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# Stability Conditions for Equilibria of Nonlinear Matrix Population Models

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In this paper we develop stability and instability criteria for equilibria of nonlinear matrix population models in which density dependence (i.e. nonlinearity) arises through a dependence of vital rates on a weighted total population size  $w$ . These criteria are based upon the net reproductive number  $n = n(w)$  as a function of  $w$  and partially address an earlier conjecture concerning the relationship between stability and the derivative  $n' = n'(w)$  (Cushing 1988a). Under rather general conditions it is shown that  $n'(w) > 0$  at equilibrium implies instability and hence that  $n'(w) \leq 0$  is necessary for stability. In general,  $n'(w) < 0$  is not sufficient for stability. Conditions under which  $n'(w) < 0$  does imply stability are also given. A variety of applications is given.

*Keywords:* nonlinear matrix equations; stability; equilibrium; net reproductive number

*Classification categories:* 92D25, 39A11

## 1. INTRODUCTION

Difference (or recursion) equations have been extensively used to describe the dynamics of biological populations since the pioneering work of Lewis [21] and Leslie [17], [18]. They have been used in a wide diversity of disciplines, including demography, ecology, epidemiology, pest control, fishery, forest management, resource renewal, and many others. One of the primary applications is to the dynamics of so-called structured populations, in which individuals are categorized according to some specified physiological classes (such as age, body size, life-cycle stages, etc.). In these applications the dynamics over discrete time intervals (of equal length) are described by a multiplicative "projection" matrix  $A$

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which maps a distribution vector  $\vec{x} = \vec{x}(t)$  of class densities at time  $t$  to a distribution vector  $\vec{x} = \vec{x}(t+1)$  at time  $t+1$  according to the formula

$$\vec{x}(t+1) = A\vec{x}(t).$$

These kinds of equations have become known as matrix population models. The book by Caswell [2] provides a comprehensive exposition of the theory and application of matrix models to population dynamics (also see [3], [5], [26], [32]).

As they do in all kinds of dynamical models, equilibria and their stability properties play important roles in matrix population models. For *linear* matrix models in which  $A$  is constant, the theory for the existence and stability of equilibria is well known. For linear models, the famous Perron-Frobenius theory and the dominant eigenvalue of the projection matrix  $A$  play a central role. For determining stability properties, an equivalent role is played by the “net reproductive number” (sometimes called the net reproductive “rate” or “value”) [7], [32]. The net reproductive number, generalized to nonlinear models, will be central to our results in this paper.

When the vital parameters, such as birth, death, and class transition rates, depend on population density, the projection matrix  $A = A(\vec{x})$  is a function of the class distribution vector  $\vec{x}$  and the matrix model describing the dynamics of the population becomes nonlinear. The existence and stability of nontrivial equilibria become in general much more difficult problems. The existence of nontrivial equilibria for general nonlinear matrix models has been studied using bifurcation theory techniques by Cushing [3], [5], [32]. In these general results the “inherent net reproductive number (the expected number of offspring per individual per lifetime at low, technically zero population density) is used as a bifurcation parameter.

Under general conditions the net reproductive number  $n = n(\vec{x})$  can be defined for a matrix population model as a function of the population distribution  $\vec{x} \geq \vec{0}$  (see [5], [32] and Definition 1 below). Biologically, this number is the expected number of offspring per individual per lifetime if the population were held fixed at the constant distribution  $\vec{x}$ . When  $\vec{x} \geq \vec{0}$  is an *equilibrium* distribution, the net reproductive number necessarily equals one, i.e.  $n(\vec{x}) = 1$ , since at equilibrium each individual exactly replaces itself. In [5] it was conjectured that there is a relationship between the stability properties of a nontrivial equilibrium  $\vec{x} \geq \vec{0}$  and the gradient  $\nabla n(\vec{x})$ , namely that  $\nabla n(\vec{x}) > \vec{0}$  implies  $\vec{x}$  is unstable. In other word, it is conjectured that  $\nabla n(\vec{x}) \leq \vec{0}$  is necessary for (local asymptotic) stability of a nontrivial equilibrium  $\vec{x}$ . This conjecture has been proved for the special case of nonlinear Leslie age-structured models in which the nonlinearities arises through a dependence of the Leslie projection matrix  $A = A(w)$  on a weighted total population size  $w = \vec{w}^T \vec{x}$  [3]. (Also see [24], [25] for related results for continuous age-structured models). Our main goal in this paper is to prove this conjecture for *general* structured population models in which

$A = A(w)$ . In this case  $n = n(w)$  is a function of  $w$  and the conjecture is that  $n'(w) > 0$  implies  $\vec{x}$  is unstable. Thus, we will prove that under very general conditions the inequality  $n'(w) \leq 0$  is necessary for the stability of a nontrivial equilibrium  $\vec{x} \geq \vec{0}$ . We will also obtain some results concerning the implication that  $n'(w) < 0$  is sufficient for equilibrium stability. We will also give a counterexample to show that the more general conjecture that  $\nabla n(\vec{x}) > \vec{0}$  implies instability is false.

The paper is organized as follows. In Section 2 the definition of the net reproductive number  $n$  is given for general matrix models. Formulas for the net reproductive number are often available for special types of matrix models [7], [32]. The existence of these formulas illustrate one advantage of the net reproductive number over the dominant eigenvalue of the projection matrix (for which such formulas are generally not available). We derive a formula for the derivative of the net reproductive number of a general nonlinear matrix equation. This formula provides the basis for the main results of the paper. In Section 3 we study necessary conditions for stability of positive equilibria. The results obtained in this section confirm the conjecture discussed above for general matrix models. These results are applied to nonlinear Leslie models, nonlinear Usher models, models with density dependent fertility, and some other examples. In Section 4 we study sufficient conditions for stability of a positive equilibrium.

## 2. THE NET REPRODUCTIVE NUMBER

Throughout this paper a matrix is denoted by a capital letter, a column vector is denoted by a lower case letter with an arrow over it. The transpose of a matrix or a vector is denoted by a superscript “ $\tau$ ”; for example,  $A^\tau$  is the transpose of the matrix  $A$  and  $\vec{x}^\tau$  is the row vector which is the transpose of the column vector  $\vec{x}$ .

Consider a population whose individual members are categorized into  $m + 1$  classes. Let  $x_k(t)$  denote the number (or the density) in the  $k^{\text{th}}$  class ( $k = 0, 1, \dots, m$ ) at time  $t = 0, 1, 2, \dots$ . Then the column vector  $\vec{x}(t) = (x_0(t), \dots, x_m(t))^\tau$  denotes the density distribution of the population at time  $t$ .

Let  $p_{ij}(t)$ ,  $0 \leq p_{ij}(t) \leq 1$ , be the (“transition”) probability that an individual in class  $j$  at time  $t$  will survive and move into class  $i$  at time  $t + 1$ . Let  $f_{ij}(t) \geq 0$  (called the “per capita fertility rate”) be the number of offspring of class  $i$  borne to an individual of class  $j$  that survive to time  $t + 1$ . The  $(m + 1) \times (m + 1)$  fertility matrix is denoted by  $F(t) = (f_{ij}(t)) \geq 0$  and the  $(m + 1) \times (m + 1)$  transition matrix is denoted by  $P(t) = (p_{ij}(t)) \geq 0$ . If we assume that the population is closed to immigration and emigration, then the density distribution vector  $\vec{x}(t + 1)$  at time  $t + 1$  is given by

$$\begin{aligned} \vec{x}(t + 1) &= A(t)\vec{x}(t) \\ A(t) &= F(t) + P(t) \geq 0. \end{aligned} \tag{1}$$

The nonnegative matrix  $A$  is usually referred to as *the projection matrix*. It is obvious from this recursive formula that the class distribution vector  $\vec{x}(t)$  is uniquely determined (and is nonnegative) for all  $t \geq 1$  once an initial nonnegative distribution vector  $\vec{x}(0) \geq \vec{0}$  is given. If  $A$  remains constant in time, then (1) is an autonomous linear system. If either the fertility or the transition matrix, and hence the projection matrix, depends on time  $t$  only through a dependency on the distribution vector  $\vec{x}(t)$ , then (1) is autonomous and nonlinear and we write

$$\begin{aligned}\vec{x}(t+1) &= A(\vec{x}(t))\vec{x}(t) \\ A(\vec{x}) &\doteq F(\vec{x}) + P(\vec{x}) \geq 0.\end{aligned}\quad (2)$$

The equilibrium equation associated with equation (2) is

$$\vec{x} = (F(\vec{x}) + P(\vec{x}))\vec{x}. \quad (3)$$

Clearly  $\vec{x} = \vec{0}$  is a trivial equilibrium. A nontrivial equilibrium  $\vec{x}$  is an eigenvector associated with the eigenvalue 1 of the projection matrix  $A(\vec{x}) = F(\vec{x}) + P(\vec{x})$ . In population problems only nonnegative, nontrivial equilibria  $\vec{x} \geq \vec{0}$  are of interest.

It is assumed that the column sums of the transition matrix  $P(\vec{x})$  are strictly less than one,

$$0 \leq \sum_{i=0}^m p_{ij}(\vec{x}) < 1, \quad \vec{x} \in R_+^n \doteq R_+ \times \dots \times R_+, \quad j = 0, 1, \dots, m. \quad (4)$$

where  $R_+ \doteq [0, +\infty)$ . The biological meaning of this “dissipative condition” is that there is always some population density loss during class transitions from every class over one unit of time (e.g. due to mortality). Because of the dissipative condition (4) the inverse of the matrix  $I - P(\vec{x})$  exists for all  $t \in R_+$  and is nonnegative

$$(I - P(\vec{x}))^{-1} = I + P(\vec{x}) + P^2(\vec{x}) + \dots \geq 0. \quad (5)$$

The matrix

$$R(\vec{x}) \doteq (I - P(\vec{x}))^{-1} F(\vec{x}) \geq 0$$

is then well defined and nonnegative for  $\vec{x} \in R_+$ . The equilibrium equation (3) is equivalent to the equation

$$\vec{x} = R(\vec{x})\vec{x}. \quad (6)$$

Thus, a nontrivial and nonnegative equilibrium  $\vec{x}$  is also an eigenvector associated with the eigenvalue 1 of the nonnegative matrix  $R(w)$ .

The theory of the nonnegative matrices implies the existence of a nonnegative dominant eigenvalue (and associated nonnegative right and left eigenvectors) [1], [2], [13]. Applied to the matrix  $R(\vec{x})$  this theory yields a nonnegative domi-

nant eigenvalue  $n = n(\vec{x}) \geq 0$  for each  $\vec{x} \in R_+^n$ . If, as is often the case in applications,  $R(\vec{x})$  is irreducible for all  $\vec{x} \in R_+^n$ , then the Perron-Frobenius theory implies  $n(\vec{x})$  is positive for all  $\vec{x} \in R_+^n$  (as are its associated right and left eigenvectors). In this case, the nonnegative equilibrium is positive.

**DEFINITION 1** For each  $\vec{x} \in R_+^n$  the dominant eigenvalue  $n = n(\vec{x}) \geq 0$  of the nonnegative matrix  $R(\vec{x})$  is called the “**net reproductive number**” at the class distribution vector  $\vec{x}$  of the matrix model (2).

The definition of the net reproductive number is a generalization of the “inherent” net reproductive number  $n(\vec{0})$  for linear matrix models [7]. Biologically  $n(\vec{x})$  is the expected number of offspring from an individual over its lifetime if the class distribution vector were held fixed at  $\vec{x}$ . That is, if class distribution vector were held fixed at  $\vec{x}$ , then an individual will produce, on average,  $n(\vec{x})$  offspring over its lifetime. A further discussion of the net reproductive number can be found in [3] and [7].  $n$  is also an eigenvalue of  $F(I - P)^{-1}$ ; see [32].

For our purposes we need an analytical formula for the derivatives of  $n(\vec{x})$ . Such a formula can be found as follows. Let  $\vec{v}(\vec{x}) = (v_0(\vec{x}), \dots, v_m(\vec{x}))^T$  be the (nonnegative) eigenvector associated with the dominant eigenvalue  $n(\vec{x})$  matrix  $R(\vec{x})$ . Then  $n(\vec{x})$  and  $\vec{v}(\vec{x})$  satisfy the equation

$$R(\vec{x})\vec{v}(\vec{x}) = n(\vec{x})\vec{v}(\vec{x})$$

or equivalently

$$F(\vec{x})\vec{v}(\vec{x}) = n(\vec{x})(I - P(\vec{x}))\vec{v}(\vec{x}).$$

From this equation it follows that

$$\begin{aligned} \frac{\partial n}{\partial x_i}(I - P)\vec{v} &= \frac{\partial F}{\partial x_i}\vec{v} + n\frac{\partial P}{\partial x_i}\vec{v} \\ &+ F(w)\frac{\partial \vec{v}}{\partial x_i} - n(I - P)\frac{\partial \vec{v}}{\partial x_i}. \end{aligned} \quad (7)$$

Suppose now that  $\vec{x} \geq \vec{0}$  is a nontrivial, nonnegative equilibrium of (2). Then  $\vec{v} = \vec{x}$ . Moreover, at this equilibrium  $n = 1$  and  $R\vec{v} = \vec{v}$ . With these relations, equation (7) becomes

$$\begin{aligned} \frac{\partial n}{\partial x_i}(I - P)\vec{x} &= \left(\frac{\partial F}{\partial x_i} + \frac{\partial P}{\partial x_i}\right)\vec{x} \\ &- (I - F - P)\frac{\partial \vec{v}}{\partial x_i}. \end{aligned} \quad (8)$$

Assume that  $A(\vec{x}) \geq 0$  is irreducible. Then  $A(\vec{x})$  has a dominant positive eigenvalue with positive eigenvectors and all other eigenvectors (associated with

all other eigenvalues) have a negative component [13]. Since  $\vec{x}$  is nontrivial and nonnegative it follows that 1 is the dominant eigenvalue and that  $\vec{x}$  is in fact positive. The matrix  $A(\vec{x})$  also has a positive left eigenvector  $\vec{u} = \vec{u}(\vec{x})$  associated with the eigenvalue 1, i.e.

$$\vec{u}(\vec{x})A(\vec{x}) = \vec{u}(\vec{x}) > 0.$$

Then

$$\vec{u}(I - F - P) = \vec{0}$$

and the inner product of the both sides of (8) with  $\vec{u} = \vec{u}(\vec{x})$  produces the equation

$$\frac{\partial n}{\partial x_i} \vec{u}(I - P)\vec{x} = \vec{u} \left( \frac{\partial F}{\partial x_i} + \frac{\partial P}{\partial x_i} \right) \vec{x}$$

or

$$\frac{\partial n}{\partial x_i} \vec{u} F \vec{x} = \vec{u} \frac{\partial A}{\partial x_i} \vec{x}. \quad (9)$$

Note that since  $\vec{u}$  is positive and  $F(\vec{x})\vec{x}$  is nonnegative

$$\vec{u}(\vec{x})F(\vec{x})\vec{x} = 0$$

would imply that

$$F(\vec{x})\vec{x} = (I - P(\vec{x}))\vec{x} = 0.$$

This contradicts the invertibility of  $I - P(\vec{x})$ . It follows that

$$\vec{u} F \vec{x} \neq 0. \quad (10)$$

Therefore, from (9) we obtain the formula

$$\frac{\partial n}{\partial x_i} = \frac{\vec{u} \frac{\partial A}{\partial x_i} \vec{x}}{\vec{u} F \vec{x}} \quad (11)$$

where all quantities are evaluated at the positive equilibrium  $\vec{x}$  of (2).

In this paper we study the important case in which the density dependence of  $A$  is through a dependence on a weighed total population size. Define the *weighted total population size*  $w = w(t)$  by

$$w(t) = \sum_{i=0}^m w_i x_i(t) = \vec{w} \vec{x}(t) \quad (12)$$

where  $\vec{w}$  is a constant nonnegative, nonzero column vector of weights, i.e.

$$\vec{w}^{\rightarrow\tau} = (w_0, \dots, w_m) \geq 0, \quad w_i \geq 0, \quad \sum_{i=0}^m w_i > 0.$$

The entries in the fertility and transition matrices  $F = (f_{ij})$  and  $P = (p_{ij})$ , and hence in  $A$ , are assumed dependent on  $w$ , i.e.  $p_{ij} = p_{ij}(w)$  and  $f_{ij} = f_{ij}(w)$ . Under these assumptions we rewrite model (2) as

$$\begin{aligned} \vec{x}(t+1) &= A(w(t))\vec{x}(t) \\ A(w) &= F(w) + P(w). \end{aligned} \quad (13)$$

Assume

$$\mathbf{A1}: f_{ij} \in C^1(R_+, R_+) \text{ and } p_{ij} \in C^1(R_+, [0, 1])$$

and the “dissipative condition”:

$$\mathbf{A2}: 0 \leq \sum_{i=0}^m p_{ij}(w) < 1, \quad w \in R_+, \quad j = 0, 1, \dots, m$$

We also assume that

$$\mathbf{A3}: A(w) \text{ is irreducible for } w \in R_+.$$

In most population models the nonnegative projection matrix  $A(w)$  is, in fact, both irreducible and primitive [2].

For models of the form (13) the net reproductive number  $n = n(w)$  is a function of  $w$ . The formula (11) yields the equation

$$n'(w)w_i = \frac{\vec{u}^{\rightarrow\tau} A'(w)w_i \vec{x}}{\vec{u}^{\rightarrow\tau} F(w)\vec{x}}$$

and since at least one weight  $w_i$  is nonzero this equation gives formula

$$n'(w) = \frac{\vec{u}^{\rightarrow\tau} A'(w)\vec{x}}{\vec{u}^{\rightarrow\tau} F(w)\vec{x}} \quad (14)$$

for the derivative of  $n(w)$  at a positive equilibrium of (13).

As an illustrative example, consider a nonlinear Usher matrix equation [28], [29], [30], [32]. In an Usher model all newborns lie in the first class and during one time interval a surviving individual either remains in its current class or advances to the next adjacent class. Thus, Usher models with a nonlinear dependence on weighted total population size  $w$  are characterized by fertility and transition matrices of the form



$$F(w) = \begin{bmatrix} f_{00}(w) & f_{01}(w) & \dots & f_{0m}(w) \\ 0 & 0 & \dots & 0 \\ \vdots & \vdots & \square & \vdots \\ 0 & 0 & \dots & 0 \end{bmatrix} \quad (15)$$

$$P(w) = \begin{bmatrix} p_{00}(w) & 0 & \dots & 0 & 0 \\ p_{10}(w) & p_{11}(w) & \dots & 0 & 0 \\ \vdots & \vdots & \square & \vdots & \vdots \\ 0 & 0 & \dots & p_{m-1,m-1}(w) & 0 \\ 0 & 0 & \dots & p_{m,m-1}(w) & p_{mm}(w) \end{bmatrix} \quad (16)$$

with

$$f_{0i}(w) \geq 0, \quad 0 \leq p_{ii}(w) < 1, \quad 0 < p_{i,i-1}(w) \leq 1.$$

Usher models are the simplest kind of “size” structured population model in which the classes are based upon a measurement of body size and an individual either remains, after one time unit, in its current size class or grows into the next size class (i.e., it is assumed that the time unit is chosen so that individuals cannot skip over the next size class nor shrink to a smaller size class). In its mathematical form, the Usher matrix equation is a generalization of the classical Leslie age-structured model. In a Leslie matrix model the population is structured by means of chronological age classes with the same length as the time step of the equation. Thus, in a Leslie matrix equation all diagonal terms vanish,  $p_{ii}(w) = 0$  (because a surviving individual necessarily advances to the next age class).

Define the positive quantities

$$e_{ij}(w) = \frac{\prod_{k=j}^i p_{k,k-1}(w)}{\prod_{k=j}^i (1 - p_{jj}(w))} > 0 \quad \text{for } i \geq j \geq 0.$$

For notational convenience  $p_{0,-1}(w)$  is defined to be identically equal to 1. The quantity  $e_{ij}$  is the amount of time an individual, starting from class  $j$ , is expected thereafter to spend in class  $i$ . Thus,  $e_{i0}$  is the amount of time an individual is expected to spend in class  $i$  over the course of its lifetime. If we denote

$$\vec{f}(w) = \begin{bmatrix} f_{00}(w) \\ f_{01}(w) \\ \vdots \\ f_{0m}(w) \end{bmatrix} \quad \text{and} \quad \vec{e}(w) = \begin{bmatrix} e_{00}(w) \\ e_{10}(w) \\ \vdots \\ e_{m0}(w) \end{bmatrix}$$

is turns out for an Usher matrix model that

$$R(w) = \begin{bmatrix} f_{00}(w)e_{00}(w) & f_{01}(w)e_{00}(w) & \dots & f_{0m}(w)e_{00}(w) \\ f_{00}(w)e_{10}(w) & f_{01}(w)e_{10}(w) & \dots & f_{0m}(w)e_{10}(w) \\ \vdots & \vdots & \square & \vdots \\ f_{00}(w)e_{m0}(w) & f_{01}(w)e_{m0}(w) & \dots & f_{0m}(w)e_{m0}(w) \end{bmatrix}$$

$$= \vec{e}(w) \vec{f}^{\tau}(w)$$

Because each row of the matrix  $R(w)$  is a multiple of the same column vector  $\vec{e}(w)$ , 0 is an eigenvalue of multiplicity  $m$ . The remaining eigenvalue is

$$n(w) = \sum_{i=0}^m f_{0i}(w)e_{i0}(w) = \vec{f}^{\tau}(w) \vec{e}(w) \quad (17)$$

and  $\vec{e}(w)$  is an eigenvector.

At a nontrivial, nonnegative equilibrium  $\vec{x}$ , we know that  $n(w) = 1$  where  $w = \vec{w}^{\tau} \vec{x}$  is the equilibrium total population size. The equilibrium  $\vec{x}$  is an eigenvector associated with  $R(w)$  and is therefore a positive multiple of  $\vec{e}(w)$ , i.e.  $\vec{x} = c \vec{e}(w)$ .

Thus, nontrivial equilibria can be found by first finding a positive root  $w$  of the equation  $n(w) = 1$  and then determining the value of  $c$  so that  $\vec{w}^{\tau} \vec{x} = w$ . This value of  $c$  is clearly  $c = \frac{w}{\vec{w}^{\tau} \vec{e}(w)}$ . Thus, for each positive root of the equation

$n(w) = 1$  there is a positive equilibrium as given by the formula

$$\vec{x} = \frac{w}{\vec{w}^{\tau} \vec{e}(w)} \vec{e}(w).$$

Although, as remarked above, we will not study the existence of nonnegative equilibria here, these calculations show that such a study reduces to a single scalar equation  $n(w) = 1$  for positive  $w$ .

A positive left eigenvector corresponding to the eigenvalue 1 of  $A(w)$  is given by

$$\vec{u}(w) = \begin{pmatrix} \frac{1}{p_{0, -1}(w)} \sum_{k=0}^m f_{0k}(w) e_{k0}(w) \\ \vdots \\ \frac{1}{p_{i, i-1}(w)} \sum_{k=i}^m f_{0k}(w) e_{ki}(w) \\ \vdots \\ \frac{1}{p_{m, m-1}(w)} f_{0m}(w) e_{mm}(w) \end{pmatrix}$$

$$= \begin{pmatrix} 1 \\ \vdots \\ \frac{1}{p_{i,i-1}(w)} \sum_{k=i}^m f_{0k}(w) e_{ki}(w) \\ \vdots \\ \frac{1}{p_{m,m-1}(w)} f_{0m}(w) e_{mm}(w) \end{pmatrix}.$$

In the formula (14), the denominator is

$$\vec{u}^\tau(w) F(w) \vec{x} = \frac{w}{w e} \vec{u}^\tau(w) F(w) \vec{e}(w) = \frac{w}{w e} \vec{u}^\tau(w) \begin{pmatrix} n(w) \\ 0 \\ \vdots \\ 0 \end{pmatrix} = \frac{w}{w e}.$$

and thus

$$n'(w) = \vec{u}^\tau(w) A'(w) \vec{e}(w)$$

$$= \begin{pmatrix} 1 \\ \vdots \\ \frac{1}{p_{i,i-1}} \sum_{k=i}^m f_{0k} e_{ki} \\ \vdots \\ \frac{1}{p_{m,m-1}} f_{0m} e_{mm} \end{pmatrix}^\tau \begin{pmatrix} f_{00} + p_{00} & \cdots & f_{0,m-1} & f_{0m} \\ p_{10} & \cdots & 0 & 0 \\ \vdots & \square & \vdots & \vdots \\ 0 & \cdots & p_{m,m-1} & p_{mm} \end{pmatrix} \begin{pmatrix} e_{00} \\ e_{10} \\ \vdots \\ e_{m0} \end{pmatrix}.$$

### 3. NECESSARY CONDITIONS FOR STABILITY

To study the local stability or instability of a positive equilibrium  $\vec{x}$  of the non-linear matrix model (13) we need to investigate the eigenvalues of the Jacobian of  $A(w)\vec{x} = A(\vec{w}, \vec{x})\vec{x}$  evaluated at the equilibrium. The linearized equation is (asymptotically) stable if all eigenvalue of its coefficient matrix are less than one in magnitude, and unstable if at least one eigenvalues has magnitude larger than one. The equilibrium  $\vec{x}$  of the original nonlinear matrix equation (13) is correspondingly (locally asymptotically) stable or unstable [16], [32].

Unfortunately, in general there is no simple way to study the stability of the linearized equation, as it depends on model parametrs, if the dimension  $m$  is large.

## STABILITY CONDITIONS FOR EQUILIBRIA

There exists no general formula for the eigenvalues of high dimensional matrices and the necessary and sufficient conditions given by the Schur-Cohn (or Jury) conditions [16], [15] are too complicated to be of practical use for parameter studies in high dimensional problems. On the other hand, formulas for the net reproductive number  $n$  and its derivative  $n'$  are often available and results that relate  $n'$  to the stability properties of an equilibrium can therefore be of use. In this section we will show that the positivity of  $n'(w)$  at a positive equilibrium of (13) implies that the equilibrium is unstable.

Assume that equation (13) has a positive equilibrium  $\vec{x}$ . A routine calculation yields the linearized equation of model (13) at  $\vec{x}$

$$\vec{z}(t+1) = J(w)\vec{z}(t), \quad w = \vec{w} \vec{x} \quad (18)$$

where the Jacobian matrix  $J(w)$  is given by

$$J(w) \doteq A(w) + A'(w)\vec{x}\vec{w}$$

with

$$A(w) = F(w) + P(w), \quad A'(w) = F'(w) + P'(w).$$

The magnitude of eigenvalue of the Jacobian matrix  $J(w)$  determines the stability properties of the positive equilibrium  $\vec{x}$ . For example, if  $J(w)$  has a real eigenvalue  $\lambda$ ,  $\lambda > 1$  then the positive equilibrium is unstable.

As a motivating example, consider the Usher model (15)-(16). A straightforward (but tedious) calculation of  $J(w)$  shows that

$$\det(I - J(w)) = -wn'(w) \prod_{i=0}^{m-1} (1 - p_{ii}(w)). \quad (19)$$

If  $n'(w) > 1$ , then the characteristic polynomial  $p(\lambda) \doteq \det(\lambda I - J(w))$  satisfies  $p(1) < 1$  and  $\lim_{\lambda \rightarrow +\infty} p(\lambda) = +\infty$ . It follows that  $p(\lambda)$  has a real root  $\lambda > 1$  and the equilibrium is unstable. This is a generalization of the same result in [3] for the Leslie model (i.e. when  $p_{ii}(w) \equiv 0$ ).

Our goal is to show that  $n'(w) > 0$  implies equilibrium instability for the general matrix model (13). The proof involves showing that  $\det(I - J(w))$  is a negative multiple of  $n'(w)$ , as in the Usher example above. In order to state our main result we need some additional notation. Let  $S(w) = (s_{ij}(w))$  be the cofactor matrix of the matrix  $I - A(w)$ , i.e.  $s_{ij}(w) = (-1)^{i+j} \det(S_{ij}(w))$  where  $S_{ij}(w)$  is a  $m \times m$  matrix obtained by deleting the  $i^{\text{th}}$  row and  $j^{\text{th}}$  column of the matrix  $I - A(w)$ . For example,

$$s_{00} = \det \begin{pmatrix} 1 - a_{11}(w) & -a_{12}(w) & \dots & -a_{1m}(w) \\ -a_{21}(w) & 1 - a_{22}(w) & \dots & -a_{2m}(w) \\ \vdots & \vdots & \square & \vdots \\ -a_{m1}(w) & -a_{m2}(w) & \dots & 1 - a_{mm}(w) \end{pmatrix}$$

where  $A(w) = (a_{ij}(w)) = (f_{ij}(w) + p_{ij}(w))$ .

**THEOREM 1** Assume A1, A2 and A3. Suppose that  $\vec{x}$  is a positive equilibrium of the nonlinear matrix equation (13) and that  $w = \vec{w}^{\tau} \vec{x} > 0$  is the corresponding weighted total population size. Assume that  $s_{ii}(w) > 0$  for all  $i$ ,  $0 \leq i \leq m$ . Then  $n'(w) > 0$  implies that  $\vec{x}$  is unstable. That is to say,  $n'(w) \leq 0$  is necessary for the (local asymptotic) stability of the positive equilibrium  $\vec{x}$ .

The proof of this theorem appears in the Appendix.

In the following two examples it is shown that the assumption  $s_{ii} > 0$  is automatically fulfilled for the two and three dimensional cases. It is an open question whether this is true for  $m \geq 3$ .

**Example 1** Consider the general two dimensional structured population model

$$\begin{pmatrix} x_0(t+1) \\ x_1(t+1) \end{pmatrix} = \begin{pmatrix} a_{00}(w) & a_{01}(w) \\ a_{10}(w) & a_{11}(w) \end{pmatrix} \begin{pmatrix} x_0(t) \\ x_1(t) \end{pmatrix} \quad (20)$$

Suppose A1, A2 and A3 hold and suppose that  $\vec{x} = (x_0, x_1)^t$  is a positive equilibrium. Then the positive components of  $\vec{x}$  satisfy the equations

$$\begin{aligned} (1 - a_{00}(w))x_0 - a_{01}(w)x_1 &= 0 \\ -a_{10}(w)x_0 + (1 - a_{11}(w))x_1 &= 0. \end{aligned}$$

For this equation  $s_{00} = 1 - a_{00}(w)$ . Clearly  $s_{00}(w) < 0$  and the second equation lead to the contradiction that  $x_1 = 0$ . If  $s_{00}(w) = 0$ , then either  $x_0 = 0$ , a contradiction, or  $a_{10}(w) = 0$ , which implies the reducibility of the matrix  $A(w)$  in contradiction to A3. Therefore, the existence of a positive equilibrium and the irreducibility of the matrix  $A(w)$  assure that  $s_{00}(w) > 0$ . A similar argument, using the first equation, shows that  $s_{11}(w) > 0$ . Thus, Theorem 1 implies that  $n'(w) \leq 0$  is necessary for the stability of the equilibrium.

**Example 2** Consider the general three dimensional structured population model (13)

$$\begin{pmatrix} x_0(t+1) \\ x_1(t+1) \\ x_2(t+1) \end{pmatrix} = \begin{pmatrix} a_{00}(w) & a_{01}(w) & a_{02}(w) \\ a_{10}(w) & a_{11}(w) & a_{12}(w) \\ a_{20}(w) & a_{21}(w) & a_{22}(w) \end{pmatrix} \begin{pmatrix} x_0(t) \\ x_1(t) \\ x_2(t) \end{pmatrix} \quad (21)$$

Suppose A1, A2 and A3 hold and that  $\vec{x} = (x_0, x_1, x_2)^T$  is a positive equilibrium.

Then the positive components of  $\vec{x}$  satisfy the equations

$$\begin{aligned} (1 - a_{00}(w))x_0 - a_{01}(w)x_1 - a_{02}(w)x_2 &= 0 \\ -a_{10}(w)x_0 + (1 - a_{11}(w))x_1 - a_{12}(w)x_2 &= 0 \\ -a_{20}(w)x_0 - a_{21}(w)x_1 + (1 - a_{22}(w))x_2 &= 0. \end{aligned} \quad (22)$$

A little algebra shows that  $s_{01}(w) < 0$  and  $s_{02}(w) < 0$  implies  $s_{00}(w) > 0$ . Thus, from the second and third equations, which imply  $s_{00}(w)x_1 = s_{01}(w)x_0$  and  $s_{00}(w)x_2 = s_{02}(w)x_0$ , it follows that  $s_{00}(w)$  cannot be negative, i.e.  $s_{00}(w) \geq 0$ . If  $s_{00}(w) = 0$  then it follows that  $s_{01}(w) = s_{02}(w) = 0$  and hence that  $a_{11} \geq 1$  and  $a_{22} \geq 1$ . These inequalities, together with the equations (22), imply that  $a_{10}(w) = a_{12}(w) = a_{20}(w) = a_{21}(w) = 0$ , which contradicts the irreducibility of  $A(w)$ . Thus, the existence of a positive equilibrium and the irreducibility of  $A(w)$  imply  $s_{00}(w) > 0$ . Similar arguments using other pairs of the equations (22) imply that  $s_{11}(w) > 0$  and  $s_{22}(w) > 0$ . Thus, Theorem 1 implies the necessity of  $n'(w) \leq 0$  for the stability of the equilibrium.

For nonlinear Leslie age-structured population models and Usher models (15)-(16), we saw above that  $n'(w) \leq 0$  is necessary for the stability of a positive equilibrium  $\vec{x}$  (see(19)). In fact, Theorem 1 implies the same result, as it can be shown that all  $s_{ii}$  are positive for an Usher model.

From (19) we see that the inequality  $n'(w) \leq 0$  is necessary for stability for Usher matrix equations even without the irreducibility to the matrix  $A$ . Thus, although the assumption A3 of irreducibility generally holds in applications, it may be relaxed at least for some special population models. The following theorem (whose proof appears in the Appendix) describes a class of models for which this is true. A matrix  $M$  is normal if  $MM^T = M^T M$  [27].

**THEOREM 2** *Assume A1 and A2. If the Jacobian  $J$  at a positive equilibrium  $\vec{x}$  of (13) is normal, then  $n'(w) \leq 0$  is necessary for the equilibrium  $\vec{x}$  to be (locally asymptotically) stable.*

A obvious corollary of this theorem is that  $n'(w) > 0$  implies equilibrium instability if  $J = J^T$ .

#### 4. SUFFICIENT CONDITIONS FOR STABILITY

We have seen in Theorem 1 that under rather general conditions the inequality  $n'(w) \leq 0$  is a necessary condition for a positive equilibrium of the nonlinear matrix equation (13) to be (locally asymptotically) stable. If this necessary condition holds, then is the positive equilibrium stable? Or more strongly, does  $n'(w) < 1$  imply equilibrium stability? The answer usually is no. The Schur-Cohn Criteria (also called the Jury Criteria) provide necessary and sufficient conditions for the roots of a polynomial to be less than one in magnitude (see [16]). These criteria consist of more than two inequalities, the first of which is that  $p(1) = \det(I - J(w)) > 0$  where  $p(\lambda)$  is the characteristic polynomial associated with  $J(w)$ . It turns out that under the conditions of Theorem 1,  $p(1)$  is a negative multiple of  $n'(w)$  (see (32) in the proof below). Thus,  $n'(w) < 1$  is equivalent to the first Schur-Cohn inequality  $p(1) > 0$  and alone cannot, in general, be sufficient for stability. The following theorem gives an added condition under which  $n'(w) < 1$  is sufficient for stability. It is motivated by the stability results for small amplitude equilibria obtained by bifurcation methods in [3], [5]. The proof appears in the Appendix.

**THEOREM 3** *Assume A1, A2 and A3. Suppose that  $\vec{x}$  is a positive equilibrium of the nonlinear matrix equation (13) and that  $w = w \vec{x} > 0$  is the corresponding weighted total population size. Assume that  $A(w) = F(w) + P(w)$  is primitive. If  $0 < |A'(w)\vec{x}|$  is sufficiently small, then  $n'(w) < 0$  implies that  $\vec{x}$  is (locally asymptotically) stable and  $n'(w) > 0$  implies that  $\vec{x}$  is unstable.*

**Remark 1** *If  $A'(w)\vec{x} = 0$ , then 1 is an eigenvalue of  $J(w) = A(w)$ . Therefore, in this case the local stability properties of the positive equilibrium  $\vec{x}$  can not be determined by the linearized model.*

In the proof of Theorem 3 the primitivity of the matrix  $A(w)$  is used to insure that any nonzero right eigenvector (left eigenvector) belonging to the eigenvalue 1 is a multiple of the positive equilibrium  $\vec{x}$  (the positive left eigenvector  $\vec{u}$ ). This added assumption is not restrictive in most applications, since it is usually the case that the projection matrix  $A$  is irreducible and primitive [2].

An important class of models is one in which the nonlinear density terms appear only in the fertility rates of model (13) (i.e. the transition matrix  $P$  is constant) and all newborns lie in the same class, e.g. without loss of generality in the first class  $i = 0$ . In this case,  $|A'(w)\vec{x}| = |F'(w)\vec{x}| = |n'(w)|x_0$ .

**COROLLARY 1** *Suppose, in addition to the assumptions of Theorem 3, that all newborns lie in the first class  $i = 0$  and that the transition matrix  $P$  is constant. If*

$0 < |n'(w)|x_0$  is sufficiently small, then  $n'(w) < 0$  implies that  $\vec{x}$  is (locally asymptotically) stable and  $n'(w) > 0$  implies that  $\vec{x}$  is unstable.

The condition that  $|A'(w)\vec{x}|$  be sufficiently small is met by equilibria of sufficiently small amplitude  $|\vec{x}|$ . The conclusion of Theorem 3 in this case yields the local stability bifurcation results of Cushing [3], [5]. The stability condition  $n'(w) < 0$  for small amplitude equilibria is equivalent to the supercritical and stable bifurcation condition  $n'(0) < 0$ ; the instability condition  $n'(w) > 0$  for small amplitude equilibria is equivalent to the subcritical and unstable bifurcation condition  $n'(0) > 0$ .

Here are some examples illustrating the use of Theorem 3 for positive equilibrium of not necessarily small amplitude.

**Example 3** Liu and Cohen [22] study the nonlinear Leslie model

$$x_0(t+1) = e^{-rw(t)} \sum_{i=0}^m f_i x_i(t) \quad (23)$$

$$x_{k+1}(t+1) = e^{-rw(t)} p_k x_k(t), \quad k = 0, 1, \dots, m-1$$

where  $r > 0$ ,  $f_i \geq 0$ ,  $f_m > 0$ , and  $p_i > 0$  are constants and  $w(t) = \sum_{i=0}^m w_i x_i(t)$ . In this model the fertility and transition matrices are

$$F(w) = e^{-rw} \begin{pmatrix} f_0 & f_1 & \dots & f_m \\ 0 & 0 & \dots & 0 \\ \vdots & \vdots & \square & \vdots \\ 0 & 0 & \dots & 0 \end{pmatrix}$$

$$P(w) = e^{-rw} \begin{pmatrix} 0 & 0 & \dots & 0 & 0 \\ p_0 & 0 & \dots & 0 & 0 \\ 0 & p_1 & \dots & 0 & 0 \\ \vdots & \vdots & \square & \vdots & \vdots \\ 0 & 0 & \dots & p_{m-1} & 0 \end{pmatrix}$$

and the projection matrix is  $A(w) = e^{-rw}L$  where  $L$  is the Leslie matrix

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$$L = \begin{pmatrix} f_0 & f_1 & \cdots & f_{m-1} & f_m \\ p_0 & 0 & \cdots & 0 & 0 \\ 0 & p_1 & \cdots & 0 & 0 \\ \vdots & \vdots & \square & \vdots & \vdots \\ 0 & 0 & \cdots & p_{m-1} & 0 \end{pmatrix}$$

The net reproductive number is

$$n(w) = e^{-rw} f_0 + e^{-2rw} f_1 p_0 + e^{-3rw} f_2 p_0 p_1 + \cdots + e^{-(m+1)rw} f_m p_0 p_1 \cdots p_{m-1}.$$

Clearly  $n'(w) < 0$  and  $\lim_{w \rightarrow +\infty} n(w) = 0$ . As a result, the equation  $n(w) = 1$  has a positive root  $w > 0$  if and only if the "inherent" net reproduction number

$$n_0 = f_0 + f_1 p_0 + f_2 p_0 p_1 + \cdots + f_m p_0 p_1 \cdots p_{m-1} \quad (24)$$

satisfies  $n_0 > 1$  (in which case the root is unique). Thus, model (23) has a unique positive equilibrium  $\vec{x}$  if and only if  $n_0 > 1$ , in which case the components of  $\vec{x}$  are defined by

$$\begin{aligned} x_0 &= cw \\ x_i &= cwe^{-irw} \prod_{k=0}^{i-1} p_k, \quad i = 1, \dots, m \end{aligned}$$

where

$$c = (w_0 + w_1 p_0 + w_2 p_0 p_1 + \cdots + w_m p_0 p_1 \cdots p_{m-1})^{-1}. \quad (25)$$

From  $A'(w)\vec{x} = -re^{-rw}L\vec{x}$  we obtain the inequality

$$|A'(w)\vec{x}| \leq \Omega(w)\|L\|$$

$$\Omega(w) = rcwe^{-rw}(1 + e^{-2rw}p_0^2 + \cdots + e^{-2mrw}p_0^2 p_1^2 \cdots p_{m-1}^2)^{1/2}.$$

Note that  $\Omega(0) = 0$  and  $\lim_{w \rightarrow +\infty} \Omega(w) = 0$ . As a result we see that  $|A'(w)\vec{x}|$  is small for equilibria of either small or sufficiently large magnitude (i.e. for  $n_0$  close to 1 or sufficiently large). The conditions of Theorem 3 hold and we conclude that all positive equilibria are (locally asymptotically) stable for either  $n_0 > 1$  sufficiently large or sufficiently near 1.

Perhaps the most common assumption in nonlinear dynamics models is that increased population density results in decreased survivability and/or fertility. Mathematically, this means that the derivatives  $f'_{ij}(w)$  and  $p'_{ij}(w)$  are negative (or at least nonpositive). This in turn generally implies that  $n'(w) < 0$  for all  $w > 0$ , as in the previous example. Not all important models have this property,

however, the most common example being those that involve a so-called ‘‘Allee effect’’ [4], [5], [9]. These models are built on the assumption that fertility and survivability are decreasing functions of population density only at high densities and that, on the contrary, some or all of these vital rates can be increasing functions of population density at low density levels. Here is an example.

**Example 4** In [31] the nonlinear Leslie model

$$x_0(t+1) = \frac{1+a^2}{1+(w(t)-a)^2} \sum_{i=0}^m f_i x_i(t)$$

$$x_{k+1}(t+1) = p_k x_k(t) \quad k = 0, 1, \dots, m-1$$

was studied. Here  $a > 0$  and the parameters  $f_i$  and  $p_i$  satisfy the same conditions as those in model (23). In this model only fertility rates are density dependent

$$F(w) = \frac{1+a^2}{1+(w-a)^2} \begin{pmatrix} f_0 & f_1 & \dots & f_m \\ 0 & 0 & \dots & 0 \\ \vdots & \vdots & \square & \vdots \\ 0 & 0 & \dots & 0 \end{pmatrix}$$

and the transition matrix

$$P = \begin{pmatrix} 0 & 0 & \dots & 0 & 0 \\ p_0 & 0 & \dots & 0 & 0 \\ 0 & p_1 & \dots & 0 & 0 \\ \vdots & \vdots & \square & \vdots & \vdots \\ 0 & 0 & \dots & p_{m-1} & 0 \end{pmatrix}$$

is constant. Note that the nonlinear term  $\frac{1+a^2}{1+(w-a)^2}$  increases for  $0 < w < a$  and decreases for  $a < w$ . The net reproductive number is

$$n(w) = \frac{1+a^2}{1+(w-a)^2} (f_0 + f_1 p_0 + f_2 p_0 p_1 + \dots + f_m p_0 p_1 \dots p_{m-1}) \quad (26)$$

For each positive root of  $n(w) = 1$  there exists a positive equilibrium  $\vec{x}$  whose components are given by

$$x_0 = cw$$

$$x_i = cw \prod_{k=0}^{i-1} p_k, \quad i = 1, \dots, m \quad (27)$$

where  $c$  is given by (25). For any positive equilibrium

$$|n'(w)|_{x_0} = 2cn_0(1+a^2) \frac{|w-a|w}{(1+(w-a)^2)^2} > 0 \quad (28)$$

Hence  $|n'(w)|_{x_0}$  can be made arbitrarily small for equilibria of sufficiently small or sufficiently large magnitude.

The positive roots of  $n(w) = 1$  are

$$0 < w_1 = a + \sqrt{n_0(1+a^2)} - 1 \quad \text{for} \quad \frac{1}{1+a^2} < n_0$$

$$0 < w_2 = a - \sqrt{n_0(1+a^2)} - 1 \quad \text{for} \quad \frac{1}{1+a^2} < n_0 < 1$$

where the inherent net reproductive number  $n_0$  is given by (24). Each of these positive roots defines a positive equilibrium by (27) which we denote by  $\vec{x}_1$  and respectively  $\vec{x}_2$ .

Consider first the positive equilibrium  $\vec{x}_2$  when the inherent net reproductive number lies in the interval  $\frac{1}{1+a^2} < n_0 < 1$ . A straightforward calculation shows that

$$n'(w_2) = \frac{2}{(1+a^2)n_0} \sqrt{n_0(1+a^2)} - 1 > 0.$$

Thus, by Theorem 1 the positive equilibrium  $\vec{x}_2$  is unstable.

For the positive equilibrium  $\vec{x}_1$ , when  $n_0 > \frac{1}{1+a^2}$ , we have the necessary condition

$$n'(w_1) = -\frac{2}{(1+a^2)n_0} \sqrt{n_0(1+a^2)} - 1 < 0$$

for stability holds. The total population size  $w_1$ , which is larger than  $a > 0$  for all  $n_0 > \frac{1}{1+a^2}$ , cannot be made arbitrarily small, but it can be made arbitrarily large by choosing  $n_0$  sufficiently large. Thus, by (28) the quantity  $|n'(w)|_{x_0}$ , can be

made arbitrarily small by taking  $n_0$  sufficiently large. By Corollary 1 the positive equilibrium  $\vec{x}_1$  is (locally asymptotically) stable for  $n_0$  sufficiently large.

The next example was constructed to show that  $|A'(w)\vec{x}|$  can be made small even if both  $|\vec{x}|$  and  $\|A'(w)\|$  are not small.

**Example 5** Consider the two dimensional matrix equation

$$\begin{aligned}x_0(t+1) &= f_0(w)x_0(t) + f_1(w)x_1(t) \\x_1(t+1) &= p_0x_0(t) + p_1x_1(t)\end{aligned}$$

where

$$\begin{aligned}f_0(w) &= \frac{1-p_1}{1-p_1+p_0} e^{-(1+\varepsilon)p_0(w-2)} \\f_1(w) &= \frac{1-p_1}{1-p_1+p_0} e^{(1-p_1)(w-2)}\end{aligned}$$

$$0 < p_0, p_1 < 1, \varepsilon \in (-\infty, +\infty), w = x_0 + x_1.$$

This matrix equation has fertility and transition matrices

$$F(w) = \begin{pmatrix} f_0(w) & f_1(w) \\ 0 & 0 \end{pmatrix}, \quad P = \begin{pmatrix} 0 & 0 \\ p_0 & p_1 \end{pmatrix}.$$

There is only one positive equilibrium  $\vec{x}$  with components given by

$$\begin{aligned}x_0 &= \frac{2(1-p_1)}{1-p_1+p_0} \\x_1 &= \frac{2p_0}{1-p_1+p_0}\end{aligned}$$

which are independent of the parameter  $\varepsilon$ . From

$$A'(w) =$$

$$\begin{pmatrix} -(1+\varepsilon)p_0 \frac{1-p_1}{1-p_1+p_0} e^{-(1+\varepsilon)p_0(w-2)} & (1-p_1) \frac{1-p_1}{1-p_1+p_0} e^{(1-p_1)(w-2)} \\ 0 & 0 \end{pmatrix}$$

we see that neither  $|\vec{x}|$  nor  $\|A'(w)\|$  can be made small by choosing  $|\varepsilon|$  small.

By direct calculation

$$\begin{aligned} n(w) &= \frac{1-p_1}{1-p_1+p_0} \left( e^{-(1+\varepsilon)p_0(w-2)} + \frac{p_0}{1-p_1} e^{(1-p_1)(w-2)} \right) \\ n'(w) &= -\varepsilon \frac{p_0(1-p_1)}{1-p_1+p_0} \\ |n'(w)|x_0 &= |\varepsilon| \frac{2p_0(1-p_1)^2}{(1-p_1+p_0)^2} > 0 \end{aligned}$$

and we see that  $|A'(w)x| = |n'(w)|x_0$  can be made arbitrary small by taking  $|\varepsilon|$  small. By Corollary 1 the equilibrium is (locally) asymptotically stable if  $\varepsilon > 0$  is sufficiently small.

By Theorem 1 the equilibrium is unstable for all  $\varepsilon < 0$  since in this case  $n'(w) > 0$ .

Our last example shows that the primitivity assumption on  $A(w)$  cannot be dropped in Theorem 3.

**Example 6** In his study of juvenile-versus-adult competition Ebenman [10], [11] introduced the age-structured population model (also see [6], [23])

$$\begin{aligned} x_0(t+1) &= bf(w)x_1(t) \\ x_1(t+1) &= sx_0(t) \end{aligned} \tag{29}$$

where  $w = \alpha x_0 + x_1$ . The constant  $\alpha \geq 0$  measures the effect that juvenile density has on adult fertility (relative to the effect of adult density). Here  $b > 0$ ,  $s \in (0, 1)$  and  $f: R_+ \rightarrow R_+$  satisfies  $f' < 0$ ,  $f(0) = 1$  and  $\lim_{w \rightarrow +\infty} f(w) = 0$ . The net reproductive number is  $n(w) = sbf(w)$  and the equation  $n(w) = 1$  has a positive root  $w > 0$  if and only if the inherent net reproductive number  $n_0 = sb \underset{>}{\geq} 1$  (in which case the root is unique). For  $n_0 > 1$  the unique positive equilibrium  $\bar{x}$  has components

$$x_0 = w \frac{1}{\alpha + s} \text{ and } x_1 = s_0.$$

The necessary condition stability condition  $n'(w) = sbf'(w) < 0$  is satisfied. The Schur-Cohn Criteria applied to the linearization at this positive equilibrium yield the following necessary and sufficient conditions for (local asymptotic) stability:

$$\begin{aligned} 0 > n'(w)x_0 > -\frac{2}{s} \\ s > \alpha. \end{aligned}$$

Thus, stability requires that  $|A'(w)x| = |n'(w)x_0|$  be sufficiently small. Note, however, that this requirement is not sufficient in this example; also needed is the

inequality  $s > \alpha$ . (In fact, if  $s < \alpha$  the matrix  $J(w)$  has a real eigenvalue  $\lambda < -1$  and the equilibrium is unstable.) This is not in contradiction to Theorem 3 (or Corollary 1), however, because

$$A(w) = \begin{pmatrix} 0 & bf(w) \\ s & 0 \end{pmatrix}$$

is not primitive.

## 5. SOME APPLICATIONS

Some applications to population models found in the literature are made in this section. In all applications the nonlinearities will satisfy the following conditions:

$$\begin{aligned} f &\in C^1(R_+ \rightarrow R_+) \\ f' &< 0, \quad f(0) = 1 \end{aligned} \tag{30}$$

$$\lim_{w \rightarrow +\infty} f(w) = \lim_{w \rightarrow +\infty} wf'(w) = 0.$$

### 5.1 Competition among newborns

DeAngelis et al. [8] studied a nonlinear Leslie age-structured model for fish populations. They assumed a birth-pulse population with the census immediately following breeding. In this case, the fertility terms are given by  $f_{0i} = p_i u_i$ . They assumed that competition occurs only among the first age class, so that  $p_0 = f(x_0)$

is density dependent. In [8]  $f(x_0) = \frac{1}{1 + cx_0}$ ,  $c > 0$ , and  $w = x_0$ , but we will consider the more general case when  $f(w)$  satisfies (30) and  $w$  is an arbitrary weighted total population size. The fertility and transition matrices are

$$F(w) = \begin{pmatrix} f(w)u_0 & p_1u_1 & \dots & p_mu_m \\ 0 & 0 & \dots & 0 \\ \vdots & \vdots & \square & \vdots \\ 0 & 0 & \dots & 0 \end{pmatrix}$$

$$P(w) = \begin{pmatrix} 0 & 0 & \dots & 0 & 0 \\ f(w) & 0 & \dots & 0 & 0 \\ 0 & p_1 & \dots & 0 & 0 \\ \vdots & \vdots & \square & \vdots & \vdots \\ 0 & 0 & \dots & p_{m-1} & p_m \end{pmatrix}$$

where  $\mu_i \geq 0$  and  $0 < p_i < 1$ . To insure irreducibility, it is also assumed that  $p_m \mu_m > 0$ .

The net reproductive number is

$$n(w) = n_0 f(w)$$

where

$$n_0 = \mu_0 + p_1 \mu_1 + \dots + p_1 p_2 \dots p_{m-1} \mu_{m-1} + \frac{p_1 p_2 \dots p_m}{1 - p_m} \mu_m$$

is the inherent net reproductive number. There exists a positive root

$$w = f^{-1}\left(\frac{1}{n_0}\right) > 0$$

of  $n(w) = 1$  if and only if  $n_0 > 1$  (in which case it is unique). Note, under the assumption made on  $f$ , that

$$\lim_{n_0 \rightarrow 1} w = 0 \quad \text{and} \quad \lim_{n_0 \rightarrow +\infty} w = +\infty \quad (31)$$

The components of the positive equilibrium are then given by

$$\begin{aligned} x_0 &= w \frac{1}{w_0 + cf(w)} \\ x_1 &= f(w)x_0 \\ x_2 &= f(w)p_1 x_0 \\ &\vdots \\ x_{m-1} &= f(w)p_1 \dots p_{m-2} x_0 \\ x_m &= f(w)p_1 \dots p_{m-1} \frac{1}{1 - p_m} x_0 \end{aligned}$$

where

$$c = w_1 + w_2 p_1 + \dots + w_{m-1} p_1 \dots p_{m-2} + w_m \frac{p_1 \dots p_{m-1}}{1 - p_m} > 0.$$

Since  $n'(w) = n_0 f'(w) < 0$ , the necessary condition for stability is met. By a direct calculation

$$\begin{aligned} |A'(w)x| &= x_0 |f'(w)| \sqrt{\mu_0^2 + 1} \\ &= \left( \frac{\sqrt{\mu_0^2 + 1}}{w_0 + cp_0(w)} \right) w |f'(w)| \end{aligned}$$

From (30) we see that  $|A'(w)x|$  is small if  $w > 0$  is either small or large. By (31) and Theorem 3 it follows that the positive equilibrium is (locally asymptotically) stable for  $n_0 > 1$  sufficiently close to 1 and for  $n_0$  sufficiently large.

## 5.2. Density dependent fertility

Levin and Goodyear [19], [20] studied a two dimensional Leslie age-population model with density-dependent fertility. The fertility and transition matrices of this model have the form

$$\begin{aligned} F(w) &= \begin{pmatrix} b_1 f(w) & b_2 f(w) \\ 0 & 0 \end{pmatrix} \\ P &= \begin{pmatrix} 0 & 0 \\ p & 0 \end{pmatrix} \end{aligned}$$

where  $0 < p < 1$ ,  $b_i > 0$ , and  $f(w)$  satisfies (30). In the Levin and Goodyear model  $f(w) = e^{-\beta w}$ ,  $\beta > 0$ .

The net reproductive number

$$\begin{aligned} n(w) &= n_0 f(w) \\ n_0 &= (b_1 + pb_2) \end{aligned}$$

satisfies the necessary condition  $n'(w) = n_0 f'(w) < 0$  for the stability of positive equilibria. The equation  $n(w) = 1$  has a unique positive solution

$$w = f^{-1}\left(\frac{1}{n_0}\right) < 0 \quad \text{for} \quad n_0 > 1.$$

The components of the positive equilibrium are

$$\begin{aligned} x_0 &= w \frac{1}{w_0 + w_1 p} \\ x_1 &= w \frac{p}{w_0 + w_1 p}. \end{aligned}$$

A simple calculation yields

$$|n'(w)|x_0 = \left( \frac{n_0}{w_0 + w_1 p} \right) w |f'(w)|$$



Corollary 1 implies that the positive equilibrium is (locally asymptotically) stable for  $n_0 > 1$  sufficiently close to 1 and for  $n_0$  sufficiently large.

### 5.3 Adult-juvenile competition

Silva and Hallam [26] studied nonlinear Leslie model with fertility and transition matrices of the form

$$F(w) = \begin{pmatrix} 0 & 0 & \dots & bf(w) \\ 0 & 0 & \dots & 0 \\ \vdots & \vdots & \square & \vdots \\ \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \dots & 0 \end{pmatrix}$$

$$P(w) = \begin{pmatrix} 0 & 0 & \dots & 0 & 0 \\ p & 0 & \dots & 0 & 0 \\ 0 & p & \dots & 0 & 0 \\ \vdots & \vdots & \square & \vdots & \vdots \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \dots & p & p \end{pmatrix}$$

where  $b > 0$ , and  $0 < p < 1$ . The density term  $f(w)$  is assumed to satisfy (30). This is a generalization of Ebenman's model [10], [11] (see Example 29) in which there are  $m$  juvenile classes and the adult class is iteroparous (adults can live and reproduce for more than one time unit). Silva and Hallam take  $w = \sum_{i=0}^m x_i$ , but we will take a general weighted total population size.

The net reproductive number of model is

$$n(w) = n_0 f(w)$$

$$n_0 = b \frac{p_m}{1-p}.$$

There exists a positive equilibrium if and only if  $n_0 > 1$  in which case

$$\begin{aligned} x_0 &= cw \\ &\vdots \\ x_{0i} &= p^i cw \quad (i = 1, 2, \dots, m-1) \\ &\vdots \\ x_m &= p^m \frac{1}{1-p} cw \end{aligned}$$

where

$$c \doteq \left[ w_0 + w_1 p + \dots + w_{m-1} p^{m-1} + w_m p^m \frac{1}{1-p} \right]^{-1}$$

and

$$w = f^{-1}\left(\frac{1}{n_0}\right).$$

Since  $n'(w) = n_0 f'(w) < 0$ , Corollary 1 implies that the positive equilibrium is (locally asymptotically) stable if

$$|n'(w)|x_0 = bc \frac{p^m}{1-p} w |f'(w)|$$

is sufficiently small, i.e. if  $w$  is sufficiently small or (by (30)) sufficiently large. (In [26] it is proved that the positive equilibrium  $\vec{x}^*$  is stable if  $0 > n'(w^*) x_0^* > -p$ .)

## 6. DISCUSSION

The magnitude of the “inherent” net reproductive number  $n(\vec{0})$  (often denoted  $R_0$  in the literature) determines the (local) stability properties of the trivial equilibrium  $\vec{x} = \vec{0}$  of the nonlinear matrix equation (13) [5], [7], [32]. At a nontrivial equilibrium  $\vec{x}$ , however, the net reproductive number  $n(\vec{x})$  always equals one and therefore its magnitude cannot be used to determine the stability properties of the equilibrium. In this paper we have investigated the relationship between nontrivial equilibrium stability and the variation of  $n$  near the equilibrium. In our main result we showed in Theorem 1, for models in which the nonlinear dependence is through a dependence on a weighted total population size  $w = \sum_{\tau} w_{\tau} x_{\tau}$ , that the inequality  $n'(w) \leq 0$  is necessary for the (local asymptotic) stability of a positive equilibrium. Although the converse of this result is false, Theorem 3 gives conditions under which  $n'(w) < 0$  implies (local asymptotic) stability of a positive equilibrium.

The nonlinearities in most matrix population models appearing in the literature do in fact arise through a dependence on a weighted total population size  $w$ . Some, however, do not and it is natural to ask whether our main result in Theorem 1 can be generalized to the matrix equation (2) when  $F = F(\vec{x})$  and  $P = P(\vec{x})$ . One natural conjecture for a generalization of Theorem 1 is that  $\nabla_{\vec{x}} n(\vec{x}) \leq \vec{0}$  is a necessary condition for the stability of a positive equilibrium  $\vec{x}$  of equation (2). The following example shows that this conjecture is, however, false.

Consider the two dimensional, nonlinear Leslie matrix equation with fertility and transition matrices

$$F(x_0, x_1) = \begin{pmatrix} \frac{9}{10}e^{x_0+x_1-2} & \frac{1}{10} \\ 0 & 0 \end{pmatrix}$$

$$P(x_0, x_1) = \begin{pmatrix} 0 & 0 \\ \frac{1}{2}e^{-7(x_0-1)} & \frac{1}{2}e^{-4(x_1-1)} \end{pmatrix}.$$

This matrix equation has the positive equilibrium  $(x_0, x_1) = (1, 1)$ . The Jacobian evaluated at this equilibrium

$$J(1, 1) = \begin{pmatrix} \frac{9}{5} & 1 \\ -3 & -\frac{3}{2} \end{pmatrix}$$

has eigenvalues  $\lambda = \frac{3}{20} \pm \frac{1}{20}i\sqrt{111}$  whose magnitudes  $|\lambda| = \left| \frac{3}{20} \pm \frac{1}{20}i\sqrt{111} \right| = \frac{1}{10}\sqrt{30}$  are less than one. Thus, the positive equilibrium  $(1, 1)$  is locally asymptotically stable. The net reproductive number is given by

$$n(x_0, x_1) = \frac{9}{10}e^{x_0+x_1-2} + \frac{1}{10}e^{-7(x_0-1)} \frac{1}{1-e^{-4(x_1-1)}}$$

from which the gradient at the equilibrium can readily be calculated to be

$$\nabla_x n(1, 1) = \left( \frac{1}{5}, \frac{1}{2} \right).$$

Thus, it is seen that  $\nabla_x n \leq \vec{0}$  is, in general, not necessary for (local asymptotic) stability.

It would be interesting to determine additional conditions under which  $\nabla_x n \leq \vec{0}$  is a necessary condition for equilibrium stability.

As a final remark, we point out a connection between the net reproductive number  $n$  and the "population growth rate"  $\lambda = \lambda(\vec{x})$ , defined as the dominant eigenvalue of the (nonnegative and irreducible) projection matrix  $A(\vec{x})$ . If  $\vec{p} = \vec{q}(\vec{x})$  is the associated eigenvector, a partial differentiation of  $A(\vec{x})\vec{q}(\vec{x}) = \lambda(\vec{x})\vec{q}(\vec{x})$  yields

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$$\frac{\partial A}{\partial x_i} \vec{q} + A \frac{\partial \vec{q}}{\partial x_i} = \frac{\partial \lambda}{\partial x_i} \vec{q} + \lambda \frac{\partial \vec{q}}{\partial x_i}.$$

When  $\vec{x}$  is an equilibrium,  $\lambda(\vec{x}) = 1$  and  $\vec{q}(\vec{x}) = \vec{x}$ , and this equation, after an inner product by the left eigenvector  $\vec{u} = \vec{u}(\vec{x})$  of  $A(\vec{x})$ , yields

$$\frac{\partial \lambda}{\partial x_i} = \frac{\vec{u} \frac{\partial A(\vec{x})}{\partial x_i} \vec{x}}{\vec{u} \vec{x}}.$$

This formula, together with (11), gives

$$\frac{\partial \lambda}{\partial x_i} = \frac{\vec{u} F(\vec{x}) \vec{x} \frac{\partial n}{\partial x_i}}{\vec{u} \vec{x}}.$$

In the case of dependence on weighted total population size  $\lambda = \lambda(w)$ , this formula in turn yields the relationship

$$\lambda'(w) = \frac{\vec{u} F(w) \vec{x}}{\vec{u} \vec{x}} n'(w)$$

between the derivatives  $\lambda'(w)$  and  $n'(w)$  at equilibrium. Thus, these two derivatives have the same sign and  $\lambda'(w)$  can replace  $n'(w)$  in our theorems. For example, by Theorem 1,  $\lambda'(w) \leq 0$  is a necessary condition for equilibrium stability. One advantage of working with the net reproductive rate  $n$  is that explicit formulas can often be obtained for it in terms of the entries in the fertility and transition (e.g. see (17) for nonlinear Usher models) [7]; such formulas for  $\lambda$  are unavailable.

## 7. APPENDIX

### 7.1 The proof of Theorem 1

The positive equilibrium  $\vec{x}$  is a right eigenvector to the eigenvalue 1 of the irreducible projection matrix  $A(\vec{x})$ . Thus, 1 is dominant and simple; thus, if  $\vec{v}$  satisfies  $A(\vec{x})\vec{v} = \vec{v} \neq 0$ , then  $\vec{v} = c\vec{x}$  for some constant  $c \neq 0$ . The irreducibility of the matrix  $A$  also implies that there exists a positive left eigenvector  $\vec{u}$ , such that

$\vec{u}^T A = \vec{u}^T$ . If a vector  $\vec{y} \neq \vec{0}$  satisfies the equation  $\vec{y}^T A = \vec{y}^T$ , then there exists a nonzero constant  $d$ , such that  $\vec{y}^T = d\vec{u}^T$ .

Define the column vectors  $\vec{\tau}_i = (s_{i0}, s_{i1}, \dots, s_{im})^T$  for  $i = 0, 1, \dots, m$ . The vector  $\vec{\tau}_i$  is the transpose of the  $i^{th}$  row vector of the cofactor matrix  $S$ . By using the properties of determinants it is readily verified that, if nonzero, the vector  $\vec{\tau}_i$  is a right eigenvector belonging to eigenvalue 1 of the matrix  $A$ . Similarly, if nonzero, the row vectors  $\vec{l}_j = (s_{0j}, s_{1j}, \dots, s_{mj})$  for  $j = 0, 1, \dots, m$  are left eigenvectors belonging to the eigenvalue 1 of the matrix  $A$ . The vector  $\vec{l}_j$  is the transpose of the  $j^{th}$  column vector of the matrix  $S$ .

By the assumption that  $s_{ii} > 0$  for all  $i$  it follows that both  $\vec{\tau}_i$  and  $\vec{l}_j$  are nonzero and are eigenvectors. Thus,  $\vec{\tau}_i = c_i \vec{x}$  and  $\vec{l}_j = d_j \vec{u}$ . From the first components, we obtain  $c_i = \frac{s_{i0}}{x_0}$  and  $d_j = \frac{s_{0j}}{u_0}$  and hence

$$\vec{\tau}_i = \frac{s_{i0}}{x_0} \vec{x}, \quad \vec{l}_j = \frac{s_{0j}}{u_0} \vec{u}.$$

Thus,

$$w \vec{\tau}_i = \frac{w}{x_0} s_{i0}.$$

By using appropriate column operations a straight forward calculation shows

$$\det(I - J) = \det(I - A) + \sum_{k=0}^m w_k \det A'_k$$

where  $A'_k$  is a  $(m + 1) \times (m + 1)$  matrix  $I - A$  with its  $k^{th}$  column replaced by the column vector  $-\vec{h} = -A'x$ . Using the fact that at equilibrium,  $\det(I - A) = 0$  and by expanding the determinant  $\det A'_k$  by its  $k^{th}$  column, we obtain

$$\begin{aligned} \det(I - J) &= - \sum_{k=0}^m w_k \sum_{j=0}^m h_j s_{jk} = - \sum_{j=0}^m \left( \sum_{k=0}^m w_k s_{jk} \right) h_j \\ &= - \sum_{j=0}^m w \vec{\tau}_j h_j = - \frac{w}{x_0} \sum_{j=0}^m s_{j0} h_j \\ &= - \frac{w \vec{\tau}^T \vec{h}}{x_0} = - \frac{w \vec{\tau}^T A'x}{x_0} \\ &= - \frac{w s_{00}}{x_0 u_0} \vec{u} A'x. \end{aligned}$$

From the formula in (14) we obtain finally that

$$\det(I - J) = -\frac{w s_{00} \vec{u}^{\tau} F(w) \vec{x}}{x_0 u_0} n'(w) \quad (32)$$

The characteristic equation  $\det(\lambda I - J)$  of the linearized model (18) is a polynomial of degree  $m + 1$ , and the coefficient of the highest term  $\lambda^{m+1}$  is 1. Therefore, if  $n'(w) > 0$ , (32) implies that  $\det(I - J) < 0$  and consequently there exists at least one real eigenvalue  $\lambda$  which is larger than 1. This proves that the positive equilibrium  $\vec{x}$  of (13) is unstable.

## 7.2 Proof of Theorem 2

Assume that  $n'(w) > 0$ . Then the dominant eigenvalue  $n((1+\varepsilon)w)$  of the matrix  $R(\varepsilon) = (I - P((1+\varepsilon)w))^{-1} F((1+\varepsilon)w)$  is greater than 1 if  $\varepsilon > 0$  is sufficiently small. Therefore, the dominant eigenvalue  $\lambda(\varepsilon)$  of  $A(\varepsilon) = F((1+\varepsilon)w) + P((1+\varepsilon)w)$  is also greater than 1 when  $\varepsilon > 0$  is sufficiently small [7]. Let  $v(\varepsilon)$  be the corresponding eigenvalue to  $\lambda(\varepsilon)$ , i.e.

$$A(\varepsilon) \vec{v}(\varepsilon) = \lambda(\varepsilon) \vec{v}(\varepsilon).$$

If in this equation we substitute the expansions

$$\lambda(\varepsilon) = 1 + \lambda_1 \varepsilon + \dots$$

$$\vec{v}(\varepsilon) = \vec{x} + \vec{v}_1 \varepsilon + \dots$$

$$A(\varepsilon) = A(w) + w A'(w) \varepsilon + \dots$$

and equate the first order  $\varepsilon$  coefficients, we obtain

$$(A(w) - I) \vec{v}_1 = \lambda_1 \vec{x} - w A'(w) \vec{x}$$

which has a solution if and only if the right hand side is orthogonal to the left eigenvector  $\vec{u}^{\tau}$  of  $A(w)$ . Without loss in generality we assume that  $\vec{u}$  is a unit vector, i.e.  $\vec{u}^{\tau} \vec{u} = 1$ . Thus,

$$\lambda_1 = w \frac{\vec{u}^{\tau} A'(w) \vec{x}}{\vec{u}^{\tau} \vec{x}}.$$

The fact that  $\lambda(\varepsilon) > 1$  for small  $\varepsilon > 0$  implies that  $\theta = \vec{u}^{\tau} A'(w) \vec{x} > 0$ . From the formula  $J(w) = A(w) + A'(w) \vec{x} w$  for the Jacobian we obtain

$$\vec{u}^{\tau} J = \vec{u}^{\tau} A + \vec{u}^{\tau} A' \vec{x} w = \vec{u}^{\tau} + \theta w$$

and

$$\vec{u}^{\tau} J J^{\tau} \vec{u} = 1 + 2\theta w^{\tau} \vec{u} + \theta^2 w^{\tau} w > 1 \quad (33)$$

The normality of the matrix  $J$  implies that the matrix  $J^T J$  is symmetric and therefore has real eigenvalues (and a complete set of orthogonal eigenvectors) [12]. It follows from (33) that the matrix  $JJ^T$  has at least one eigenvalue  $\lambda_0 > 1$ . If we let  $\vec{z}(0)$  be the eigenvector corresponding to  $\lambda_0$  of matrix  $J^T J$ , then the resulting solution of the linearized equation  $\vec{z}(t+1) = J\vec{z}(t)$  is exponentially unbounded; specifically

$$\lim_{t \rightarrow \infty} \vec{z}(t) = \lim_{t \rightarrow \infty} \lambda_0^t \vec{z}(0) = +\infty.$$

Thus, the positive equilibrium of (13) is unstable.

### 7.3. Proof of Theorem 3

The Jacobian  $J$  of the linearized model at  $\vec{x}$  has the form (18)

$$J(w) = A(w) + A'(w)\vec{x}\vec{w}^T$$

Let  $\vec{u}^T$  be the unit left positive eigenvector corresponding to eigenvalue 1 of matrix  $A(w)$  and define  $\varepsilon = |A'(w)\vec{x}|$ . Recall from (14) that

$$n'(w) = \frac{\vec{u}^T A'(w)\vec{x}}{\vec{u}^T F(w)\vec{x}}.$$

The positive equilibrium  $\vec{x}$  is an eigenvector of  $A(w)$  associated with eigenvalue 1. The irreducibility and primitivity of matrix  $A(w)$  implies that 1 is a strictly dominant, simple eigenvalue [13]. From the formula for  $J$  it follows that if  $\varepsilon$  is sufficiently small  $J$  has a strictly dominant, simple eigenvalue  $\lambda_b$  near 1. Let  $\vec{y}^T$  be the left unit eigenvector of matrix  $J$  corresponding to  $\lambda_b$ ; that is

$$\vec{y}^T A(w) + \vec{y}^T A'(w)\vec{x}\vec{w}^T = \lambda_b \vec{y}^T.$$

As  $\varepsilon \rightarrow 0$ , note that  $J \rightarrow A$  and  $\vec{y}^T \rightarrow \vec{u}^T$ . From this equation subtract

$$\vec{u}^T A(w) = \vec{u}^T$$

to obtain

$$(\vec{y}^T - \vec{u}^T)A(w) + \vec{y}^T A'(w)\vec{x}\vec{w}^T = \lambda_b \vec{y}^T - \vec{y}^T + \vec{y}^T - \vec{u}^T$$

or

$$(\vec{y}^T - \vec{u}^T)(A(w) - I) = (\lambda_b - 1)\vec{y}^T - \vec{y}^T A'(w)\vec{x}\vec{w}^T.$$

The singularity of  $A(w) - I$  requires that the right hand side be orthogonal to the right nullspace of  $A(w) - I$ , i.e. orthogonal to the equilibrium  $\vec{x}$ . This yields

$$(\lambda_b - 1)\vec{y}^T \vec{x} = \vec{y}^T A'(w)\vec{x}\vec{w}^T \vec{x}$$

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or

$$\lambda_b - 1 = \frac{\frac{\partial \tau}{\partial y} A'(w) x w x}{\frac{\partial \tau}{\partial y} x}.$$

Thus, for  $\varepsilon$  sufficiently small

$$\lambda_b - 1 \approx \frac{\frac{\partial \tau}{\partial u} A'(w) x w x}{\frac{\partial \tau}{\partial u} x} = n'(w) \frac{\frac{\partial \tau}{\partial u} F(w) x w x}{\frac{\partial \tau}{\partial u} x}$$

and the sign of  $\lambda_b - 1$  is the same as that of  $n'(w)$ . If  $n'(w) > 0$  then  $\lambda_b > 1$  and the equilibrium  $\bar{x}$  is unstable. On the other hand if  $n'(w) < 0$  then the dominant eigenvalue  $\lambda_b$  of the Jacobian  $J$  is less than 1 and the equilibrium  $\bar{x}$  is (locally asymptotically) stable. This proves the theorem.

### References

- [1] Berman, Abraham and Robert J. Plemmons (1979), *Nonnegative Matrices in the Mathematical Sciences*, Academic Press Inc., New York
- [2] Caswell, Hal (1989), *Matrix Population Models*, Sinauer Associates Inc., Sunderland, MA
- [3] Cushing, J.M. (1988), Nonlinear matrix models and population dynamics, *Natural Resource Modeling* 2 (No. 4), 539-580
- [4] Cushing, J.M. (1988), The Allee effect in age-structured population dynamics, *Mathematical Ecology* (Hallam, Gross & Levin eds.), World Scientific, Singapore, 479-505
- [5] Cushing, J.M. (1994), Nonlinear matrix models for structured populations, *Mathematical Population Dynamics: Analysis of Heterogeneity, Volume III: Mathematical Methods and Modeling of Data*, (O. Arino, D. Axelrod, M. Kimmel, Michel Langlais, editors), Wuerz Publishing Ltd, Winnipeg
- [6] Cushing, J.M., and Jia Li (1989), On Ebenman's model for the dynamics of a population with competing juveniles and adults, *Bull. Math. Biol.* 51, No. 6, 687-713
- [7] Cushing, J.M., and Zhou Yicang (1994), The net reproductive value and stability in structured population models, *Natural Resource Modeling* 8 (No. 4), 1-37
- [8] DeAngelis, D.S., L.J. Svoboda, S.W. Christensen, and D.S. Vaughan (1980), Stability and return times of Leslic matrices with density-dependent survival: applications to fish population, *Ecological Modelling* 8, 149-163
- [9] Dennis, B. (1989), Allee effects: population growth, critical density, and the chance of extinction, *Natural Resource Modeling* 3, 481-538
- [10] Ebenman, Bo (1988), Dynamics of age- and size-structured populations: intraspecific competition, *Size-structured Populations* (B. Ebenman and L. Person, eds.) Springer-Verlag, Berlin, 127-139
- [11] Ebenman, Bo (1988), Competition between age classes and population dynamics, *J. Theor. Biol.* 131, 389-400
- [12] Franklin, J.N. (1968), *Matrix Theory*, Prentice-Hall, Inc. Englewood Cliffs, New Jersey
- [13] Gantmacher, F.R. (1959), *Application of the Theory of Matrices*, Interscience publishers Inc., New York
- [14] Impagliazzo, John (1985), *Deterministic Aspects of Mathematical Demography*, Springer-Verlag, Berlin, Heidelberg
- [15] Jury, E.I. (1982), *Inners and stability of Dynamics Systems*, Robert E. Krieger Publ. Malabar, Florida
- [16] LaSalle, J.P. (1986), *The Stability and Control of Discrete Processes*, Springer-Verlag, Berlin
- [17] Leslie, P.H. (1945), On the use of matrices in certain population mathematics, *Biometrika* 33, 183-212
- [18] Leslie, P.H. (1948), Some further notes on the use of matrices in population mathematics, *Biometrika* 35, 213-245



- [19] Levin, S.A. and C.P. Goodyear (1980), Analysis of an age-structured fishery model. *J. Math. Biol.* 9, 245-274
- [20] Levin, S.A. (1981), Age-structure and stability in multiple-age spawning population, *Renewable Resource Management* (T.L. Vincent and J.M. Skowronski, eds.), Springer-Verlag, Berlin, 21-45
- [21] Lewis, E.G. (1942), On the generation and growth of a population, *Sankhya* 6, 93-96
- [22] Liu, L. and J.E. Cohen (1987), Equilibrium and local stability in a logistic matrix model for age-structured populations, *J. of Math. Biol.* 25, 73-88
- [23] Loreau, M. (1990), Competition between age-classes and the stability of stage-structured population: a re-examination of Ebenman's model, *J. of Theor. Biol.* 144, 567-571
- [24] Rorres, Chris (1976), Stability of an age-specific population with density dependent fertility, *Theor. Pop. Biol.* 10, 26-46
- [25] Rorres, Chris (1979), Local stability of a population with density dependent fertility, *Theor. Pop. Biol.* 16, 283-300
- [26] Silva, Jacques A.L., and Thomas G. Hallam (1992), Compensation and stability in nonlinear matrix models, *Math. Biosci.* 110, 67-101
- [27] Stewart, G.W. and Ji-Guang Sun (1990), *Matrix Perturbation Theory*, Academic Press Inc., Harcourt Brace Jovanovich Publisher, Boston
- [28] Usher, M.B. (1966), A matrix approach to the management of renewable resources with special reference to forest, *J. of Appl. Ecology* 3, 355-367
- [29] Usher, M.B. (1969), A matrix model for forest management, *Biometrics* 25, 309-315
- [30] Usher, M.B. (1972), Developments in the Leslie matrix model, *Mathematical Models in Ecology* (J.M.R. Jeffers, editor), Blackwell Scientific Publishers, London, 29-60
- [31] Yicang, Zhou and Li Xiwen (1996), The dynamics and application of the nonlinear matrix model of the disabled population, *J. Engineering Mathematics* 13, No. 3, 69-81
- [32] Cushing J.M. (1998), *An Introduction to Structured Population Dynamics*, CBMS-NSF Conf. Series in Applied Mathematics, SIAM, Philadelphia