Figures 1-3. All three figures show the (parabolic) bifurcation diagram with the positive x_2 component of the continuum of positive equilibria plotted as a function of R_0 . The strong Allee effect occurs in the region enclosed by the vertical dashed lines, caused by the backward bifurcation. Figure 1 illustrates Case 1 in which a strong Allee effect occurs throughout the interval $R_0^{\min} < R_0 < 1$ and a unique stable positive equilibrium exists for $R_0 > 1$.

Figure 2 illustrates Case 2 in which a strong Allee effect occurs throughout the interval $R_0^{\min} < R_0 < 1$, but in this case the unique positive equilibrium loses its stable as R_0 increases above $R_0^* > 1$, at which point stable 2-cycles appear as shown in the phase plane plots (b) and (c).

Finally Figure 3 illustrates Case 3 in which a strong Allee effect occurs involving equilibria on the subinterval $R_0^{\min} < R_0 < R_0^*$ and involving a stable 2-cycle on the subinterval $R_0^* < R_0 < 1$.

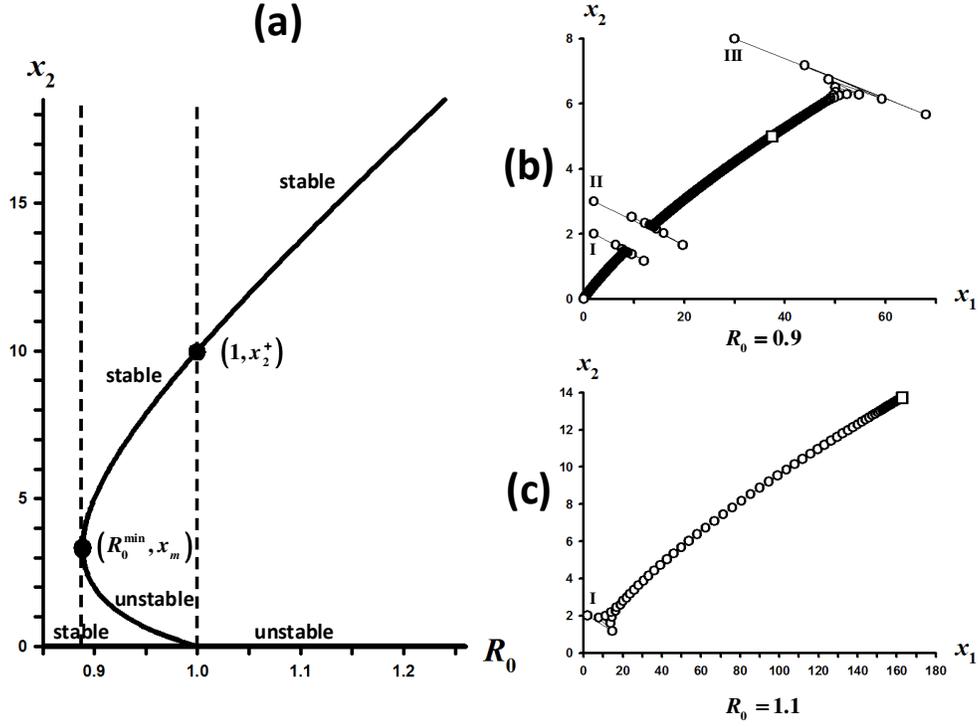


Figure 1. Parameter values are $s_2 = 0.5$ and $s_1 = 0.1$, $a = 0.3$, $c = 0.1$.

(a) The x_2 component of the positive equilibria from the bifurcating continuum \mathcal{C} are shown plotted against R_0 . The two equilibria that mark the strong Allee interval (shown as solid circles) are $(R_0^{\min}, x_m) = (8/9, 10/3)$ and $(1, x_2^+) = (1, 10)$.

(b) For $R_0 = 0.9 < 1$ a strong Allee effect is present. To illustrate this, three sample orbits in the phase plane are shown. The orbit with initial condition $(x_1, x_2) = (2, 2)$, designated by I, tends to the extinction equilibrium while the orbits with initial conditions at $(x_1, x_2) = (2, 3)$ and at $(x_1, x_2) = (30, 8)$, designated by II and III respectively, tend to the survival equilibrium $(x_1, x_2) = (37.5, 5)$, indicated by the open square.

(c) For $R_0 = 1.1 > 1$ there is a unique positive equilibrium and it is stable. In particular, the orbit with initial condition $(x_1, x_2) = (2, 2)$, designated by I, now tends to the survival equilibrium $(x_1, x_2) \approx (162.88, 13.73)$, indicated by the open square.

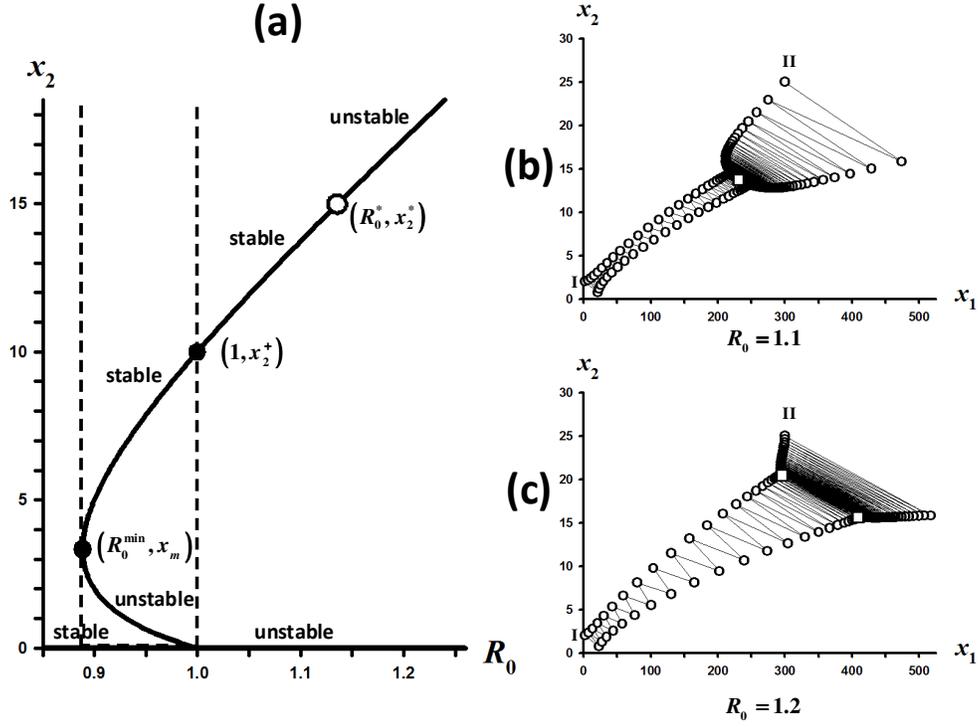


Figure 2. Parameter values are $s_2 = 0.29 < 1/3$ and $s_1 = 0.1$, $a = 0.3$, $c = 0.1$.

(a) The x_2 component of the positive equilibria from the bifurcating continuum \mathcal{C} are shown plotted against R_0 . The two equilibria that mark the strong Allee interval (shown as solid circles) are $(R_0^{\min}, x_m) = (8/9, 10/3)$ and $(1, x_2^+) = (1, 10)$. The open circle at $(R_0^*, x_2^*) \approx (1.13, 14.87)$ denotes where the positive equilibrium destabilizes.

(b) For $R_0 = 1.1 < R_0^*$ two sample orbits are shown. Orbit with initial conditions $(x_1, x_2) = (2, 2)$ and $(x_1, x_2) = (300, 25)$, designated by I and II respectively, tend to the positive equilibrium $(x_1, x_2) \approx (231.29, 13.73)$, indicated by the open square.

(c) For $R_0 = 1.1 > R_0^*$ two sample orbits are shown whose initial conditions are the same as in (b). Both orbits now tend to a periodic 2-cycle whose points are $(x_1, x_2) \approx (409.10, 15.66)$ and $(x_1, x_2) \approx (296.22, 20.49)$, which are located at the open squares.

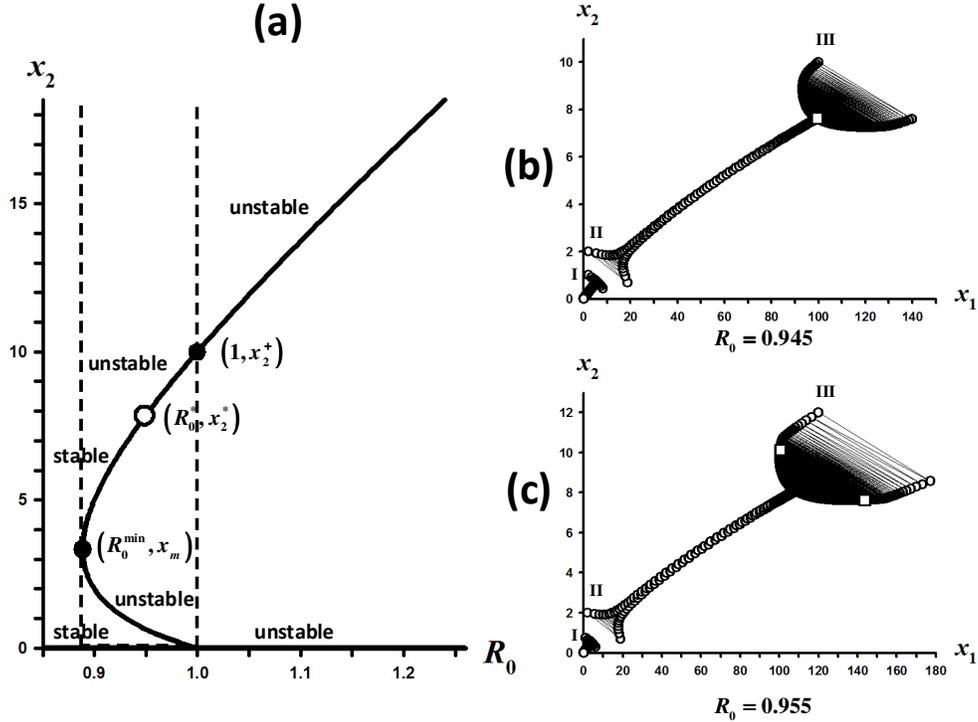


Figure 3. Parameter values are $s_2 = 0.26 < 1/3$ and $s_1 = 0.1$, $a = 0.3$, $c = 0.1$.

(a) The x_2 component of the positive equilibria from the bifurcating continuum \mathcal{C} are shown plotted against R_0 . The two equilibria that mark the strong Allee interval (shown as solid circles) are $(R_0^{\min}, x_m) = (8/9, 10/3)$ and $(1, x_2^+) = (1, 10)$. The open circle at $(R_0^*, x_2^*) \approx (0.95, 7.88)$ denotes where the positive equilibrium destabilizes.

(b) For $R_0 = 0.945 < R_0^*$ three sample orbits are shown. The orbit with initial condition $(x_1, x_2) = (2, 1)$, designated by I, tends to the extinction equilibrium while the orbits with initial conditions at $(x_1, x_2) = (2, 2)$ and at $(x_1, x_2) = (100, 10)$, designated by II and III respectively, tend to the positive equilibrium $(x_1, x_2) = (99.53, 7.63)$, which is located at the open square.

(c) For $R_0 = 0.955 > R_0^*$ three sample orbits are shown. The orbit with initial condition $(x_1, x_2) = (1, 0.75)$, designated by I, tends to the extinction equilibrium while the orbits with initial conditions at $(x_1, x_2) = (2, 2)$ and at $(x_1, x_2) = (120, 12)$, designated by II and III respectively, tend to the survival periodic 2-cycle whose points are $(x_1, x_2) \approx (143.80, 7.64)$ and $(x_1, x_2) \approx (100.70, 10.14)$, which are located at the open squares.

5 Concluding remarks

We have seen that the interplay of positive feedback effects at low population densities (component Allee effects) and negative feedback effects at high population densities can together produce, in population matrix models, a strong Allee effect for an interval of inherent net reproductive numbers r (equivalently R_0) with values less than 1. In general, strong Allee effects occur when there is a backward (transcritical) bifurcation at $r = R_0 = 1$ and a saddle-node (blue-sky or tangent) bifurcation at a value of r (or R_0) less than 1. This approach using bifurcation theory is different from that taken in [24] where different criteria for the occurrence of a strong Allee effect are obtained.

A strong Allee effect allows for the survival of a population when r (or R_0) is less than 1, provided its density remains sufficiently high, i.e. does not lie in the basin of attraction of the extinction equilibrium (the Allee basin). The boundary of the Allee basin constitutes a threshold in phase space between extinction and survival. For $r > 1$ (equivalently $R_0 > 1$) the extinction equilibrium is unstable and a strong Allee effect cannot occur.

For a strong Allee effect to occur in this way, the component Allee (positive feedback) effects at low population density must be sufficiently large in magnitude, relative to any negative feedback terms (in the sense that κ defined by (7) is positive), in order to produce a backward bifurcation of the bifurcating continuum \mathcal{C} of positive equilibria. The negative feedback effects at high population densities cause the backward bifurcating continuum \mathcal{C} to “turn around” or “fold over” at a saddle-node bifurcation point, as illustrated in bifurcation diagrams in Figures 1(a)-3(a). It is this folding over of the continuum that accounts for the multiple positive equilibria for $r < 1$ (equivalently $R_0 < 1$) and, as a result, for the possibility of a strong Allee effect (should one of the positive equilibria be stable).

We focussed in this paper on strong Allee effects in which a stable extinction equilibrium coexists with a stable positive (survival) equilibrium. However, in the example in Section 4 we saw that a strong Allee effect can occur in matrix models in which a stable extinction equilibrium coexists with a positive attractor other than an equilibrium (namely, a stable 2-cycle).

Because the fundamental bifurcation Theorems 1 and 2 are the result of general bifurcation theorems and techniques from nonlinear functional analysis, analogs of these theorems have been proved for population dynamic models based on many other types of mathematical equations, including autonomous and periodically forced ordinary and partial differential equations, integro-differential equations and integro-difference equations. For some examples see [6, 7, 8, 9, 10, 11, 12, 13, 15, 16, 19, 26]. The approach taken here towards strong Allee effects via backward bifurcations can also be taken for these types of model equations.

Acknowledgement. *The author was partially supported by NSF grant DMS 0917435.*

References

- [1] W. C. Allee, *Animal Aggregations, a Study in General Sociology*, University of Chicago Press, Chicago, 1931
- [2] W. C. Allee, *The Social Life of Animals*, 3rd edition, William Heineman Ltd, London and Toronto, 1941
- [3] W. C. Allee, O. Park, T. Park, and K. Schmidt, *Principles of Animal Ecology*, W. B. Saunders Company, Philadelphia, 1949

- [4] H. Caswell, *Matrix Population Models: Construction, Analysis and Interpretation*, Second Edition, Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts, 2001
- [5] F. Courchamp, L. Berec and J. Gascoigne, *Allee Effects in Ecology and Conservation*, Oxford University Press, Oxford, Great Britain, 2008
- [6] J. M. Cushing, *Bifurcation of periodic solutions of integro-differential equations with applications to time delay models in population dynamics*, SIAM Journal of Applied Mathematics 33, No. 4 (1977), 640-654
- [7] J. M. Cushing, *Periodic Kolmogorov systems*, SIAM Journal of Mathematical Analysis 13, No. 5 (1982), 811-827
- [8] J. M. Cushing, *Existence and stability of equilibria in age-structured population dynamics*, Journal of Mathematical Biology 20, No. 3 (1984), 259-276
- [9] J. M. Cushing, *Equilibria in structured populations*, Journal of Mathematical Biology 23, No. 1 (1985), 15-39
- [10] J. M. Cushing, *Global branches of equilibrium solutions of the McKendrick equations for age-structured population growth*, Computers and Mathematics with Applications 11 (1985), 175-188
- [11] J. M. Cushing, *Periodic Lotka-Volterra competition equations*, Journal of Mathematical Biology 24 (1986), 381-403
- [12] J. M. Cushing, *An Introduction to Structured Population Dynamics*, CBMS-NSF Regional Conference Series in Applied Mathematics, Vol. 71, SIAM, Philadelphia, 1998
- [13] J. M. Cushing, *A juvenile-adult model with periodic vital rates*, Journal of Mathematical Biology 53 (2006), 520-539
- [14] J. M. Cushing, *Matrix models and population dynamics*, appearing in *Mathematical Biology* (Mark Lewis, A. J. Chaplain, James P. Keener, Philip K. Maini eds.), IAS/Park City Mathematics Series Vol 14, American Mathematical Society, Providence, RI, 2009, p. 47-150
- [15] J. M. Cushing, *A bifurcation theorem for Darwinian matrix models*, Nonlinear Studies 17, No. 1 (2010), 1-13
- [16] J. M. Cushing and Jarred Hudson, *Evolutionary dynamics and strong Allee effects*, *Journal of Biological Dynamics* 6, No. 2 (2012), 941-958
- [17] J. M. Cushing and Zhou Yicang, *The net reproductive value and stability in structured population models*, *Natural Resource Modeling* 8, No. 4 (1994), 1-37
- [18] B. Dennis, *Allee effects: population growth, critical density, and the chance of extinction*, *Natural Resource Modeling* 3 (1989), 481-538
- [19] Henson, S. M. 1996. *Existence and stability of nontrivial periodic solutions of periodically forced discrete dynamical systems*, *Journal of Difference Equations and Applications*, 2:315-331.

- [20] H. Keilhöfer, *Bifurcation Theory: An Introduction with Applications to PDEs*, Applied Mathematical Sciences 156, Springer, New York, 2004
- [21] J. P. LaSalle, *The Stability of Dynamical Systems*, CBMS-NSF Regional Conference Series in Applied Mathematics, Vol. 25, SIAM, Philadelphia, 1976
- [22] C.-K. Li and H. Schneider, *Applications of Perron-Frobenius theory to population dynamics*, Journal of Mathematical Biology 44 (2002), 450-462
- [23] G. Livadiotis and S. Elaydi, *General Allee effect in two-species population biology*, Journal of Biological Dynamics 6 (2012), 959-973
- [24] S. J. Schreiber, *On Allee effects in structured populations*, Proceedings of the American Mathematical Society 132 (2004), 3047-3053
- [25] P. H. Rabinowitz, *Some global results for nonlinear eigenvalue problems*, Journal of Functional Analysis 7, No. 3 (1971), 487-513
- [26] S. L. Robertson and J. M. Cushing, *A bifurcation analysis of stage-structured density dependent integrodifference equations*, Journal of Mathematical Analysis and Applications 388 (2012), 490-499

Appendices

A Proof of Theorem 1.

We show that $\mathcal{C} \setminus \{(1,0)\} \subset R_+ \times R_+^n$ by contradiction. If this set inclusion were not true, then since \mathcal{C} is a continuum it would follow that $\mathcal{C} \setminus \{(1,0)\} \cap \partial(R_+ \times R_+^n) \neq \emptyset$ and we could choose a point $(r^*, x^*) \in \mathcal{C} \setminus \{(1,0)\} \cap \partial(R_+ \times R_+^n)$ and a sequence $(r_i, x_i) \in \mathcal{C} \setminus \{(1,0)\}$ such that $(r_i, x_i) \rightarrow (r^*, x^*)$. Suppose first that $x^* \neq 0$. Then from $x_i = r_i \bar{P}(x_i) x_i$ we find, by taking the limit as $i \rightarrow \infty$, that $x^* = r^* \bar{P}(x^*) x^*$. Therefore $r^* \neq 0$ and since $x^* \in \partial(R_+ \times R_+^n)$ it follows that $x^* \in \partial(R_+^n)$. This is a contradiction to the Perron-Frobenius result (2b). Suppose, on the other hand, that $x^* = 0$. Then from $x_i = r_i \bar{P}(x_i) x_i$ we have, since $x_i \in \mathcal{C} \setminus \{(1,0)\}$ and hence $x_i \neq 0$,

$$\frac{x_i}{|x_i|} = r_i \bar{P}(x_i) \frac{x_i}{|x_i|} \tag{19}$$

for all i . Take a subsequence, if necessary, so that the positive unit vectors $u_i = x_i/|x_i| \in R_+^n$ converge: $u_i \rightarrow u^* \in \partial(R_+^n)$ and $|u^*| = 1$. By taking the limit as $i \rightarrow \infty$ in (19) we see that $u^* = r^* \bar{P}(x^*) u^*$. Since $u^* \neq 0$ it follows that $r^* > 0$. Since $u^* \in \partial(R_+^n)$ we have again contradicted the Perron-Frobenius result (2b).

The proof is complete when we have ruled out Rabinowitz Alternative (ii). Suppose it were true that \mathcal{C} meets $(\hat{r}, 0)$ where $\hat{r} \neq 1$ is a real characteristic value of $\bar{P}(0)$. Then there exists a sequence $(r_i, x_i) \in \mathcal{C} \setminus \{(1,0)\}$ such that $(r_i, x_i) \rightarrow (\hat{r}, 0)$. We've shown above that $x_i \in R_+^n$ are positive vectors and therefore (19) holds for this sequence. Extracting a convergent subsequence from the positive unit vectors $u_i = x_i/|x_i| \in R_+^n$ that converges to a unit vector $u^* \in \text{cl}(R_+^n)$ we have, by passing to the limit, that $u^* = \hat{r} \bar{P}(0) u^*$. Since $\hat{r} \neq 1$ and u^* is a nonnegative eigenvector of $\bar{P}(0)$ we arrive at a contradiction to the Perron-Frobenius result (2b).

B Proof of Theorem 3.

Under assumptions A1 and A2 the trivial equilibrium is stable and there exists an unstable positive equilibrium for $r \lesssim 1$. Assumption A3 implies the existence of a positive equilibrium that is also stable. The proof of this follows from a straightforward application of the implicit function theorem to the equilibrium equation

$$r\bar{P}(x)x - x = 0 \tag{20}$$

centered on the pair $(r, x) = (1, x_+)$. The condition $\rho[J(x_+)] < 1$ in A3 implies that the Jacobian of $r\bar{P}(x)x - x$ evaluated at $(r, x) = (1, x_+)$ is nonsingular. It follows that the equilibrium equation (20) has a solution $x = x(r) \in \mathcal{C}^2$ for $r \approx 1$ that satisfies $x(1) = x_+$. Since $x_+ \in R_+^n$ and $\rho[J(x_+)] < 1$ it follows (by continuity) that $x(r) \in R_+^n$ and $\rho[J(x(r))] < 1$ for $r \approx 1$. Therefore, the positive equilibria $x(r)$ are (locally asymptotically) stable for $r \approx 1$.