

This article was downloaded by: [Cushing, Jim M]

On: 3 May 2011

Access details: Access Details: [subscription number 746291984]

Publisher Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Journal of Biological Dynamics

Publication details, including instructions for authors and subscription information:

<http://www.informaworld.com/smpp/title~content=t744398444>

On the relationship between r and R_0 and its role in the bifurcation of stable equilibria of Darwinian matrix models

J. M. Cushing^a

^a Department of Mathematics, Interdisciplinary Program in Applied Mathematics, University of Arizona, Tucson, AZ, USA

First published on: 29 June 2010

To cite this Article Cushing, J. M.(2011) 'On the relationship between r and R_0 and its role in the bifurcation of stable equilibria of Darwinian matrix models', Journal of Biological Dynamics, 5: 3, 277 – 297, First published on: 29 June 2010 (iFirst)

To link to this Article: DOI: 10.1080/17513758.2010.491583

URL: <http://dx.doi.org/10.1080/17513758.2010.491583>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.informaworld.com/terms-and-conditions-of-access.pdf>

This article may be used for research, teaching and private study purposes. Any substantial or systematic reproduction, re-distribution, re-selling, loan or sub-licensing, systematic supply or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

On the relationship between r and R_0 and its role in the bifurcation of stable equilibria of Darwinian matrix models

J.M. Cushing*

Department of Mathematics, Interdisciplinary Program in Applied Mathematics,
University of Arizona, Tucson, AZ 85721, USA

(Received 24 April 2010; final version received 1 May 2010)

If the demographic parameters in a matrix model for the dynamics of a structured population are dependent on a parameter u , then the population growth rate $r = r(u)$ and the net reproductive number $R_0 = R_0(u)$ are functions of u . For a general matrix model, we show that r and R_0 share critical values and extrema at values $u = u^*$ for which $r(u^*) = R_0(u^*) = 1$. This allows us to re-interpret, in terms of the more analytically tractable quantity R_0 , a fundamental bifurcation theorem for non-linear Darwinian matrix models from the evolutionary game theory that concerns the destabilization of the extinction equilibrium and creation of positive equilibria. Two illustrations are given: a theoretical study of trade-offs between fertility and survivorship in the evolution of an evolutionarily stable strategies and an application to an experimental study of the evolution to a genetic polymorphism.

Keywords: Darwinian matrix models; bifurcation; equilibria; net reproductive number; the evolutionary game theory

AMS 2000 Mathematics Subject Classification codes: 92D25; 92D15; 37N25

1. Introduction

Matrix models of the form

$$\hat{x}(t + 1) = P\hat{x}(t), \quad \hat{x}(0) \geq \hat{0} \tag{1}$$

are commonly used to describe the dynamics of structured populations [1,8,10]. Here $\hat{x}(t)$ is, at times $t = 0, 1, 2, \dots$, a column m -vector of numbers or densities of individuals in a specified set of classes or categories (e.g. based on age, size, or life cycle stage). The entries of the non-negative, $m \times m$ matrix projection matrix P are vital birth and death rates and transition probabilities among classes (per unit time). If P is irreducible, then its dominant eigenvalue $r > 0$ gives the inherent growth rate of the population. If $r < 1$, the population goes extinct (the extinction equilibrium $\hat{x} = \hat{0}$ is globally asymptotically stable); if $r > 1$, the population will grow exponentially (solutions with $\hat{x} \neq \hat{0}$ grow exponentially). If $r = 1$, the model has infinitely many equilibrium solutions (positive scalar multiples of a positive eigenvalue associated with $r = 1$); that is to say, a vertical

*Email: cushing@math.arizona.edu

continuum of non-extinction ‘equilibrium pairs’ $(r, \hat{x}) = (1, \hat{0})$. Thus, $r = 1$ is a bifurcation point separating population extinction from long-term persistence.

We can also express this fundamental bifurcation theorem in terms of another important quantity in population dynamics, namely the inherent net reproductive number R_0 . This number is defined as follows [12]. The projection matrix $P = F + T$ is additively decomposed by separating the birth processes, contained in the matrix F , and the survival and class transition probabilities, contained in matrix $T \neq 0$. Specifically, the i, j -entry in $F = (f_{ij})$ is the number of j -class offspring from an i -class individual (per unit time) and the i, j -entry in $T = (\tau_{ij})$ is the fraction of j -class individuals that move to class i in a unit of time. Thus, these entries satisfy

$$f_{ij} \geq 0, \quad 0 \leq \tau_{ij} \leq 1, \quad \sum_{i=1}^m \tau_{ij} \leq 1. \tag{2}$$

We assume $I - T$ is invertible (so that individuals do not have infinite life expectancy); a sufficient (but not necessary) condition for this is that all sums $\sum_{i=1}^m \tau_{ij} < 1$ (i.e. there is some loss in every class at each point in time). We also assume $F(I - T)^{-1}$ has a simple, dominant eigenvalue R_0 which has a non-negative (right) eigenvector. A basic relationship between R_0 and r is given in [12] (also see [8,10,17]): R_0 and r are both equal 1 or are both less than 1, or are both greater than 1. As a result, the fundamental bifurcation theorem described above can be expressed equivalently in terms of r or R_0 .

With regard to the analysis of population models, and in particular the basic question of extinction versus persistence, an analytic advantage in using R_0 is that, unlike r , there is often a tractable formula for R_0 expressible in terms of the entries in the fertility and transition matrices F and T .

For example, if the classification scheme is such that all newborns lie in the same class – say class $i = 1$ – then all rows of F except the first row consist entirely of zeros. This means R_0 is simply the first row, first column entry in the matrix $F(I - T)^{-1}$. Since the first column of $(I - T)^{-1}$ consists of the expected amounts of time spent in each class, it follows that R_0 is the expected number of offspring per newborn per lifetime. Specific examples include the standard size-structured population (or Usher) matrix model [1]

$$F = \begin{bmatrix} f_{11} & f_{12} & \cdots & f_{1,m-1} & f_{1m} \\ 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & 0 & 0 \end{bmatrix}, \quad T = \begin{bmatrix} \tau_{11} & 0 & \cdots & 0 & 0 \\ \tau_{21} & \tau_{22} & \cdots & 0 & 0 \\ 0 & \tau_{32} & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & \tau_{m,m-1} & \tau_{mm} \end{bmatrix} \tag{3}$$

for which

$$(I - T)^{-1} = \begin{bmatrix} \frac{1}{1 - \tau_{11}} & 0 & \cdots & 0 \\ \frac{\tau_{21}}{(1 - \tau_{11})(1 - \tau_{22})} & \frac{1}{1 - \tau_{22}} & \cdots & 0 \\ \vdots & \vdots & \cdots & 0 \\ \prod_{j=1}^i \frac{\tau_{j,j-1}}{1 - \tau_{jj}} & \prod_{j=2}^i \frac{\tau_{j,j-1}}{1 - \tau_{jj}} & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ \prod_{j=1}^m \frac{\tau_{j,j-1}}{1 - \tau_{jj}} & \prod_{j=2}^m \frac{\tau_{j,j-1}}{1 - \tau_{jj}} & \cdots & \frac{1}{1 - \tau_{mm}} \end{bmatrix}$$

and hence

$$R_0 = \sum_{i=1}^m f_{1i} \prod_{j=1}^i \frac{\tau_{j,j-1}}{1 - \tau_{jj}}. \tag{4}$$

Here, $\tau_{10} = 1$ for notational convenience. Also, $0 \leq \tau_{ii} < 1$ and hence this formula includes, as a special case, the Leslie matrix model for age-structured populations in which $\tau_{ii} = 0$ for $i = 1, 2, \dots, m - 1$.

If the entries of $P = P(\hat{x})$ are dependent on the distribution vector \hat{x} , then the matrix model (1) is non-linear and $r = r(\hat{x})$ becomes a function of \hat{x} . The extension of the fundamental bifurcation theorem, described above for linear matrix models, to nonlinear matrix models follows from theorems in [8]. For example, using the inherent growth rate $r = r(\hat{0})$ as a bifurcation parameter, these theorems imply that a global continuum of non-extinction equilibrium pairs (r, \hat{x}) bifurcates from $(1, \hat{0})$ (under suitable smoothness conditions). However, the continuum in the non-linear case is not in general vertical, as it is for linear models; that is to say, the spectrum (the set of $r = r(\hat{0})$ values obtained from equilibrium pairs (r, \hat{x}) on the bifurcating continuum) does not consist of a single point, but rather is an interval of real numbers. Moreover, the (local asymptotic) stability of the equilibria \hat{x} is determined, at least for equilibrium pairs (r, \hat{x}) near the bifurcation point $(1, \hat{0})$, by the direction of bifurcation. (This is the familiar exchange of stability property that occurs at transcritical bifurcations.) If the bifurcation is to the right (supercritical), the non-extinction equilibria are stable while if the bifurcation is to the left, they are unstable. (The bifurcation is to the right if $r > 1$ for non-extinction equilibrium pairs (r, \hat{x}) near $(1, \hat{0})$ and to the left if $r < 1$.)

The theorems in [8] allows for the fundamental bifurcation theorem for non-linear matrix models to be expressed in terms of other model parameters as well, including the inherent net reproductive number $R_0 = R_0(\hat{0})$ (denoted by n in [8]). Moreover, the bifurcation theorem (linear and non-linear) has also been proved valid in other contexts, including periodically forced matrix models (for populations in periodically fluctuating environments) [7,13], integro-matrix models (for structured populations in spatial environments) [19], for both autonomous and periodically models for continuously structured populations in continuous time [3–6], and for general structured population models set in an infinite dimensional setting [21].

Recently, the author extended the fundamental bifurcation theorem to a type of non-linear matrix model obtained when evolutionary game theoretic methods are used to extend a population matrix model to an evolutionary context [22]. This methodology includes the dynamics of evolving (mean) phenotypic traits (that possess heritable components) under the influence of natural selection. According to this theory, if the demographic parameters appearing in the entries of the projection matrix P depend on one (mean) phenotypic trait u that, having a heritable component, evolves according to natural selection, then model equations describing the population dynamics and the trait dynamics (together called the Darwinian dynamics) are

$$\hat{x}(t + 1) = P(\hat{x}(t), u(t))\hat{x}(t) \tag{5a}$$

$$u(t + 1) = u(t) + \sigma^2 \frac{r'(\hat{x}, u)}{r(\hat{x}, u)} \Big|_{(\hat{x}, u) = (\hat{x}(t), u(t))}. \tag{5b}$$

Here, $r = r(\hat{x}, u)$ denotes the dominant eigenvalue of $P(\hat{x}, u)$ and throughout this paper the prime “’” denotes partial differentiation with respect to u :

$$r'(\hat{x}, u) = \frac{\partial r(\hat{x}, u)}{\partial u}.$$

The quantity σ^2 in Equation (5b) is the variance of the trait (around its mean u) that occurs in the population at each point in time. It is a measure of the speed of evolution.

If no evolution occurs ($\sigma^2 = 0$), so that $u(t) \equiv u^*$ is constant in time, then the Darwinian model (5) reduces to the population dynamic model (1) with projection matrix $P = P(\hat{x}, u^*)$ for which the fundamental bifurcation theorem described above holds.

For $\sigma^2 > 0$, a fundamental bifurcation theorem is proved for the Darwinian model (5) in [11] using the inherent population growth rate $r = r(\hat{0}, u^*)$ as a bifurcation parameter, where u^* is a certain critical trait value (see Section 3). A goal here is to show that this bifurcation theorem can be stated equivalently in terms of the inherent net reproductive number $R_0 = R_0(\hat{0}, u^*)$. To do this, we establish a relationship between $r(\hat{0}, u)$ and $R_0(0, u)$ and between their first two derivatives with respect to u when evaluated at the critical value $u = u^*$. These relationships are proved in Section 2 and the re-reformulated bifurcation theorem appears in Section 3. The main advantage of this version of the fundamental bifurcation theorem is that, as pointed out above, it is often the case that explicit formulas are available for R_0 even when they are not available for r . This often allows for analyses that are not possible using r . Two applications that illustrate this point appear in Section 4.

2. Some relationships between r and R_0

Let $U \subseteq \mathbb{R}^1$ be an open interval of real numbers and consider the $m \times m$ matrix valued functions $F(u) = (f_{ij}(u))$ and $T(u) = (\tau_{ij}(u))$ whose entries satisfy

$$A1: \begin{cases} f_{ij}, \tau_{ij} \in C^1(U \rightarrow \mathbb{R}^1) \text{ and, for all } u \in U, \\ f_{ij}(u) \geq 0, \quad 0 \leq \tau_{ij}(u) \leq 1, \quad \sum_{i=1}^m \tau_{ij}(u) \leq 1. \end{cases}$$

Let $\rho(M)$ denote the spectral radius of a matrix M . Assume

$$A2: \begin{cases} P(u) = F(u) + T(u) \text{ is primitive,}^1 \\ T(u) \neq 0_{m \times m} \text{ and } \rho(T(u)) < 1 \text{ for all } u \in U. \end{cases}$$

and

$$A3: \begin{cases} \text{For } u \in U \text{ the matrix } F(u)(I - T(u))^{-1} \text{ has a simple, dominant eigenvalue} \\ \text{which has non-negative right and left eigenvectors } \hat{w}_r(u) \text{ and } \hat{w}_l(u). \end{cases}$$

Define

$$r(u) \triangleq \rho(P(u))$$

$$R_0(u) \triangleq \rho(F(u)(I - T(u))^{-1}).$$

A fundamental fact about these two quantities is that if one of them equals 1 then so must the other (and otherwise they both lie on the same side of 1) [12]. On the other hand, as functions of the trait u , these two quantities do not necessarily share the same properties. For example, in general, the critical points and extrema of $r(u)$ and $R_0(u)$ do not necessarily occur at the same trait values u . The next theorem shows, however, that they do share extrema if they equal 1 at a critical trait.

THEOREM 1 *Suppose A1, A2, and A3 hold.*

(a) *Then for $u^* \in U$*

$$r(u^*) = 1 \text{ if and only if } R_0(u^*) = 1. \tag{6}$$

(b) If Equation (6) holds for $u^* \in U$, then there exists a constant $k > 0$ such that $R'_0(u^*) = kr'(u^*)$. As a result,

$$r'(u^*) = 0 \text{ if and only if } R'_0(u^*) = 0. \tag{7}$$

(c) If Equations (6) and (7) hold for $u^* \in U$, then $R''_0(u^*) = kr''(u^*)$ and as a result

$$r''(u^*) < 0 \text{ if and only if } R''_0(u^*) < 0. \tag{8}$$

It also follows that Equation (8) remains valid if ' $<$ ' is replaced by ' $>$ ' or by ' $=$ '.

Proof of (a) The equivalence (6) is proved in [12]. (Also see [17].) ■

Proof of (b) Let $\hat{v}_l(u)$ and $\hat{v}_r(u)$ be left (row) and right (column) positive eigenvectors of $P(u) = F(u) + T(u)$ associated with the dominant eigenvector $r(u)$

$$\begin{aligned} \hat{v}_l(u)P(u) &= r(u)\hat{v}_l(u) \\ P(u)\hat{v}_r(u) &= r(u)\hat{v}_r(u) \end{aligned}$$

normalized so that $\hat{v}_l(u)\hat{v}_r(u) = 1$. For notational simplicity, we drop the functional notation ' (u) '. Thus, we write (valid for all $u \in U$)

$$\begin{aligned} \hat{v}_l(F + T) &= r\hat{v}_l \\ (F + T)\hat{v}_r &= r\hat{v}_r \\ \hat{v}_l\hat{v}_r &= 1. \end{aligned} \tag{9}$$

A differentiation of the second equation with respect to u implies

$$(F + T - rI)\hat{v}'_r = (r'I - F' - T')\hat{v}_r,$$

where I is the $m \times m$ identity matrix. It follows that $\hat{v}_l(r'I - F' - T')\hat{v}_r = 0$ or

$$r' = \hat{v}_l(F' + T')\hat{v}_r. \tag{10}$$

From the defining equations for the eigenvectors \hat{v}_r and \hat{v}_l , we derive the equations

$$\begin{aligned} \hat{w}_l F(I - T)^{-1} &= R_0\hat{w}_l \\ F(I - T)^{-1}\hat{w}_r &= R_0\hat{w}_r \\ \hat{w}_l\hat{w}_r &= 1 \end{aligned} \tag{11}$$

for \hat{w}_l and \hat{w}_r , and, similarly, obtain

$$R'_0 = \hat{w}_l[F(I - T)^{-1}]'\hat{w}_r.$$

To simplify this formula, we differentiate $(I - T)(I - T)^{-1} = I$ to obtain

$$[(I - T)^{-1}]' = (I - T)^{-1}T'(I - T)^{-1}$$

and

$$\begin{aligned} R'_0 &= \hat{w}_l[F'(I - T)^{-1} + F(I - T)^{-1}T'(I - T)^{-1}]\hat{w}_r \\ R'_0 &= \hat{w}_l(F' + R_0T')(I - T)^{-1}\hat{w}_r. \end{aligned} \tag{12}$$

To prove (b), assume $u = u^*$ is a point where $r = R_0 = 1$. Then setting $u = u^*$ in the first equations in Equation (9) and in Equation (11) implies

$$\begin{aligned} \hat{v}_l F(I - T)^{-1} &= \hat{v}_l \\ \hat{w}_l F(I - T)^{-1} &= \hat{w}_l \end{aligned}$$

which, because $R_0 = 1$ is simple and both \hat{v}_l and \hat{w}_r are non-negative vectors, implies $\hat{v}_l = k_1 \hat{w}_l$ for some positive constant $k_1 > 0$. Also when $u = u^*$ we have

$$\begin{aligned} (F + T)\hat{v}_r &= \hat{v}_r \\ F\hat{v}_r &= (I - T)\hat{v}_l \\ F(I - T)^{-1}(I - T)\hat{v}_r &= (I - T)\hat{v}_l \end{aligned}$$

and hence

$$(I - T)\hat{v}_r = k_2 \hat{w}_r$$

for some positive constant $k_2 > 0$.

In summary, at a point $u = u^*$ where $r = R_0 = 1$, there are *positive* constants $k_1 > 0$ and $k_2 > 0$ so that

$$\hat{v}_l = k_1 \hat{w}_l \tag{13}$$

$$\hat{v}_r = k_2 (I - T)^{-1} \hat{w}_r. \tag{14}$$

Substituting these into Equation (12) we obtain, at a point $u = u^*$ where $r = R_0 = 1$, that

$$\begin{aligned} R'_0 &= k_1^{-1} \hat{v}_l F' k_2^{-1} \hat{v}_r + k_1^{-1} \hat{v}_l T' (I - T)^{-1} k_2^{-1} \hat{v}_r \\ &= k_1^{-1} k_2^{-1} (\hat{v}_l F' \hat{v}_r + \hat{v}_l T' \hat{v}_r) \\ &= k_1^{-1} k_2^{-1} r'. \end{aligned}$$

It follows that at such a point $u = u^*$, the derivative $R'_0 = 0$ if and only if $r' = 0$. ■

Proof of (c) We need to investigate the second derivatives R''_0 and r'' evaluated at point $u = u^*$, where both $r = R_0 = 1$ and $r' = R'_0 = 0$. We will prove (c) by showing that

$$R''_0 = k_1^{-1} k_2^{-1} r'' \tag{15}$$

at $u = u^*$. Recall that both $k_i > 0$.

As a preliminary step, we derive relationships between the derivatives \hat{v}'_l , \hat{v}'_r and \hat{q}'_r , \hat{w}'_l evaluated at the point $u = u^*$, where we have, for notational convenience, defined

$$\hat{q}_r \triangleq (I - T)^{-1} \hat{w}_r.$$

From Equations (9) and (11) we have (for all u)

$$\begin{aligned} (F + T)\hat{v}_r &= r\hat{v}_r \\ F(I - T)^{-1} \hat{w}_r &= R_0 \hat{w}_r. \end{aligned}$$

We re-write this pair of equations as

$$\begin{aligned} (F + T)\hat{v}_r &= r\hat{v}_r \\ (F + R_0 T)\hat{q}_r &= R_0 \hat{q}_r \end{aligned}$$

Downloaded By: [Cushing, Jim M] At: 20:33 3 May 2011

and differentiate both with respect to u to obtain

$$\begin{aligned} (F + T)\hat{v}'_r + (F + T)'\hat{v}_r &= r\hat{v}'_r + r'\hat{v}_r \\ (F + R_0T)\hat{q}'_r + (F + R_0T)'\hat{q}_r &= R_0\hat{q}'_r + R'_0\hat{q}_r. \end{aligned}$$

An evaluation at $u = u^*$ leads to (refer to Equation (14))

$$\begin{aligned} (F + T)\hat{v}'_r + (F' + T')\hat{v}_r &= \hat{v}'_r \\ (F + T)\hat{q}'_r + (F' + T')\hat{q}_r &= \hat{q}'_r \end{aligned}$$

and hence

$$\begin{aligned} (F + T)\hat{v}'_r &= \hat{v}'_r - (F' + T')\hat{v}_r \\ (F + T)\hat{q}'_r &= \hat{q}'_r - k_2^{-1}(F' + T')\hat{v}_r. \end{aligned}$$

Let \hat{v}_r^0 denote the unique solution of

$$\begin{aligned} (F + T)\hat{x} &= \hat{x} - (F' + T')\hat{v}_r \\ \hat{v}_r^T \hat{x} &= 0, \end{aligned}$$

(where the superscript ‘T’ denotes the transpose of a vector). This solution exists because the non-homogeneous term $-(F' + T')\hat{v}_r$ is orthogonal to \hat{v}_l (which spans the nullspace of $(F + T) - I$) and hence to $\hat{w}_l = k_1^{-1}\hat{v}_l$. This is because r' vanishes at $u = u^*$ (see (10)). We conclude that

$$\begin{aligned} \hat{v}'_r &= c_1\hat{v}_r + \hat{v}_r^0 \\ \hat{q}'_r &= c_2\hat{v}_r + k_2^{-1}\hat{v}_r^0 \end{aligned} \tag{16}$$

for constants c_1, c_2 .

A similar set of calculations holds for the derivatives of the vectors \hat{v}_l, \hat{w}_l . We have from Equation (9) and (11)

$$\begin{aligned} \hat{v}_l(F + T) &= r\hat{v}_l \\ \hat{w}_l F(I - T)^{-1} &= R_0\hat{w}_l \end{aligned}$$

(valid for all u) by differentiation that

$$\begin{aligned} \hat{v}_l(F + T)' + \hat{v}'_l(F + T) &= r\hat{v}'_l + r'\hat{v}_l \\ \hat{w}_l(F + R_0T)' + \hat{w}'_l(F + R_0T) &= R_0\hat{w}'_l + R'_0\hat{w}_l. \end{aligned}$$

These equations, when evaluated at $u = u^*$, yield

$$\begin{aligned} \hat{v}_l(F' + T') + \hat{v}'_l(F + T) &= \hat{v}'_l \\ \hat{w}_l(F' + T') + \hat{w}'_l(F + T) &= \hat{w}'_l \end{aligned}$$

or

$$\begin{aligned} \hat{v}'_l(F + T) &= \hat{v}'_l - \hat{v}_l(F' + T') \\ \hat{w}'_l(F + T) &= \hat{w}'_l - \hat{w}_l(F' + T'). \end{aligned}$$

Thus, since Equation (13) implies $\hat{w}_l = k_1^{-1}\hat{v}_l$, we get

$$\begin{aligned} \hat{v}'_l &= c_1\hat{v}_l + \hat{v}_l^0 \\ \hat{w}'_l &= c_2\hat{v}_l + k_1^{-1}\hat{v}_l^0 \end{aligned} \tag{17}$$

for constants c_1, c_2 , where \hat{v}_l^0 is the unique solution of

$$\begin{aligned} \hat{y}(F + T) &= \hat{y} - \hat{v}_l(F' + T') \\ \hat{v}_l^T \hat{y} &= 0. \end{aligned}$$

We turn now to a calculation of the second derivatives r'' and R''_0 evaluated at $u = u^*$. From Equations (10) and (12), we obtain by differentiation that

$$\begin{aligned} r'' &= \hat{v}'_l(F' + T')\hat{v}_r + \hat{v}_l(F'' + T'')\hat{v}_r + \hat{v}_l(F' + T')\hat{v}'_r \\ R''_0 &= \hat{w}'_l(F' + R_0T')\hat{q}_r + \hat{w}_l[(F' + R_0T')]'\hat{q}_r + \hat{w}_l(F' + R_0T')\hat{q}'_r. \end{aligned}$$

An evaluation at $u = u^*$ yields

$$\begin{aligned} r'' &= \hat{v}'_l(F' + T')\hat{v}_r + \hat{v}_l(F'' + T'')\hat{v}_r + \hat{v}_l(F' + T')\hat{v}'_r \\ R''_0 &= \hat{w}'_l(F' + T')\hat{q}_r + \hat{w}_l[(F' + R_0T')]'\hat{q}_r + \hat{w}_l(F' + T')\hat{q}'_r \end{aligned}$$

and from Equations (16) and (17) we obtain

$$\begin{aligned} r'' &= (c_1\hat{v}_l + \hat{v}_l^0)(F' + T')\hat{v}_r + \hat{v}_l(F'' + T'')\hat{v}_r + \hat{v}_l(F' + T')(c_1\hat{v}_r + \hat{v}_r^0) \\ R''_0 &= (c_2\hat{v}_l + k_1^{-1}\hat{v}_l^0)(F' + T')\hat{q}_r + \hat{w}_l(F'' + T'')\hat{q}_r + \hat{w}_l(F' + T')(c_2\hat{v}_r + k_2^{-1}\hat{v}_r^0). \end{aligned}$$

If we make use of $r' = \hat{v}_l(F' + T')\hat{v}_r = 0$ and $\hat{q}_r \triangleq (I - T)^{-1}\hat{w}_r = k_2^{-1}\hat{v}_r$, together with Equations (14) and (13), we can write these equations as

$$\begin{aligned} r'' &= \hat{v}_l^0(F' + T')\hat{v}_r + \hat{v}_l(F'' + T'')\hat{v}_r + \hat{v}_l(F' + T')\hat{v}_r^0 \\ R''_0 &= k_1^{-1}k_2^{-1}\hat{v}_l^0(F' + T')\hat{v}_r + k_1^{-1}k_2^{-1}\hat{v}_l(F'' + T'')\hat{v}_r + k_1^{-1}k_2^{-1}\hat{v}_l(F' + T')\hat{v}_r^0 \end{aligned}$$

and hence we see that $R''_0(u^*) = kr''(u^*)$. ■

3. The fundamental bifurcation theorem and R_0

Let \bar{R}_+^m denote the closure of the positive cone R_+^m in R^m and let Ω be an open set in R^m that contains \bar{R}_+^m . Recall that $U \subseteq R^1$ is an open interval. Consider the Darwinian matrix model (5) with a projection matrix $P(\hat{x}, u) = (p_{ij}(\hat{x}, u))$ that satisfies

$$\text{H0: } \begin{cases} p_{ij} \in C^2(\Omega \times U \rightarrow \bar{R}_+^1); \\ (\hat{x}, u) \in (\Omega \cap \bar{R}_+^m) \times U \text{ and } P(\hat{x}, u)\hat{x} = \hat{0} \text{ imply } \hat{x} = \hat{0}; \\ P(\hat{x}, u) \text{ is primitive for } (\hat{x}, u) \in (\Omega \cap \bar{R}_+^m) \times U. \end{cases}$$

The dominant eigenvalue $r(\hat{x}, u) \triangleq \rho(P(\hat{x}, u))$ is the *population growth rate at* (\hat{x}, u) and $r(\hat{0}, u)$ is called the *inherent population growth rate at trait* u .

Downloaded By: [Cushing, Jim M] At: 20:33 3 May 2011

We consider projection matrices that have the form [8,10]

$$P(\hat{x}, u) = F(\hat{x}, u) + T(\hat{x}, u) \tag{18}$$

where the entries in the $m \times m$ matrices $F(\hat{x}, u) = (f_{ij}(\hat{x}, u))$ and $T(\hat{x}, u) = (\tau_{ij}(\hat{x}, u))$ satisfy

$$\text{H1: } \begin{cases} f_{ij}, \tau_{ij} \in C^2(\Omega \times U \rightarrow \bar{R}_+^1) \text{ and, for all } (\hat{x}, u) \in (\Omega \cap \bar{R}_+^m) \times U, \\ f_{ij}(\hat{x}, u) \geq 0, \quad 0 \leq \tau_{ij}(\hat{x}, u) \leq 1, \quad \sum_{i=1}^m \tau_{ij}(\hat{x}, u) \leq 1. \end{cases}$$

In order to use Theorem 1, we also need the hypotheses

$$\text{H2: } \begin{cases} \text{for } u \in U \text{ assume } T(\hat{0}, u) \neq 0_{m \times m}, \quad \rho(T(\hat{0}, u)) < 1 \text{ and} \\ F(\hat{0}, u)(I - T(\hat{0}, u))^{-1} \text{ has a simple, dominant eigenvalue which} \\ \text{has non-negative right and left eigenvectors } \hat{w}_l(u) \text{ and } \hat{w}_r(u). \end{cases}$$

The dominant eigenvalue $r(\hat{0}, u) \triangleq \rho(P(\hat{0}, u))$ is called the *inherent population growth rate at trait u*. The dominant eigenvalue

$$R_0(\hat{0}, u) \triangleq \rho(F(\hat{0}, u)(I - T(\hat{0}, u))^{-1})$$

is called the *inherent net reproductive number at trait u* [8,10,12].

A non-negative equilibrium $(\hat{x}(t), u(t)) \equiv (\hat{x}_e, u_e) \in \Omega \times U$ of the Darwinian model (5) satisfies the equations (when $\sigma^2 > 0$)

$$\hat{x}_e = P(\hat{x}_e, u_e)\hat{x}_e \tag{19a}$$

$$r'(\hat{x}_e, u_e) = 0. \tag{19b}$$

The point $(\hat{0}, u)$ is an equilibrium if $u = u^*$, where $r'(\hat{0}, u^*) = 0$. We call such a trait u^* a *critical trait*.

Theorems 2 and 3 below are re-statements of Theorems 2 and 3 in [11] in terms of the inherent net reproductive number at a critical trait, which, in these theorems, is denoted by

$$\lambda \triangleq R_0(\hat{0}, u^*). \tag{20}$$

Theorems 2 and 3 in [11] are instead stated in terms of the inherent population growth rate $r(\hat{0}, u^*)$. These re-statements in terms of $R_0(\hat{0}, u^*)$ are valid in light of Theorem 1 proved in Section 2. These theorems deal with a transcritical bifurcation of equilibria of the Darwinian model (5) that occurs at the extinction equilibrium $(\hat{0}, u^*)$ at $\lambda = 1$ and results in the existence of non-extinction equilibria (\hat{x}_e, u_e) , $\hat{x}_e \in R_+^m$, of Equation (5) for λ near $\lambda = 1$. They also deal with the stability of these bifurcating non-extinction equilibria and how it depends on the direction of bifurcation.

Before stating the theorems, we give some preliminaries. If (\hat{x}_e, u_e) is an equilibrium of a Darwinian model (5) for which the inherent net reproductive number $R_0(\hat{0}, u^*)$ equals the value λ_e , then we call $(\lambda_e, (\hat{x}_e, u_e))$ an *equilibrium pair* of Equation (5). If $\hat{x}_e = \hat{0}$, then the equilibrium pair is an *extinction pair* and if $\hat{0} \neq \hat{x}_e \in R_+^m$ then it is a *non-extinction pair*. If $\hat{x}_e \in R_+^m$ it is a *positive pair*. An equilibrium pair $(\lambda, (\hat{x}_e, u_e))$ is *stable* if the equilibrium (\hat{x}_e, u_e) is *locally asymptotically stable* as an equilibrium of the Darwinian equations (5).

The following theorem concerns the stability of the extinction equilibrium $(\hat{x}_e, u_e) = (\hat{0}, u^*)$ as it depends on the value of the inherent net reproductive number $\lambda = R_0(\hat{0}, u^*)$.

THEOREM 2 Assume H_0 and that $u^* \in U$ is a critical trait of the Darwinian model (5).

(a) If $R_0''(\hat{0}, u^*) < 0$, then the extinction equilibrium pair $(\lambda, (\hat{0}, u^*))$ (where λ is given by Equation (20)) is

(i) unstable if $\lambda > 1$;

(ii) stable if $\lambda < 1$ provided the speed of evolution σ^2 is sufficiently small, specifically provided

$$\sigma^2 < -\frac{2}{R_0''(\hat{0}, u^*)}. \tag{21}$$

(b) If $R_0''(\hat{0}, u^*) > 0$, then the extinction equilibrium pair $(\lambda, (\hat{0}, u^*))$ is unstable for all $\lambda \in R_+^1$.

We point out that the derivation of the Darwinian equation (5) requires, in general, that σ^2 be small [22] and, consequently, Equation (21) is not restrictive with respect to applications of the theorem.

If $R_0''(\hat{0}, u^*) < 0$, Theorem 2 implies the loss of stability of the extinction equilibrium as the value of the inherent net reproductive number $\lambda = R_0(\hat{0}, u^*)$ at the critical trait u^* increases through 1. This suggests that a necessary condition for the persistence of a population is $R_0(\hat{0}, u^*) > 1$. This conclusion needs qualification, however, since the stability assertion in the theorem when $R_0(\hat{0}, u^*) < 1$ is not global. It is a valid conclusion for populations initiating at low densities. On the other hand, positive equilibrium pairs, even stable ones, can exist when $\lambda = R_0(\hat{0}, u^*) < 1$ as, for example, when Allee effects of sufficient magnitude are present [8,10].

THEOREM 3 Assume $u^* \in U$ is a critical trait of the Darwinian model (5) such that $R_0''(\hat{0}, u^*) \neq 0$. Assume H_0, H_1 , and H_2 .

(a) Then there exists a continuum of positive equilibrium pairs $(\lambda, (\hat{x}_e, u_e)) \in R_+^1 \times (R_+^m \times U)$ of the Darwinian equations (5), with $\lambda = R_0(\hat{0}, u^*)$, that contains the extinction pair $(1, (\hat{0}, u^*))$ in its closure.

(b) Suppose $R_0''(\hat{0}, u^*) < 0$ and σ^2 is small (i.e. Equation (21) holds). Define $p_{ij}(\hat{x}, u) \triangleq f_{ij}(\hat{x}, u) + \tau_{ij}(\hat{x}, u)$ and

$$\kappa^* \triangleq -\hat{v}_l[\nabla_{\hat{x}} p_{ij}(\hat{0}, u^*)\hat{v}_r]\hat{v}_r. \tag{22}$$

If σ^2 is small (i.e. Equation (21) holds), then the positive equilibrium pairs near the bifurcation point are stable if the bifurcation is to the right, i.e. if $\kappa^* > 0$, and are unstable if the bifurcation is to the left, i.e. if $\kappa^* < 0$.

(c) If $R_0''(\hat{0}, u^*) > 0$, then near the bifurcation point $(1, (\hat{0}, u^*))$ the positive equilibrium pairs $(\lambda, (\hat{x}_e, u_e))$ are unstable.

Theorems 2 and 3 in [11] treat the transcritical bifurcation described in Theorems 2 and 3 in terms of the inherent population growth rate at the critical trait value $\lambda = r(\hat{0}, u^*)$ rather than in terms of the inherent net reproductive number $\lambda = R_0(\hat{0}, u^*)$ as is done here. In effect, Theorems 2 and 3 show that this fundamental bifurcation phenomenon can be studied – in so far as the location of critical traits, the stability of the extinction equilibrium, and the existence and stability of positive equilibria near the bifurcation point are concerned – by using either the inherent growth rate $r(\hat{0}, u^*)$ or the inherent net reproductive number $R_0(\hat{0}, u^*)$. As pointed out in Section 2, one advantage of this result is that tractable formulas are often available for R_0 , whereas this is rarely the case for r . See Figure 1 for a schematic representation of the bifurcation possibilities for the general Darwinian matrix model (5) as given by Theorems 2 and 3.

In formula (22) for κ^* , the vectors \hat{v}_l and \hat{v}_r are positive. (They are left and right eigenvectors of $P(\hat{0}, u^*)$ associated eigenvalue $r(\hat{0}, u^*) = 1$; see the proof of Theorem 1.) The sign of κ^* is

Downloaded By: [Cushing, Jim M] At: 20:33 3 May 2011

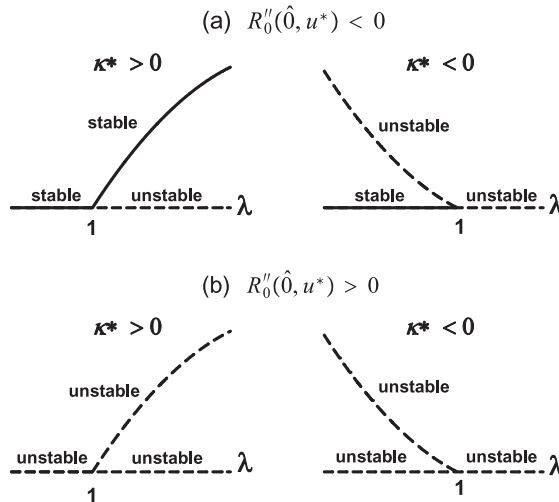


Figure 1. (a) If $R_0''(\hat{0}, u^*) < 0$, Theorems 2 and 3 imply the familiar alternatives of the fundamental bifurcation theorem occur for the Darwinian matrix model (5). (b) On the other hand, if $R_0''(\hat{0}, u^*) > 0$, then even though the bifurcation of positive equilibria occurs, the usual exchange of stability does not hold. In these schematic plots, the horizontal axis λ can be either the inherent net reproductive number $R_0(\hat{0}, u^*)$ or the inherent growth rate $r(\hat{0}, u^*)$ at a critical trait u^* . The vertical axis represents equilibrium pairs (\hat{x}_e, u_e) , $\hat{x}_e \in R_+^m$ of Equation (5). Points on the horizontal axis represent extinction equilibrium pairs $(\lambda, (\hat{0}, u^*))$ and those above the horizontal axis represent positive equilibrium pairs $(\lambda, (\hat{x}_e, u_e))$, $\hat{x}_e \in R_+^m$.

therefore determined by the signs of the first-order derivatives of $p_{ij}(\hat{x}, u)$ with respect to the components of \hat{x} evaluated at $(\hat{0}, u^*)$. Thus, the first-order derivatives of the fertility $f_{ij}(\hat{x}, u)$ and transition $\tau_{ij}(\hat{x}, u)$ terms determine the direction of bifurcation and, as a result, the stability of the bifurcating positive equilibria. In models for which increased densities lead to decreased fertility and survivorships (at least at low densities), these derivatives are negative and consequently $\kappa^* > 0$. Thus, from this simple negative feedback property of density-dependent fertility and survivorship (which is the most common assumption in population models), one can conclude from Theorem 3(b) that a stable bifurcation occurs; there is no need to calculate κ^* explicitly or to perform a separate stability analysis (involving, for example, the linearization of the model equations).

COROLLARY 4 *Under the assumptions of Theorem 3(b), a bifurcation to the right (of a branch of stable positive equilibria) occurs if the following holds:*

$$\text{H3: } \begin{cases} \text{when evaluated at } (\hat{x}, u) = (\hat{0}, u^*), \text{ all partial derivatives of} \\ f(\hat{x}, u) \text{ and } \tau_{ij}(\hat{x}, u) \\ \text{with respect to each component of } \hat{x} \text{ are non-positive and at least} \\ \text{one is negative.} \end{cases}$$

In order for $\kappa^* < 0$ (and an unstable bifurcation to occur) at least one of the first-order derivatives must be positive (i.e. there must exist some positive feedback caused by increased population density, a phenomenon known as an Allee effect). The occurrence of such positive derivatives is not sufficient for $\kappa^* > 0$, however; those derivatives would have to be of sufficient magnitude so as to outweigh any negative derivatives appearing in the formula for κ^* .

Assume H2 holds with $\hat{0}$ replaced by $\hat{x} \in \Omega$. The dominant eigenvalue

$$R_0(\hat{x}, u) \triangleq \rho(F(\hat{x}, u)(I - T(\hat{x}, u))^{-1})$$

is the net reproductive number at population level \hat{x} and trait u . Let (\hat{x}_e, u_e) be an equilibrium of Equation (19) and consider the projection matrix $P(\hat{x}_e, u) = F(\hat{x}_e, u) + T(\hat{x}_e, u)$ as a function of u with \hat{x} held fixed at \hat{x}_e . The population growth rate $r(\hat{x}_e, u)$ and net reproductive number $R_0(\hat{x}_e, u)$ become functions of u and the equilibrium equations (19) and Theorem 1 imply

$$r(\hat{x}_e, u_e) = 1, \quad r'(\hat{x}_e, u_e) = 0$$

and

$$R_0(\hat{x}_e, u_e) = 1, \quad R_0'(\hat{x}_e, u_e) = 0. \tag{23}$$

Thus, when r and R_0 are treated as functions of the trait u with the population density held constant at the equilibrium \hat{x}_e , we see that equilibria of the Darwinian model (5) occur at critical traits of both these functions where both equal 1. In particular, consider an equilibrium from the bifurcating branch of positive equilibrium pairs in Theorem 3(b) when $R_0''(\hat{0}, u^*) < 0$. By continuity (and Theorem 1) we have, for equilibrium pairs near the bifurcation point, that

$$r''(\hat{x}_e, u_e) < 0, \quad R_0''(\hat{x}_e, u_e) < 0.$$

Similarly, in case (b) when $R_0''(\hat{0}, u^*) > 0$ these two inequalities are reversed.

COROLLARY 5 *Let (\hat{x}_e, u) be a positive equilibrium of the Darwinian model (5) near the bifurcation point $(\hat{0}, u^*)$, as guaranteed by Theorem 3. As functions of u (with \hat{x}_e held fixed), both $r(\hat{x}_e, u)$ and $R_0(\hat{x}_e, u)$ have local maxima of 1 at $u = u_e$ in case (b) when $R_0''(\hat{0}, u^*) < 0$. In case (c) when $R_0''(\hat{0}, u^*) > 0$, both $r(\hat{x}_e, u)$ and $R_0(\hat{x}_e, u)$ have local minima of 1 at $u = u_e$.*

Under the dynamic of the Darwinian equations (5), \hat{x} will not remain fixed as u varies in time. If, for each \hat{x} , we think of $r(\hat{x}, u)$ and $R_0(\hat{x}, u)$ as defining fitness landscapes as functions of the trait u , then under the dynamic of Equation (5) both the landscape and u change in time. However, the asymptotic limit of a trajectory approaching the stable positive equilibrium (\hat{x}_e, u_e) will result in both $r(\hat{x}_e, u)$ and $R_0(\hat{x}_e, u)$ attaining (local) maxima of 1. Geometrically, the fitness landscapes can be drawn at a fixed point in time t by plotting graphs of $r(\hat{x}(t), u)$ and $R_0(\hat{x}(t), u)$ as functions of u . As t changes, these landscape plots change and as $t \rightarrow +\infty$ they approach the landscape plots $r(\hat{x}_e, u)$ and $R_0(\hat{x}_e, u)$. The points $(u(t), r(\hat{x}(t), u(t)))$ and $(u(t), R_0(\hat{x}(t), u(t)))$, located on the changing fitness landscape, will asymptotically arrive at (local) peaks of height 1 on the landscape plots $r(\hat{x}_e, u)$ and $R_0(\hat{x}_e, u)$. This occurs, for example, when the bifurcation in Theorem 3(c) is to the right ($\kappa^* > 0$). In this case, (nearby) trajectories will approach a (local) peak on both fitness landscapes. However, if the bifurcation is the left ($\kappa^* < 0$), the trajectories will not evolve towards, but be repelled from these positive equilibria. The corresponding points on the fitness landscapes will evolve away from the peaks associated with these equilibria (even though they are local maximum of $r(\hat{x}_e, u)$ and $R_0(\hat{x}_e, u)$).

A similar argument shows that when $R_0''(\hat{0}, u^*) > 0$ both $r(\hat{x}_e, u)$ and $R_0(\hat{x}_e, u)$ will have local minima of 1 at $u = u_e$. According to Theorem 1(b), in this case the bifurcating positive equilibria are unstable, regardless of the direction of bifurcation. Nearby trajectories will evolve away from the local minima (valleys) in the fitness landscapes associated with the bifurcating positive equilibria.

If the focus is on finding conditions under which there exist (evolutionarily) stable non-extinction equilibria then, in so far as the bifurcation of such equilibria from the extinction

equilibrium is concerned, one searches for critical traits u^* at which $R_0(\hat{0}, u)$ is maximized (i.e. $R'_0(\hat{0}, u^*) = 0$ and $R''_0(\hat{0}, u^*) < 0$) and $\kappa^* > 0$. Stable non-extinction equilibria will bifurcate from the extinction equilibrium as the value of $R_0(\hat{0}, u^*)$ increases through 1 (Theorem 3(a)). This is the goal in the applications in the following section.

4. Applications

The inherent growth rate $r(\hat{0}, u)$ is an eigenvalue of the $m \times m$ matrix $P(\hat{0}, u)$. The inherent reproduction number $R_0(\hat{0}, u)$ is an eigenvalue of the $m \times m$ matrix $F(\hat{0}, u)(I - T(\hat{0}, u))^{-1}$. If, however, there are only n newborn classes (i.e. $F(\hat{0}, u)$ has only n nonzero rows), then $R_0(\hat{0}, u)$ is an eigenvalue of an $n \times n$ matrix [8,10,12]. In applications, the number of newborn classes n is frequently small (indeed often $n = 1$) and this is the source of the tractability of calculating formulas for $R_0(\hat{0}, u)$ in terms of the entries in the projection matrix.

For example, suppose all newborns lie in a single class, which we take without loss in generality to be the first class. Then the fertility matrix F in the Darwinian model (5) with projection matrix (18) has the form

$$F = \begin{bmatrix} f_{11} & f_{12} & \cdots & f_{1m} \\ 0 & 0 & \cdots & 0 \\ \vdots & \vdots & & \vdots \\ 0 & 0 & \cdots & 0 \end{bmatrix}.$$

In this case, R_0 is the vector product

$$R_0 = \sum_{i=1}^m f_{1i} e_{i1}$$

of the first row in F with the first column in the matrix $(I - T)^{-1} = (e_{ij})$. Here e_{i1} is the expected amount of time spent in class i by an individual starting in class 1 (i.e. starting as a newborn) during its lifetime. Thus, R_0 is the expected number of newborns produced per newborn per lifetime. Any convenient formula (e.g. the cofactor formula) for a matrix inverse that gives these expectations leads to a formula for R_0 expressed explicitly in terms of the demographic coefficients f_{1i} and τ_{ij} of the model.

For example, for the standard size structured model (3) (and, as a special case, a Leslie age-structured model), we have

$$e_{i1} = \prod_{j=1}^i \frac{\tau_{j,j-1}}{1 - \tau_{jj}},$$

which leads to formula (4). This formula allows one to determine the critical (mean) traits at which the fundamental bifurcations Theorems 2 and 3 apply, and what type of bifurcation (stable or unstable) occurs, from the properties of the functional dependences of the basic demographic parameters $f_{ij} = f_{ij}(u)$ and $\tau_{ij} = \tau_{ij}(u)$ on the trait u . This can be done using R_0 even if one wishes to use the inherent growth rate $r(\hat{0}, u^*)$ as the bifurcation parameter instead of $R_0(\hat{0}, u^*)$.

We give two applications. The first concerns a general juvenile–adult model for which the methods developed here provide a study of trade-offs between fertility and survivorship as functions of the (mean) trait u [20]. The second application involves a more specific model that has been used to study experimental results in which the evolution of a certain trait was observed and quantified.

4.1. A juvenile–adult model

Consider a matrix model for a population in which all newborns lie in the first class $i = 1$ and only individuals in the last class $i = m$ are reproductive. Thus, the population is assumed to have $m - 1$ juvenile classes through which an individual must pass before becoming reproductively mature. We assume that adult fertility and all juvenile survivorships are dependent on a (mean) trait u . Then

$$F(\hat{x}, u) = \begin{bmatrix} 0 & 0 & \cdots & f(\hat{x}, u) \\ 0 & 0 & \cdots & 0 \\ \vdots & \vdots & & \vdots \\ 0 & 0 & \cdots & 0 \end{bmatrix}, \tag{24}$$

where $f(\hat{x}, u) = f_{1m}(\hat{x}, u)$ is *adult fertility*. The net reproductive number (expected newborns produced per newborn per lifetime) is

$$R_0(\hat{x}, u) = f(\hat{x}, u)e(\hat{x}, u).$$

Here, $e(\hat{x}, u) = e_{m1}(\hat{x}, u)$ is the *expected amount of time a newborn will spend as an adult during its lifetime* (when possessing mean trait u and the population is at density \hat{x}). This quantity encapsulates the survivorship probabilities that determine the likelihood a newborn will reach adulthood as well as the probability of adult survival.

We make no special assumptions about the structure of the transition matrix T (e.g., it is not necessarily a Leslie or Usher transition matrix), which includes probabilities of transfers between any two classes (given survival). In general, it is allowed in this model that an adult could (if it survived) stay an adult or return to a juvenile stage (with a chance that it will again reach the adult stage in the future). In this application, however, we will not model these survival and/or transition probabilities explicitly as functions of u . Indeed, it is not necessary to do so in order to apply the bifurcation theorems since R_0 depends only on the composite quantity $e(\hat{x}, u)$.

We can study the fundamental bifurcation properties of this general model of arbitrary dimension (using Theorems 2 and 3) by means of just the two (biologically meaningful) quantities $f(\hat{0}, u)$ and $e(\hat{0}, u)$ appearing in the formula

$$R_0(\hat{0}, u) = f(\hat{0}, u)e(\hat{0}, u)$$

for the inherent net reproductive number. The goal in this application is to determine conditions under which a right, stable bifurcation of non-extinction (positive) equilibria occurs.

We assume only negative feedback density terms appear in adult fertility $f(\hat{x}, u)$ and all transition probabilities $\tau_{ij}(\hat{x}, u)$. That is to say, we assume H3 holds. By Corollary 4, a (right) bifurcation will occur and produce stable, positive equilibria for values of $\lambda = R_0(\hat{0}, u) \gtrsim 1$ provided there exists a critical u^* for which $R_0(\hat{0}, u)$ has a local maximum:

$$R'_0(\hat{0}, u^*) = 0, \quad R''_0(\hat{0}, u^*) < 0 \tag{25}$$

(and σ^2 is small).

Our goal here is to interpret these conditions for a stable bifurcation in terms of the inherent adult fertility $f(\hat{0}, u)$ and the inherent expected amount of time $e(\hat{0}, u)$ a newborn will spend as an adult during its lifetime (adult longevity). In terms of these two quantities, the conditions (25) are

$$f(\hat{0}, u^*)e'(\hat{0}, u^*) + f'(\hat{0}, u^*)e(\hat{0}, u^*) = 0 \tag{26}$$

and

$$f(\hat{0}, u^*)e''(\hat{0}, u^*) + 2f'(\hat{0}, u^*)e'(\hat{0}, u^*) + f''(\hat{0}, u^*)e(\hat{0}, u^*) < 0, \tag{27}$$

where the prime denotes partial differentiation with respect to u .

Downloaded By: [Cushing, Jim M] At: 20:33 3 May 2011

Note that the first constraint (26) requires either that $f'(\hat{0}, u^*)$ and $e'(\hat{0}, u^*)$ have opposite signs or that both equal 0. If, when u is changed, $f(\hat{0}, u)$ and $e(\hat{0}, u)$ change in opposite directions, then a trade-off has occurred in the following sense: an increase in the trait u causes an increase in adult fertility and a corresponding decrease adult longevity (or vice versa).

DEFINITION 6 A trade-off between (inherent) adult fertility and longevity at a trait $u = u^*$ occurs if $f(\hat{0}, u)$ and $e(\hat{0}, u)$ have opposite monotonicities as functions of u in a deleted neighbourhood of u^* .

Theorems 2, 3 and Corollary 4 imply the following result.

THEOREM 7 Consider the Darwinian model (5) with a fertility matrix of the form (24) in its projection matrix (18). Assume H0, H1, H2, and H3.

- (a) For the right (stable) bifurcation of positive equilibria described in Theorem 3(b) to occur, it is necessary that there exists a critical trait u^* at which a trade-off between (inherent) adult fertility and longevity occurs or at least one of these is maximized.
- (b) Suppose there exists a critical trait u^* at which a trade-off between (inherent) adult fertility and longevity occurs. Then the right (stable) bifurcation of positive equilibria described in Theorem 3(b) occurs provided inequality (27) holds.

If the inequality (27) is reversed, then by Theorem 3(c) the bifurcating positive equilibria are unstable.

As pointed out above, a trade-off between inherent adult fertility and longevity at a trait $u = u^*$ occurs in two different ways:

- (a) $f(\hat{0}, u)$ and $e(\hat{0}, u)$ have extrema at $u = u^*$ of opposite type or
- (b) $f'(\hat{0}, u)$ and $e'(\hat{0}, u)$ have opposite signs.

See Figure 2.

In Case (a), when $f(\hat{0}, u)$ has a maximum and $e(\hat{0}, u)$ has a minimum at $u = u^*$ (or vice versa), condition (27) for a stable, right bifurcation (Theorem 7(b)) reduces to

$$f(\hat{0}, u^*)e''(\hat{0}, u^*) + f''(\hat{0}, u^*)e(\hat{0}, u^*) < 0.$$

This implies that at least one of the second derivatives $f''(\hat{0}, u^*)$ or $e''(\hat{0}, u^*)$ is negative and of sufficiently large magnitude. Thus, in this case, the condition for the existence of stable, positive equilibria requires the maximized of the two quantities $f(\hat{0}, u)$ or $e(\hat{0}, u)$ must be sufficiently narrowly distributed at $u = u^*$ (compared with the distribution of the minimized quantity). This case is illustrated by the example below.

Case (b) is interesting because at the equilibrium at which evolution arrives neither adult fertility nor adult survivorship is maximized. This is illustrated in the application in Section 4.2.

Example As an illustration of Theorem 3, consider an Usher model (3) with one newborn class and one adult class. Specifically, consider the fertility matrix (24) with $f(\hat{x}, u) = \beta\varphi(\hat{x}, u)$ and

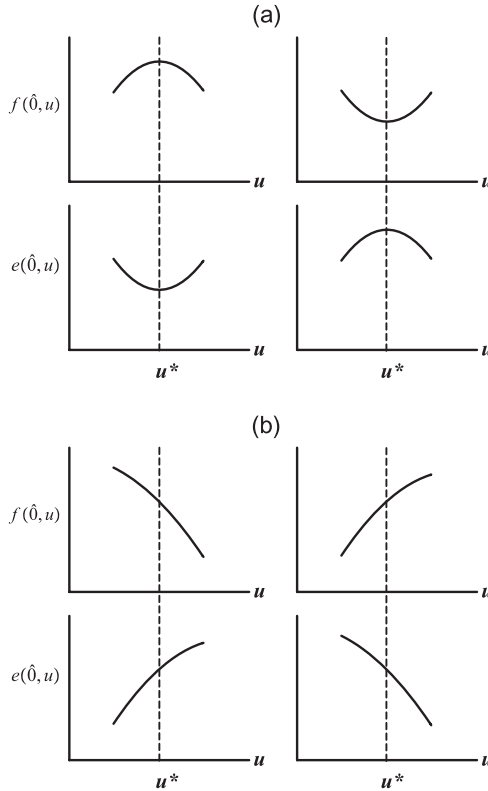


Figure 2. To obtain stable positive equilibria from a right bifurcation for a model with a single newborn class and a finite number of juvenile stages, as given by the fertility matrix (24), the inherent adult fertility $f(\hat{0}, u)$ and the inherent expected time spent as an adult $e(\hat{0}, u)$ must exhibit a trade-off at the critical trait u^* . Either these quantities must have (a) opposite extrema or (b) opposite monotonicities at $u = u^*$.

the transition matrix

$$T = \begin{bmatrix} \tau_{11}(\hat{x}) & 0 & \cdots & 0 & 0 \\ \tau_{21}(\hat{x}) & \tau_{22}(\hat{x}) & \cdots & 0 & 0 \\ 0 & \tau_{32}(\hat{x}) & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & \tau_{m,m-1}(\hat{x}) & \tau_{mm}(\hat{x}, u) \end{bmatrix}.$$

Here, it is assumed that the trait u affects only adult fertility $f(\hat{x}, u)$ and adult survivorship $\tau_{mm}(\hat{x}, u)$. We assume density dependence is a negative feedback (i.e. φ and τ_{ij} satisfy H3 as functions of \hat{x}). For φ and τ_{mm} at $\hat{x} = \hat{0}$, we assume

$$\varphi(\hat{0}, u) = \exp\left(-\frac{u^2}{2v_f}\right), \quad \tau_{mm}(\hat{0}, u) = 1 - \tau \exp\left(-\frac{u^2}{2v_\tau}\right) \tag{28}$$

$$v_f, v_\tau > 0 \text{ and } 0 < \tau < 1.$$

Here, inherent adult fertility $f(\hat{0}, u)$ is normally distributed around trait $u = 0$, with a maximum of $\beta > 0$; v_f measures the concavity (variance) of this distribution. The adult death rate is similarly distributed around $u = 0$ with a maximum of τ and variance v_τ . This means that the inherent adult

survivorship $\tau_{mm}(\hat{0}, u)$ has a minimum (of $1 - \tau$) at $u = 0$. These sub-models for adult fertility and mortality describe a trade-off between inherent adult fertility and longevity. To see this, we calculate from Equation (4) that

$$f(\hat{0}, u) = \beta\varphi(\hat{0}, u), \quad e(\hat{0}, u) = \frac{\tau_{m,m-1}}{1 - \tau_{mm}(\hat{0}, u)} \prod_{j=1}^{m-1} \frac{\tau_{j,j-1}}{1 - \tau_{jj}}$$

and hence

$$f(\hat{0}, u) = \beta \exp\left(-\frac{u^2}{2v_f}\right), \quad e(\hat{0}, u) = \alpha \exp\left(\frac{u^2}{2v_\tau}\right)$$

$$\alpha \triangleq \frac{\tau_{m,m-1}}{\tau} \prod_{j=1}^{m-1} \frac{\tau_{j,j-1}}{1 - \tau_{jj}}.$$

Clearly, $f(\hat{0}, u)$ has a (global) maximum and $e(\hat{0}, u)$ a (global) minimum at trait $u = 0$. It follows that there is a trade-off of type (a) as described in Figure 2.

Theorem 7(b) implies a right bifurcation if the inequality (27) holds, i.e. if $R_0''(\hat{0}, 0) < 0$ holds (so that $R_0(\hat{0}, u) = f(\hat{0}, u)e(\hat{0}, u)$ has a local maximum at $u = 0$). A calculation shows that this inequality reduces to

$$\alpha\beta \left(\frac{1}{v_\tau} - \frac{1}{v_f}\right) < 0.$$

If $v_f < v_\tau$, we conclude that there exist stable positive equilibria for $\lambda = \beta\varphi(\hat{0}, 0)e(\hat{0}, 0) = \alpha\beta \gtrsim 1$, or equivalently for

$$\beta \gtrsim \frac{\tau}{\tau_{m,m-1}} \prod_{j=1}^{m-1} \frac{1 - \tau_{jj}}{\tau_{j,j-1}}.$$

The inequality $v_f < v_\tau$ means that there is less variability in the adult birth rate than there is in the adult mortality rate as a function of the trait u . In the opposite case $v_f > v_\tau$, the bifurcating positive equilibria are unstable (Theorem 3(c)).

4.2. Evolution of a polymorphism

Rael *et al.* [18] use a three-dimensional ($m = 3$) evolutionary game theory (EGT) Leslie matrix model to describe and explain the evolution of a genetic polymorphism observed in an experiment involving the flour beetle *Tribolium castaneum* [16]. The matrix model used to describe the population dynamics is the LPA model [14,15] (also see [1,2,8–10]):

$$F(\hat{x}, u) = \begin{pmatrix} 0 & 0 & b(u) \exp(-c_{el}x_1 - c_{ea}x_3) \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix} \tag{29a}$$

$$T(\hat{x}, u) = \begin{pmatrix} 0 & 0 & 0 \\ 1 - \mu_l(u) & 0 & 0 \\ 0 & \exp(-c_{pa}x_3) & 1 - \mu_a(u) \end{pmatrix}. \tag{29b}$$

Here, $\hat{x} = \text{col}(x_1, x_2, x_3)$ is the vector of larval, pupal, and adult beetle densities. In this application, the trait u is a genetically determined phenotype occurring in *T. castaneum* that results from variation in a gene that regulates sensitivity to corn oil. In this classic single locus, two allele

Downloaded By: [Cushing, Jim M] At: 20:33 3 May 2011

case, individuals homozygous for the ‘cos’ allele are unable to properly digest the unsaturated fatty-acid present in corn oil, which in turn affects fecundity and mortality when cultured in a corn oil medium [16]. Individuals have one of three genotypes: cos/cos, cos/+, or +/+, where + represents the wild-type allele. The trait u in the model is the (mean) frequency of the +allele.

Using population and genetic data from the experiment, Rael *et al.* determine the following relationships among fertility and survivorship and the +allele frequency u :

$$\begin{aligned} b(u) &= -18u^2 + 21u + 11 \\ \mu_l(u) &= 0.10u^2 - 0.13u + 0.51 \\ \mu_a(u) &= 0.10u^2 - 0.13u + 0.11. \end{aligned} \tag{30}$$

We note that the non-linear terms (caused by cannibalism in this model) are all decreasing functions of x_i and therefore H3 is satisfied. To determine the critical trait values u^* at which bifurcation from the extinction equilibrium can occur, we need to solve Equation (26) for $u = u^*$, i.e. we need to solve the equation $R'_0(\hat{0}, u) = 0$ for $u = u^*$ on the interval $0 \leq u \leq 1$, where

$$\begin{aligned} R_0(\hat{0}, u) &= f(\hat{0}, u)e(\hat{0}, u) \\ f(\hat{0}, u) &= b(u) = -18u^2 + 21u + 11 \\ e(\hat{0}, u) &= \frac{1 - \mu_l(u)}{\mu_a(u)} = \frac{-0.10u^2 + 0.13u + 0.49}{0.10u^2 - 0.13u + 0.11}. \end{aligned}$$

It is straightforward to calculate $R'_0(\hat{0}, u)$ and find that $u^* \approx 0.62415$. Since

$$f'(\hat{0}, u^*) \approx -1.4694, \quad e'(\hat{0}, u^*) \approx 15.331$$

have opposite signs, we see that there is a trade-off between inherent adult fertility and inherent time spent as an adult at the trait $u^* \approx 0.62415$. This is an example of a type (b) trade-off in Figure 2 (see Figure 3).

To show the occurrence of a stable bifurcation, all that remains is to verify the inequality (27), i.e. to show that $R''_0(\hat{0}, u^*) < 0$. A straightforward calculation shows that $R''_0(\hat{0}, 0.62415) \approx -728.77$. We conclude that a right bifurcation of stable positive equilibria occurs in the EGT LPA model with Equation (30) at $R(\hat{0}, u^*) = 1$, where the critical +allele frequency is $u^* \approx 0.62415$. It is noteworthy that the experimentally observed frequency was estimated to be 0.6 [18].

An interesting observation in this example concerns the component u_e in an equilibrium (\hat{x}_e, u_e) . At an equilibrium (\hat{x}, u) we know that $R'_0(\hat{x}_e, u_e) = 0$ (see (23)). For the LPA model, a calculation shows

$$R'_0(\hat{x}, u) = \left(b(u) \frac{1 - \mu_l(u)}{\mu_a(u)} \right)' \exp(-c_{el}x_1 - c_{ea}x_3) \exp(-c_{pa}x_3),$$

which equals 0 if and only if the first factor equals 0, i.e. if and only if $u = u^*$. That is to say, for any equilibrium (\hat{x}_e, u_e) of the EGT LPA model, the trait u must equal the critical trait u^* . Thus, whereas the demographic components \hat{x}_e of the equilibria change along the bifurcating branch, the trait u remains fixed at the critical value u^* . This critical frequency implies (since it is equal to neither 0 nor 1) that the stable equilibria are polymorphisms with both alleles present.

For more details about this application, see [18].

Downloaded By: [Cushing, Jim M] At: 20:33 3 May 2011

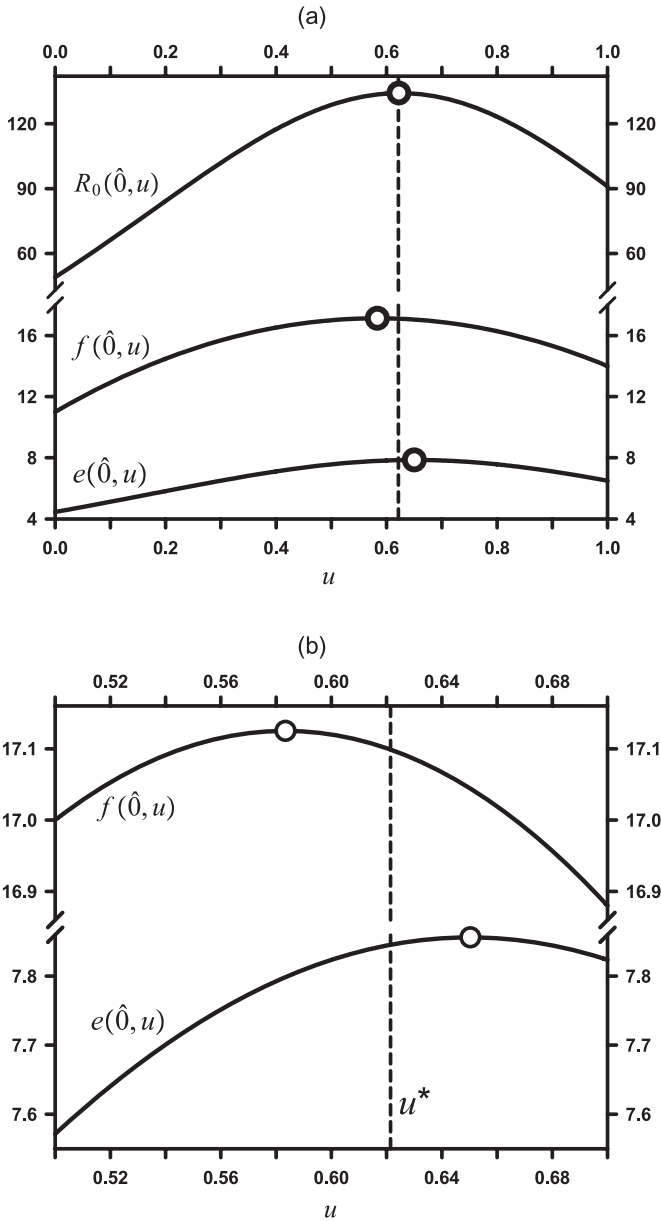


Figure 3. (a) Graphs of the inherent net reproductive number $R_0(\hat{0}, u)$, the inherent adult fertility $f(\hat{0}, u)$, and inherent time spent as an adult $e(\hat{0}, u)$ as functions of the +allele frequency u for the LPA model (29) with (30). The vertical, dashed line is located at the critical trait value $u^* \approx 0.62415$ where $R_0(\hat{0}, u)$ has a maximum. The maxima of $f(\hat{0}, u)$ and $e(\hat{0}, u)$ lie on either side of u^* . (b) $f(\hat{0}, u)$ and $e(\hat{0}, u)$ have opposite monotonicity at u^* .

5. Concluding remarks

As functions of a trait u , the inherent growth rate r and the inherent reproductive number R_0 are on the same side of 1 [12,17]. They do not, however, in general share monotonicity and extremum properties as functions of u . We showed that at values $u = u^*$ where one of these quantities equals 1 (and hence both equal 1) they do have the same monotonicity. Moreover, at

Downloaded By: [Cushing, Jim M] At: 20:33 3 May 2011

such points where one of these quantities has (and hence both have) a critical point, they have the same concavity and hence the same extremum properties (Theorem 1). Since it is these properties of r that determine the nature of the bifurcation of non-extinction equilibria of the Darwinian model (5) [11], the results in Theorem 1 allow one to determine the properties of this fundamental bifurcation phenomenon in terms of R_0 . That is to say, one can locate the bifurcation and determine its stability properties by studying R_0 as a function of the trait u , a more tractable quantity than r .

We found (Figure 1(a)) that the familiar transcritical bifurcation and exchange of stability property occur in the general Darwinian model (5) at $R_0(\hat{0}, u^*) = 1$, where u^* is a critical trait (i.e. $R'_0(\hat{0}, u^*) = 0$), when $R''_0(\hat{0}, u^*) < 0$ (and hence $R_0(\hat{0}, u)$ has a local maximum at $u = u^*$). In this case, the stability of the bifurcating non-extinction equilibria is determined by the direction of bifurcation. With regard, then, to a search for stable non-extinction equilibria of a Darwinian model (5), our results provide their existence when this bifurcation is to the right, i.e. for values of $R_0(\hat{0}, u^*) \gtrsim 1$. The usual negative feedback assumed for density-dependent demographic parameters always produces a stable bifurcation. Only in the case of sufficiently strong positive feedback effects at low density (Allee effects) will the bifurcation be to the left and unstable.

The bifurcation result in Theorem 3 only concerns non-extinction equilibria of Equation (5) near the bifurcation point, i.e. equilibria (\hat{x}, u) near $(\hat{0}, u^*)$ for values of $R_0(\hat{0}, u^*)$ near 1. Other stable and/or unstable non-extinction equilibria might exist for other, or even the same, values of $R_0(\hat{0}, u^*)$. Furthermore, stable bifurcating equilibria can lose their stability as $R_0(\hat{0}, u^*)$ is further increased beyond 1, resulting in bifurcations of non-equilibrium attractors (cycles, chaotic, etc.). This occurs, for example, in the Darwinian LPA model in Section 4.2 and is relevant to the application to the *Tribolium* experiment [18].

The Darwinian model (5) is derived from EGT. EGT was developed in the context of the theory of evolutionarily stable strategies (ESS) [22]. The ESS theory concerns the invasibility of a species by other (mutant) species. The ESS maximum principle states that a necessary condition for the trait u_e in a non-extinction equilibrium (\hat{x}_e, u_e) be an ESS is that $r(\hat{x}_e, u)$ attain a *global* maximum on U at u_e . If, in addition, (\hat{x}_e, u_e) is a stable equilibrium of Equation (5) (i.e. a convergent equilibrium in the language of [22]), then u_e is an ESS.

For any non-extinction equilibrium, the equilibrium equations (19a) and (19b) imply $r(\hat{x}_e, u_e) = 1$ and $r'(\hat{x}_e, u_e) = 0$. Clearly, the only candidates for ESS among the bifurcation scenarios in Figure 1 correspond to the stable, non-extinction equilibria along the right bifurcation case in Figure 1(a) (when $\kappa^* > 0$). In this case, $R''_0(\hat{0}, u^*) < 0$ and hence $r''(\hat{0}, u^*) < 0$ (by Theorem 1). By continuity, $r''(\hat{x}_e, u_e) < 0$ for (\hat{x}_e, u_e) near the bifurcation point $(\hat{0}, u^*)$. It follows that in this case, $r(\hat{x}_e, u)$ has a *local* maximum (equal to 1) at $u = u_e$. If $r(\hat{x}_e, u)$ has a global maximum at $u = u^*$ (on U), then it is an ESS. Unfortunately, the global maximum of $r(\hat{x}_e, u)$ cannot be determined from $R_0(\hat{x}_e, u)$. In applications, the global maximum of $r(\hat{x}_e, u)$ is usually determined by numerically graphing $r(\hat{x}_e, u)$ as a function of u . In the case of a left bifurcation (when $\kappa^* > 0$ in Figure 1(a)), u_e is not an ESS even if it is a global maximum. This is because the bifurcating equilibria (\hat{x}_e, u) are unstable (are not a convergent equilibria in the language of [22]). Nor do the bifurcating equilibria in Figure 1(b) correspond to ESS traits – both because they are unstable and because $r(\hat{x}_e, u)$ has a local minimum at $u = u_e$.

Acknowledgements

Research supported by NSF grant DMS 0917435.

Note

1. A non-negative matrix is primitive if it is irreducible and its dominant eigenvalue is strictly dominant. This is equivalent to requiring that some integer power of the matrix is positive.

References

- [1] H. Caswell, *Matrix Population Models: Construction, Analysis and Interpretation*, 2nd ed., Sinauer Associates, Inc. Publishers, Sunderland, MA, 2001.
- [2] R.F. Costantino, R.A. Desharnais, J.M. Cushing, B. Dennis, S.M. Henson, and A.A. King, *The flour beetle Tribolium as an effective tool of discovery*, Adv. Ecol. Res. 37 (2005), pp. 101–141.
- [3] J.M. Cushing, *Bifurcation of time periodic solutions of the McKendrick equations with applications to population dynamics*, Comput. Math. Appl. 9(3) (1982), pp. 459–478 (Reprinted in *Advances in Hyperbolic Differential Equations*, Vol. 1, edited by M. Witten, Pergamon Press, New York, 1983).
- [4] J.M. Cushing, *Existence and stability of equilibria in age-structured population dynamics*, J. Math. Biol. 20(3) (1984), pp. 259–276.
- [5] J.M. Cushing, *Equilibria in structured populations*, J. Math. Biol. 23(1) (1985), pp. 15–39.
- [6] J.M. Cushing, *Periodic McKendrick equations for age-structured population growth*, Comput. Math. Appl. 12A(45) (1986), pp. 513–526.
- [7] J.M. Cushing, *Periodically forced nonlinear systems of difference equations*, J. Differ. Equ. Appl. 3 (1998), pp. 547–561.
- [8] J.M. Cushing, *An Introduction to Structured Population Dynamics*, CBMS-NSF Regional Conference Series in Applied Mathematics, Vol. 71, SIAM, Philadelphia, 1998.
- [9] J.M. Cushing, *The LPA model*, Fields Inst. Commun. 43 (2004), pp. 29–55.
- [10] J.M. Cushing, *Matrix models and population dynamics*, in *Mathematical Biology*, M.A. Lewis, M.A.J. Chaplain, J.P. Keener, and P.K. Maini, eds., IAS/Park City Mathematics Series, American Mathematical Society, Providence, RI, 2009, pp. 47–150.
- [11] J.M. Cushing, *A bifurcation theorem for Darwinian matrix models*, Nonlinear Stud. 17(1) (2010), pp. 1–13.
- [12] J.M. Cushing and Z. Yicang, *The net reproductive value and stability in matrix population models*, Nat. Resour. Model. 8 (1994), pp. 297–333.
- [13] J.M. Cushing and S.M. Henson, *Global dynamics of some periodically forced, monotone difference equations*, J. Differ. Equ. Appl. 7 (2001), pp. 859–872.
- [14] J.M. Cushing, R.F. Costantino, B. Dennis, R.A. Desharnais, and S.M. Henson, *Chaos in Ecology: Experimental Nonlinear Dynamics*, Academic Press, New York, 2003.
- [15] B. Dennis, R.A. Desharnais, J.M. Cushing, and R.F. Costantino, *Nonlinear demographic dynamics: Mathematical models, statistical methods, and biological experiments*, Ecol. Monogr. 65 (1995), pp. 261–281.
- [16] R.A. Desharnais and R.F. Costantino, *Genetic analysis of a population of Tribolium. VII. stability: Response to genetic and demographic perturbations*, Can. J. Genet. Cytol. 22 (1980), pp. 577–589.
- [17] C.-K. Li and H. Schneider, *Applications of Perron-Frobenius theory to population dynamics*, J. Math. Biol. 44 (2002), pp. 450–462.
- [18] R.C. Rael, R.F. Costantino, J.M. Cushing, and T.L. Vincent, *Using stage-structured evolutionary game theory to model the experimentally observed evolution of a genetic polymorphism*, Evol. Ecol. Res. 11 (2009), pp. 141–151.
- [19] S. Robertson, *Spatial patterns in stage-structured populations with density dependent dispersal*, Ph.D. dissertation, University of Arizona, 2009.
- [20] D.A. Roff, *Life History Evolution*, Sinauer Associates Inc., MA, 2002.
- [21] H. Thieme, *Spectral bound and reproduction number for infinite-dimensional population structure and time heterogeneity*, SIAM J. Appl. Math. 70(1) (2009), pp. 188–211.
- [22] T.L. Vincent and J.S. Brown, *Evolutionary Game Theory, Natural Selection, and Darwinian Dynamics*, Cambridge University Press, 2005.