

**STRUCTURED-POPULATION
MODELS IN MARINE,
TERRESTRIAL, AND
FRESHWATER SYSTEMS**

Edited by

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Dedicated to Shubha and Anjali, and Solange and Erin
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CHAPTER 6

Nonlinear Matrix Equations and Population Dynamics

J. M. Cushing

Classical models for the dynamics of biological populations, such as the famous logistic and Lotka-Volterra equations, involve population-level statistics and parameters. In the “structured” population models of this book, individual members of the population are classified in some manner, usually by means of certain physiological characteristics, and the distribution of individuals based upon this classification is dynamically modeled.

A popular approach to modeling structured populations is to make both time and the structuring variable(s) discrete. This approach leads to a system of difference equations or, in the most commonly used form, a matrix equation for the population distribution. The chapter by Caswell (Chapter 2) discusses linear matrix models in detail. A linear theory cannot be used for long-term predictions for growing populations because it implies unlimited growth. If regulatory effects of some kind are taken into account (such as the adverse effects of population density on fertility, survival, and growth rates), then the matrix equations become nonlinear.

The goal of this chapter is to present a general theory for the asymptotic dynamics of nonlinear matrix equations as they apply to the dynamics of structured populations. The point of view taken is that of bifurcation theory. By this is meant that changes in dynamics are studied as a function of a single model parameter.

Models for population dynamics are generally replete with parameters describing various kinds of vital rates and other modeling

coefficients. In principle, any parameter appearing in a particular application can be used as a bifurcation parameter. That is, the dynamics implied by the model equations can in principle be studied as a function of any one of the parameters appearing in the equations, and an investigator may have good reasons for choosing one particular model parameter over another in a specific application. In this chapter, however, I show how a biologically significant parameter (the inherent net reproductive number of the population) can always be defined, introduced into the model equations, and successfully used as a bifurcation parameter in a completely general setting.

I hope to show how several rewards can be gained from the point of view taken here. First, the approach establishes general results concerning the existence and stability of equilibrium distributions, which are then available for any particular application. Second, it makes available powerful analytical techniques for obtaining results about the asymptotic dynamics of what might otherwise be intractable model equations. Finally, the approach serves to organize one's study of any particular model in terms of a general, biologically meaningful parameter. Moreover, even when one or more of the general results fail to apply to a specific model (because of the failure of some required hypothesis or other), the approach often gives insights into what exceptional phenomena occur and what analytical steps should next be taken.

First, the approach is applied to linear matrix equations. This is done to present the point of view of bifurcation theory in such a way that a straightforward extension can be made to nonlinear equations. Next, this extension is made, and results concerning the existence and stability of equilibria are given. The following section illustrates these equilibrium results with some applications.

1 Linear Matrix Models

The earliest matrix models structure a population into age classes of a common length and then follow the number of individuals in each age class over discrete time steps of the same length.

Let $x_i(t)$ denote the number of individuals in the i th age class at time t , $1 \leq i \leq m$, and suppose that the time unit is taken, without loss in generality, to be 1. If $\tau_{i+1,i} \in (0, 1]$ is the fraction of individuals in age class i that survives to age class $i + 1$, for $i = 0, 1, \dots, m - 1$, and if $f_{1j} \geq 0$ is the number of offspring

produced by an individual in age class j , then (as in Chapter 2),

$$\mathbf{x}(t+1) = \mathbf{A}\mathbf{x}(t), \quad t = 0, 1, 2, \dots$$

where

$$\mathbf{x}(t) = \begin{bmatrix} x_1(t) \\ x_2(t) \\ \vdots \\ x_m(t) \end{bmatrix}$$

$$\mathbf{A} = \begin{bmatrix} f_{11} & f_{12} & \cdots & f_{1,m-1} & f_{1m} \\ \tau_{21} & 0 & \cdots & 0 & 0 \\ 0 & \tau_{32} & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & \tau_{m,m-1} & 0 \end{bmatrix} \quad (1)$$

$$f_{1j} \geq 0 \text{ (not all 0)}, \quad 0 < \tau_{j+1,j} \leq 1.$$

This model assumes no immigration or emigration, and it assumes that no individual ever reaches age $m+1$. Sometimes the final class, $i = m$, is defined to be the class of individuals of age greater than m , with survival to all ages permitted, in which case a fraction τ_{mm} appears in the lower right-hand corner of \mathbf{A} .

Note that this projection matrix can be additively decomposed as $\mathbf{A} = \mathbf{F} + \mathbf{T}$, where $\mathbf{F} = [f_{ij}]$ is a fertility matrix and $\mathbf{T} = [\tau_{ij}]$ is a class-transition matrix.

For a population structured by any means into n classes (or stages), a nonnegative projection matrix \mathbf{A} can be constructed whose entries are nonnegative and represent births, deaths, and transitions between classes and which, by multiplication on the left, takes the population's class-distribution vector at time t to its distribution vector at time $t+1$ (see Chapter 2, by Caswell):

$$\mathbf{x}(t+1) = \mathbf{A}\mathbf{x}(t), \quad t = 0, 1, 2, \dots \quad (2)$$

In general, such a matrix can be additively decomposed into a fertility and a class-transition matrix:

$$\mathbf{A} = \mathbf{F} + \mathbf{T} \geq 0,$$

where

$$\mathbf{F} = [f_{ij}], \quad f_{ij} \geq 0, \quad (3)$$

$$\mathbf{T} = [\tau_{ij}], \quad \tau_{ij} \in [0, 1], \quad \sum_{i=1}^m \tau_{ij} \leq 1, \quad (4)$$

where f_{ij} is the number of i -class offspring produced by a j -class individual (per unit of time) and τ_{ij} is the fraction of j -class individuals that lie in class i after one unit of time (or the probability that a j -class individual survives and moves to class i in one unit of time). Writing $\mathbf{A} \geq 0$ for a matrix (or a vector) means that every entry in \mathbf{A} is greater than or equal to 0.

If the projection matrix \mathbf{A} is constant (i.e., if the fertilities f_{ij} and the transition probabilities τ_{ij} are all constants, unchanging in time), the dynamics are described using the methods in Chapter 2, by Caswell. Let the dominant eigenvalue of matrix \mathbf{A} be called λ_1 . The population becomes extinct if $\lambda_1 < 1$ and grows geometrically if $\lambda_1 > 1$. Mathematically, we say that the “trivial equilibrium” $\mathbf{x} = \mathbf{0}$ is (*globally asymptotically stable*) in the first case and is *unstable* in the second case. In other words, the trivial equilibrium state loses its stability as the dominant eigenvalue of \mathbf{A} increases through the critical value of 1.

When the dynamics of population models are studied as a function of the entries in the projection matrix \mathbf{A} , the critical value $\lambda_1 = 1$ delineates the boundary between the radically different dynamic cases of population extinction and population survival. As shown below, this delineation carries through to nonlinear models as well, but in a more complicated way.

The asymptotic dynamics implied by the linear model (2) may also be characterized by another fundamental biological quantity. This, the “net reproductive number,” has a more explicit biological meaning than λ_1 and is often a more convenient quantity with which to analyze matrix models, as we see below.

Consider the age-structured case and its Leslie matrix (1). The product

$$\tau_{21}\tau_{32}\cdots\tau_{j,j-1} = \prod_{k=0}^{j-1} \tau_{k+1,k}$$

is the probability of living to age j . (For notational convenience, $\tau_{10} = 1$, by definition.) The expected number of offspring that an individual of age j will produce in one unit of time is therefore

$$f_{1j} \prod_{k=0}^{j-1} \tau_{k+1,k}.$$

Adding over all age classes yields the expected number of offspring

per individual over its lifetime. This quantity, defined as

$$n = \sum_{j=1}^m f_{1j} \prod_{k=0}^{j-1} \tau_{k+1,k},$$

is called the net reproductive number for the age-structured population.

To define the net reproductive number for the general linear model (2), two assumptions are made about the transition and fertility matrices \mathbf{T} and \mathbf{F} .

First, we suppose that the inverse exists:

$$\mathbf{E} = (\mathbf{I} - \mathbf{T})^{-1}. \tag{5}$$

If we denote $\mathbf{E} = [e_{ij}]$, then e_{ij} is the expected amount of time that an individual starting initially in class j will spend in class i during its lifetime.

A sufficient condition for the matrix $\mathbf{I} - \mathbf{T}$ to have an inverse is that the following inequalities hold:

$$\sum_{i=1}^m \tau_{ij} < 1 \quad \text{for all } j = 1, 2, \dots, m \tag{6}$$

(i.e., the sum of the column entries in \mathbf{T} must be strictly less than 1). Since $\sum_{i=1}^m \tau_{ij}$ is the total fraction of individuals leaving class j in one unit of time, it is clear that this sum must satisfy the condition that $\sum_{i=1}^m \tau_{ij} \leq 1$. Therefore, the biological meaning of assumption (6) is that there is always some loss of individuals from every class over each unit of time (due, for example, to deaths).

Assumption (6) is sufficient for the existence of the inverse $\mathbf{E} = (\mathbf{I} - \mathbf{T})^{-1}$, but it is not necessary. This can be seen from the case of a Leslie matrix (1) for which

$$\mathbf{F} = \begin{bmatrix} f_{11} & f_{12} & \cdots & f_{1,m-1} & f_{1m} \\ 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & 0 & 0 \end{bmatrix},$$

$$\mathbf{T} = \begin{bmatrix} 0 & 0 & \cdots & 0 & 0 \\ \tau_{21} & 0 & \cdots & 0 & 0 \\ 0 & \tau_{32} & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & \tau_{m,m-1} & 0 \end{bmatrix}.$$

In this case, we find that

$$\mathbf{I} - \mathbf{T} = \begin{bmatrix} 1 & 0 & \cdots & 0 & 0 \\ -\tau_{21} & 1 & \cdots & 0 & 0 \\ 0 & -\tau_{32} & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & -\tau_{m,m-1} & 1 \end{bmatrix}$$

is always invertible (its determinant equals 1), even if inequality (6) does not hold. In fact, the inverse of $\mathbf{I} - \mathbf{T}$ here is

$$\mathbf{E} = [e_{ij}], \quad e_{ij} = \prod_{k=0}^{i-1} \tau_{k+1,k} \quad \text{for all } j$$

(a matrix with identical columns).

Returning to the general case, the second assumption is that there is a strictly dominant positive eigenvalue for the matrix defined by

$$\mathbf{R} = \mathbf{E}\mathbf{F}. \quad (7)$$

Because $\mathbf{T} \geq 0$ and $(\mathbf{I} - \mathbf{T})^{-1} = \mathbf{I} + \mathbf{T} + \mathbf{T}^2 + \cdots$, it follows that $\mathbf{E} = (\mathbf{I} - \mathbf{T})^{-1} \geq 0$. Therefore, since $\mathbf{F} \geq 0$ by assumption (3), it follows that the product $\mathbf{R} = \mathbf{E}\mathbf{F}$ is also nonnegative. Thus, assumption (7) holds if, for example, \mathbf{R} is irreducible and primitive.

As an example, for a Leslie matrix, we find that

$$\mathbf{R} = [r_{ij}], \quad r_{ij} = f_{1j} \prod_{k=0}^{i-1} \tau_{k+1,k}.$$

Since every column of this matrix is a multiple of the same column, it follows that 0 is an eigenvalue of multiplicity $m - 1$. The remaining eigenvalue is easily calculated to be the net reproductive number, namely,

$$\sum_{j=1}^m f_{1j} \prod_{k=0}^{j-1} \tau_{k+1,k}.$$

This eigenvalue of \mathbf{R} (not of \mathbf{A} !) is nonzero, and hence strictly dominant, if not all f_{1j} are zero, that is, if at least one age class is fertile.

It can be shown in general for any matrix $\mathbf{A} = \mathbf{F} + \mathbf{T}$ satisfying assumptions (5) and (7) that the dominant eigenvalue of the matrix $\mathbf{R} = (\mathbf{I} - \mathbf{T})^{-1}\mathbf{F}$ is equal to the expected number of offspring per individual over its lifetime (Cushing & Zhou 1995). Given this biological meaning for \mathbf{R} , we make the following definition.

Definition 1 Consider the nonnegative matrix $\mathbf{A} = \mathbf{F} + \mathbf{T}$, where \mathbf{T} and \mathbf{F} satisfy conditions (3) and (4). If assumptions (5) and (7) hold, then the net reproductive number n associated with the matrix equation (2) is defined to be the strictly dominant eigenvalue of the matrix $\mathbf{R} = (\mathbf{I} - \mathbf{T})^{-1}\mathbf{F}$.

Assuming that projection matrix \mathbf{A} in (2) has a strictly dominant eigenvalue λ_1 , in addition to satisfying assumptions (4) and (7), what is the connection between the net reproductive number n and the dominant eigenvalue λ_1 ? In partial answer to this question, it has been shown that

$$\lambda_1 > 1 \quad (\text{or } < 1 \text{ or } = 1)$$

if and only if

$$n > 1 \quad (\text{or } < 1 \text{ or } = 1, \text{ respectively})$$

(Cushing & Zhou 1995). It follows that the trivial equilibrium is asymptotically stable if $n < 1$ and is unstable if $n > 1$ and that positive equilibria exist if and only if $n = 1$. Given the biological meaning of the net reproductive number, n , these statements are biologically reasonable.

Both the geometric growth (or decay) rate of the population, λ_1 , and the net reproductive number, n , determine the stability properties of the trivial equilibrium (i.e., determine whether a population whose dynamics are described by the linear model (2) survives or becomes extinct). From a mathematical standpoint, it can sometimes be more convenient for certain kinds of questions concerning the dynamics of the population to use and study n rather than λ_1 . This is because an analytical formula for n is often available when no such formula for λ_1 exists.

Here is an example. Consider an Usher (1972) matrix, for which

$$\mathbf{T} = \begin{bmatrix} \tau_{11} & 0 & \cdots & 0 & 0 \\ \tau_{21} & \tau_{22} & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & \tau_{m,m-1} & \tau_{mm} \end{bmatrix},$$

$$\mathbf{F} = \begin{bmatrix} f_{11} & f_{12} & \cdots & f_{1,m-1} & f_{1m} \\ 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & 0 & 0 \end{bmatrix},$$

and hence, if $\tau_{ii} < 1$, the inverse $\mathbf{E} = (\mathbf{I} - \mathbf{T})^{-1}$ is a matrix with

identical columns,

$$\mathbf{E} = [e_{ij}], \quad e_{ij} = \prod_{k=0}^{i-1} \frac{\tau_{k+1,k}}{1 - \tau_{k+1,k+1}} \quad \text{for all } j.$$

It follows that

$$\mathbf{R} = \mathbf{E}\mathbf{F} = [r_{ij}], \quad r_{ij} = f_{1j} \prod_{k=0}^{i-1} \frac{\tau_{k+1,k}}{1 - \tau_{k+1,k+1}}.$$

(Again, for notational convenience, $\tau_{10} = 1$.) Since all the columns of \mathbf{R} are multiples of the same column, this matrix has 0 as an eigenvalue of multiplicity $m - 1$. The remaining eigenvalue is calculated to be

$$n = \sum_{j=1}^m f_{1j} \prod_{k=0}^{j-1} \frac{\tau_{k+1,k}}{1 - \tau_{k+1,k+1}},$$

which is positive, and hence dominant, provided that not all f_{1j} are zero (i.e., there must be at least one fertile class). This is a generalization of the formula for the Leslie matrix. It may be used to study, for example, the sensitivities of the net reproductive number to changes in these vital parameters.

As a numerical example, consider the matrix

$$\mathbf{A} = \begin{bmatrix} 0.72 & 0 & 0 & 0.74 & 1.04 & 9.03 \\ 0.28 & 0.69 & 0 & 0 & 0 & 0 \\ 0 & 0.31 & 0.75 & 0 & 0 & 0 \\ 0 & 0 & 0.25 & 0.77 & 0 & 0 \\ 0 & 0 & 0 & 0.23 & 0.63 & 0 \\ 0 & 0 & 0 & 0 & 0.37 & 0 \end{bmatrix}$$

used by Usher in a study of the dynamics of a Scots pine forest (Usher 1966). The formula for n above easily yields a net reproductive rate of 15.1 (to three significant digits). Thus, the trivial equilibrium is unstable, and this population is growing geometrically. It is not as easy to find the dominant eigenvalue, which is a root of the sixth-degree characteristic polynomial. (Numerically, we find that $\lambda_1 \approx 1.20$.)

One way to study or answer questions about the stability properties of linear model (2) is by means of the net reproductive number, n . All of the entries in the projection matrix \mathbf{A} , of course, contribute to the value of n in a complicated way. It would be more convenient if n appeared explicitly in the dynamic equation (2).

One way to introduce n explicitly into the equation is to normalize the fertilities in the matrix \mathbf{F} as follows. Suppose that the assumptions (5) and (7) for the transition and fertility matrices \mathbf{T} and \mathbf{F} hold, so that n is well defined. Then define β_{ij} to be the ratio of the class-specific fertility, f_{ij} , to the net reproductive rate, n . That is, define β_{ij} such that $f_{ij} = n\beta_{ij}$. Then, $\mathbf{F} = n\mathbf{N}$, where these normalized fertilities are described by the nonnegative matrix $\mathbf{N} = [\beta_{ij}] \geq 0$. The linear matrix equation (2) then becomes

$$\mathbf{x}(t + 1) = (n\mathbf{N} + \mathbf{T}) \mathbf{x}(t), \quad t = 0, 1, 2, \dots, \tag{8}$$

where now it is true that the matrix $\mathbf{Q} = (\mathbf{I} - \mathbf{T})^{-1}\mathbf{N}$ has a strictly dominant eigenvalue equal to 1.

As a simple example, the Leslie matrix (1) for the classical age-structured matrix equation can be rewritten

$$\mathbf{A} = n \begin{bmatrix} \beta_{11} & \beta_{12} & \cdots & \beta_{1,m-1} & \beta_{1m} \\ 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & 0 & 0 \end{bmatrix} + \begin{bmatrix} 0 & 0 & \cdots & 0 & 0 \\ \tau_{21} & 0 & \cdots & 0 & 0 \\ 0 & \tau_{32} & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & \tau_{m,m-1} & 0 \end{bmatrix},$$

where the normalized fertilities β_{ij} and the survival probabilities $\tau_{j+1,j}$ are assumed to satisfy the condition that

$$\sum_{j=1}^m \beta_{1j} \prod_{k=0}^{j-1} \tau_{k+1,k} = 1.$$

Given the changes in the stability properties of the trivial equilibrium $\mathbf{x} = \mathbf{0}$ of the general linear matrix equation (8) and hence in the fate of the population as n increases through the critical value of 1, the point $(n, \mathbf{x}) = (1, \mathbf{0})$ is called a “bifurcation point.” One way to represent these facts schematically or graphically is by means of a so-called bifurcation diagram in which some measure of the magnitude of equilibria is plotted against the “bifurcation parameter” n . For example, the sum of the components, that is, the total population size, could be plotted against n . Such a dia-

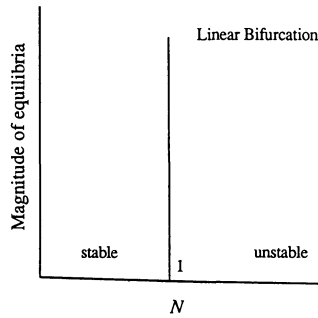


FIGURE 1. If the magnitudes of the positive equilibria of general linear matrix equation (9) are plotted against the net reproductive number, n , then a vertical line is obtained at the critical value $n = 1$; at this line, the trivial equilibrium, $\mathbf{x} = \mathbf{0}$ (which exists for all n), loses its stability. This is because positive equilibria exist if and only if $n = 1$; there are, in fact, infinitely many positive equilibria given by $\mathbf{x} = c\mathbf{v}_1$ ($c > 0$). The graph of the trivial equilibrium coincides with the n -axis, and hence the intersection of these two continuous branches of equilibria where $(n, \mathbf{x}) = (1, \mathbf{0})$ constitutes a bifurcation.

gram, for the linear matrix equation (2), consists of the vertical straight line obtained from the nontrivial equilibria at $n = 1$ and the horizontal straight line of trivial equilibria for all n (which lies on the n -axis in the diagram and therefore cannot be seen). See Figure 1.

Furthermore, if the matrix $\mathbf{A} = \mathbf{F} + \mathbf{T}$ has a strictly dominant eigenvalue for all n greater than 0 (for example, if it is irreducible and primitive for all n greater than 0), then the trivial equilibrium is stable, the population becomes extinct for all n less than 1, and the population grows geometrically without bound for all n greater than 1. There is a loss of stability as n increases through the bifurcation value, where $n = 1$. This is also indicated in the bifurcation diagram.

This bifurcation diagram is not the classical way to view and think about the dynamics of a linear matrix model (2). However, it is one way to view the dynamics implied by a linear model, since it depends on the vital parameters in its projection matrix. Moreover, this point of view lends itself very nicely to a generalization to nonlinear models, as we see in the next section.

2 Nonlinear Matrix Models

If the vital parameters appearing in the fertility matrix \mathbf{F} and/or the transition matrix \mathbf{T} are not all constants, but instead depend on population density, then projection matrix \mathbf{A} in equation (2) depends on the entries in the distribution vector \mathbf{x} :

$$\mathbf{A}(\mathbf{x}) = \mathbf{F}(\mathbf{x}) + \mathbf{T}(\mathbf{x}). \quad (9)$$

The matrix equation for the dynamics of the distribution vector then becomes nonlinear:

$$\mathbf{x}(t+1) = \mathbf{A}[\mathbf{x}(t)] \mathbf{x}(t), \quad t = 0, 1, 2, \dots \quad (10)$$

Here we assume that the entries in the projection matrix do not explicitly depend on time t ; thus, this nonlinear matrix equation is autonomous. Because equation (10) is nonlinear, the asymptotic dynamics of its solutions as $t \rightarrow +\infty$ can be considerably more varied and complicated than that of the linear equation (2).

A first step toward understanding the dynamics of a nonlinear equation such as equation (10) is to determine its (nonnegative) equilibrium solutions and their stability properties. An equilibrium is a constant solution, $\mathbf{x}(t) = \mathbf{e} \in R^m$, of the algebraic equations

$$\mathbf{e} = \mathbf{A}(\mathbf{e})\mathbf{e}.$$

Clearly, $\mathbf{e} = \mathbf{0}$ is always an equilibrium of equation (10). The existence of other equilibria depends on the properties of the matrix \mathbf{A} and presumably depends on the parameters in this matrix.

One way to study the equilibria of the nonlinear matrix equation (10) is to consider their existence and stability as a function of some selected parameter(s) in the projection matrix \mathbf{A} . The approach here, motivated by the approach to linear systems in the preceding section, is to define and introduce into the equation a single parameter n for this purpose, namely, an “inherent” net reproductive number. Biologically, this number is the expected number of offspring per individual over its lifetime when the population level is low, that is, when density effects on vital rates are negligible. Once n is introduced into the equation, bifurcation theory can be useful not only in organizing one’s thinking about equilibria (and other asymptotic states), but in analyzing the dynamics of a general matrix equation. Certainly other approaches are possible, particularly in specific applications. However, one main advantage of the approach taken here is the generality of its appli-

cability. It provides an overview of any particular application, in terms of a biologically meaningful parameter. Moreover, it provides analytical techniques that can yield information about equilibrium states for specific applications that might otherwise be quite intractable.

Existence of Equilibria

Consider the nonlinear matrix equation (10) with the projection matrix given by the additive decomposition in (9). The entries $\tau_{ij}(\mathbf{x})$ and $f_{ij}(\mathbf{x})$ in the transition and fertility matrices

$$\mathbf{T} = [\tau_{ij}(\mathbf{x})] \quad \text{and} \quad \mathbf{F} = [f_{ij}(\mathbf{x})]$$

are assumed to be twice-continuous differentiable functions of all x_i on some open domain D in R_m that contains the origin, $\mathbf{x} = \mathbf{0}$. Thus, we assume that

$$\tau_{ij}, f_{ij} \in C^2(D; R^m),$$

$$0 \leq \tau_{ij}(\mathbf{x}) \leq 1, f_{ij}(\mathbf{x}) \geq 0 \quad \text{for all } \mathbf{x} \in D. \quad (11)$$

Next, assume that the following inverse exists for all $\mathbf{x} \in D$:

$$\mathbf{E}(\mathbf{x}) = [\mathbf{I} - \mathbf{T}(\mathbf{x})]^{-1}. \quad (12)$$

Sufficient for this assumption to hold is that there is some loss at each time interval, in each class, at all population density levels; that is,

$$\sum_{i=1}^m \tau_{ij}(\mathbf{x}) < 1.$$

This inequality is not necessary for equation (12), however.

Suppose we define the matrix

$$\mathbf{R}(\mathbf{x}) = \mathbf{E}(\mathbf{x})\mathbf{F}(\mathbf{x}).$$

The final assumption is that

$$\begin{aligned} R(\mathbf{0}) \text{ has a strictly dominant, simple real eigenvalue } n > \\ 0, \text{ which is associated with a positive right eigenvector } \\ \mathbf{v} > \mathbf{0} \text{ and a nonnegative left eigenvector } \mathbf{w} \geq \mathbf{0} (\neq \mathbf{0}). \end{aligned} \quad (13)$$

Without loss in generality we can assume that the scalar product $\langle \mathbf{v}, \mathbf{w} \rangle = 1$ (scalar products are defined in Chapter 2, by Caswell).

Definition 2 Consider the nonnegative matrix $\mathbf{A}(\mathbf{x}) = \mathbf{F}(\mathbf{x}) + \mathbf{T}(\mathbf{x})$, where $\mathbf{T}(\mathbf{x})$ and $\mathbf{F}(\mathbf{x})$ satisfy conditions (11). If assumptions (12) and (13) hold, then the inherent net reproductive number n associated with matrix equation (2) is defined to be the strictly dominant eigenvalue of the matrix $\mathbf{R}(\mathbf{0}) = [\mathbf{I} - \mathbf{T}(\mathbf{0})]^{-1} \mathbf{F}(\mathbf{0})$.

As for the linear equation, n is introduced into the model equation (10) by normalizing the fertility rates $f_{ij}(\mathbf{x})$ relative to n . That is, the normalized fertility rates $\beta_{ij}(\mathbf{x})$ are defined by

$$f_{ij}(\mathbf{x}) = n\beta_{ij}(\mathbf{x})$$

and

$$\mathbf{F}(\mathbf{x}) = n\mathbf{N}(\mathbf{x}),$$

where

$$\mathbf{N}(\mathbf{x}) = [\beta_{ij}(\mathbf{x})] \geq 0.$$

This, together with assumption (13), implies that

$$\mathbf{Q}(\mathbf{0}) \text{ has dominant eigenvalue } 1, \quad (14)$$

where

$$\mathbf{Q}(\mathbf{x}) = [\mathbf{I} - \mathbf{T}(\mathbf{x})]^{-1} \mathbf{N}(\mathbf{x}) \geq 0.$$

With the explicit introduction of the net reproductive number, n , into the nonlinear matrix equation (10) in this manner, the projection matrix $\mathbf{A} = \mathbf{A}(\mathbf{x}, n)$ can be considered a function of n as well as of \mathbf{x} , where

$$\mathbf{A}(\mathbf{x}, n) = n\mathbf{N}(\mathbf{x}) + \mathbf{T}(\mathbf{x}) = [a_{ij}(\mathbf{x}, n)].$$

Matrix equation (10) becomes

$$\mathbf{x}(t+1) = [n\mathbf{N}(\mathbf{x}) + \mathbf{T}(\mathbf{x})] \mathbf{x}(t), \quad t = 0, 1, 2, \dots, \quad (15)$$

and the equilibrium equation

$$\mathbf{e} = [n\mathbf{N}(\mathbf{e}) + \mathbf{T}(\mathbf{e})] \mathbf{e}$$

can be rewritten as

$$\mathbf{e} = n[\mathbf{I} - \mathbf{T}(\mathbf{e})]^{-1} \mathbf{N}(\mathbf{e}) \mathbf{e}$$

or

$$\mathbf{e} = n\mathbf{Q}(\mathbf{e}) \mathbf{e}. \quad (16)$$

From this form of the equilibrium equations, the following general existence result for equilibria can be proved (Cushing 1995; see also Cushing 1988a).

Theorem 1 *Under assumptions (11), (12), and (13), the matrix equation (10) has a “global” continuum of nontrivial “equilibrium pairs,” $[n, \mathbf{x}(t)] = (n, \mathbf{e})$. At least near the bifurcation point, the equilibrium pairs $(n, \mathbf{e}) \neq (1, \mathbf{0})$ from the continuum are positive; that is, $\mathbf{e} > \mathbf{0}$.*

By “global” in this theorem is meant that either the continuum contains a pair $(n_0, \mathbf{0})$ where $n_0 (\neq 1)$ is a characteristic value (i.e., the reciprocal of an eigenvalue) of $\mathbf{Q}(\mathbf{0})$ or the continuum connects to the boundary of $(0, +\infty) \times D$. This is referred to as the “Rabinowitz alternative” (Rabinowitz 1971). Incidentally, it is a fundamental fact of bifurcation theory that the only candidates for bifurcation points $(n, \mathbf{0})$ for nontrivial equilibria that bifurcate from the trivial equilibrium, $\mathbf{e} = \mathbf{0}$, are the characteristic values for n of $\mathbf{Q}(\mathbf{0})$.

In the special case of linear equations, let \mathbf{v}_1 be the right eigenvalue of \mathbf{A} corresponding to the dominant eigenvalue λ_1 . The bifurcating continuum is just the set of equilibrium pairs $(n, \mathbf{e}) = (1, c\mathbf{v}_1)$ for positive constants c greater than 0. Thus, the bifurcation of positive equilibria in this case is “vertical”; that is, the “spectrum” of n values along the continuum consists of a single point where $n = 1$, leading to the vertical straight line in the bifurcation graph in Figure 1. For nonlinear equations, however, the graph of the bifurcating continuum is not in general vertical, and the spectrum of n values is some interval containing $n = 1$. See Figure 2.

Although Theorem 1 does guarantee the existence of positive equilibria for nonlinear matrix equations under general circumstances, in specific applications one would like to know much more about the bifurcating branch. Are all of the equilibria on the continuum positive? What is the “spectrum” of n values along the bifurcating continuum (i.e., for what values of n does there exist a positive equilibrium)? For a given value of n is there a unique positive equilibrium? Or can there exist several positive equilibria for some n ? Are the equilibria from the continuum bounded or unbounded as a function of n ? And, most important, what are the stability properties of the equilibria?

Detailed answers to these questions depend on the specific details of the matrix equation and its nonlinearities. Some useful things, however, can be said under rather general conditions.

In applications, the first part of the Rabinowitz alternative can often and easily be ruled out by the nature of the model equations. In any case, it is clear from the equilibrium equation (16) that the

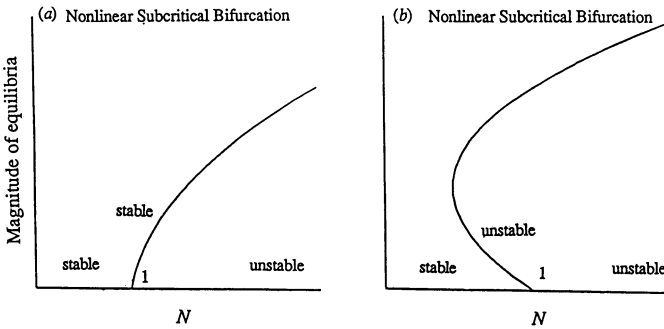


FIGURE 2. If the magnitudes of the positive equilibria of general nonlinear matrix equation (16), whose existence is guaranteed by Theorem 1, are plotted against the inherent net reproductive number, n , then a continuous branch is obtained that bifurcates from the trivial equilibrium, $\mathbf{x} = \mathbf{0}$, at the critical value $n = 1$, where the trivial equilibrium loses stability. In this nonlinear case, the bifurcation is in general not vertical and is either (a) “supercritical” or (b) “subcritical.” In the supercritical case, the bifurcating positive equilibria are (locally asymptotically) stable, at least for n near 1. In the subcritical case, the bifurcating positive equilibria are unstable for n close to 1.

only equilibrium when $n = 0$ is $\mathbf{e} = \mathbf{0}$; consequently, the spectrum of n values along the continuum guaranteed by Theorem 1 must be positive (negative values of n make no biological sense, of course). Should the first alternative occur, however, it is known that n_0 must be of odd geometric multiplicity (Rabinowitz 1971).

With regard to the second part of the Rabinowitz alternative, in applications the domain D under assumption (11) on which the problem is posed is usually unbounded, and in fact $D = R^m$. In this case, “connects to the boundary” means that the continuum of equilibrium pairs (n, \mathbf{e}) is unbounded in $R \times R^m$. This means that either the spectrum of n values from the continuum is unbounded or the set of equilibrium \mathbf{e} from the continuum is unbounded (or both).

If $q(\mathbf{e})$ is the eigenvalue of the matrix $\mathbf{Q}(\mathbf{e})$ for which $q(\mathbf{0}) = 1$, then $nq(\mathbf{e})$ is an eigenvalue of the matrix $\mathbf{R}(\mathbf{e}) = n\mathbf{Q}(\mathbf{e})$. The equilibrium form (16) of equation (15) implies that if $\mathbf{e} \neq \mathbf{0}$ is an equilibrium, then

$$nq(\mathbf{e}) = 1. \tag{17}$$

In principle, this scalar equation defines \mathbf{e} as a function of n (actually,

it more conveniently defines $n = 1/q(\mathbf{e})$ as a function of \mathbf{e}). This equation can often be used in applications to derive properties of the bifurcating continuum of equilibria; see the examples below. Biologically, equation (17) states that the net reproductive rate at equilibrium necessarily equals 1.

In population models, of course, we would like to know if all nontrivial equilibria from the bifurcating continuum are positive (or, more mathematically, if the equilibria from the continuum remain in the positive cone of R^m). If they are not, the continuum would have to contain a pair (n, \mathbf{e}) with n greater than 0 and a nonnegative, nontrivial equilibrium \mathbf{e} that contains at least one zero component. This can often be ruled out by an examination of the projection matrix \mathbf{A} . In most applications, the only possible nonnegative, nontrivial equilibria are positive, and the second Rabinowitz alternative is ruled out. Such is the case, for example, if $\mathbf{Q}(\mathbf{0})$ has no positive real characteristic value other than when $n = 1$; or if it does, then eigenvectors associated with any other characteristic value are negative (which is true if $\mathbf{Q}(\mathbf{0})$ is irreducible; see Gantmacher 1960, p. 63).

Consider models in which all newborn individuals belong to class $i = 1$; each newborn has a nonzero probability of eventually reaching every class ($\tau_{i,i+1}(\mathbf{x}) > 0$ for $i \leq m-1$); and at least one class is inherently fertile ($f_{1i}(0) > 0$ for some i). For these kinds of model populations, it can be shown that the bifurcating continuum of equilibrium pairs is unbounded in $R_+ \times R_+$ and that all nontrivial equilibria along the continuum are positive (Cushing 1995).

An important example is the nonlinear matrix for which

$$\mathbf{N}(\mathbf{x}) = \begin{bmatrix} \beta_1(\mathbf{x}) & \beta_2(\mathbf{x}) & \cdots & \beta_{m-1}(\mathbf{x}) & \beta_m(\mathbf{x}) \\ 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & 0 & 0 \end{bmatrix},$$

$$\mathbf{T}(\mathbf{x}) = \begin{bmatrix} 0 & 0 & \cdots & 0 & 0 \\ \tau_1(\mathbf{x}) & 0 & \cdots & 0 & 0 \\ 0 & \tau_2(\mathbf{x}) & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & \tau_{m-1}(\mathbf{x}) & \tau_m(\mathbf{x}) \end{bmatrix}, \quad (18)$$

where there is a nonzero probability of surviving each of the first $m-1$ time units (i.e., $\tau_i(\mathbf{x}) > 0$ for $1 \leq i \leq m-1$) and where the

m th age class is fertile (i.e., $f_m(0) > 0$). Equation (18) describes a Leslie matrix if $\tau_m = 0$. In this case,

$$[\mathbf{I} - \mathbf{T}(\mathbf{x})]^{-1} = \begin{bmatrix} 1 & 0 & \cdots & 0 & 0 \\ \tau_1(\mathbf{x}) & 1 & \cdots & 0 & 0 \\ \tau_1(\mathbf{x})\tau_2(\mathbf{x}) & \tau_1(\mathbf{x}) & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ \frac{\prod_{j=1}^{m-1} \tau_j(\mathbf{x})}{1 - \tau_m(\mathbf{x})} & \frac{\prod_{j=2}^{m-1} \tau_j(\mathbf{x})}{1 - \tau_m(\mathbf{x})} & \cdots & \frac{\tau_{m-1}(\mathbf{x})}{1 - \tau_m(\mathbf{x})} & \frac{1}{1 - \tau_m(\mathbf{x})} \end{bmatrix}$$

exists and consequently assumption (12) holds. A calculation shows that

$$\mathbf{Q}(\mathbf{x}) = [\beta_1(\mathbf{x})\mathbf{v}(\mathbf{x}) \quad \beta_2(\mathbf{x})\mathbf{v}(\mathbf{x}) \quad \cdots \quad \beta_m(\mathbf{x})\mathbf{v}(\mathbf{x})],$$

where $\mathbf{v}(\mathbf{x})$ is the column vector

$$\mathbf{v}(\mathbf{x}) = \begin{bmatrix} 1 \\ \tau_1(\mathbf{x}) \\ \tau_1(\mathbf{x})\tau_2(\mathbf{x}) \\ \vdots \\ \frac{\prod_{j=1}^{m-1} \tau_j(\mathbf{x})}{1 - \tau_m(\mathbf{x})} \end{bmatrix} > \mathbf{0}.$$

Since all of the columns of $\mathbf{Q}(\mathbf{x})$ are multiples of the same positive vector $\mathbf{v}(\mathbf{x})$, the number 0 is an eigenvalue of multiplicity $m - 1$. The remaining eigenvalue, which is positive and simple, is given by the formula

$$q(\mathbf{x}) = \beta_1(\mathbf{x}) + \sum_{i=2}^{m-1} \beta_i(\mathbf{x}) \prod_{j=1}^{i-1} \tau_j(\mathbf{x}) + \beta_m(\mathbf{x}) \frac{\prod_{j=1}^{m-1} \tau_j(\mathbf{x})}{1 - \tau_m(\mathbf{x})}, \quad (19)$$

where the normalization of the β_i implies that $q(\mathbf{0}) = 1$. As above, positive equilibria must satisfy equation (17); that is,

$$n \left[\beta_1(\mathbf{x}) + \sum_{i=2}^{m-1} \beta_i(\mathbf{x}) \prod_{j=1}^{i-1} \tau_j(\mathbf{x}) + \beta_m(\mathbf{x}) \frac{\prod_{j=1}^{m-1} \tau_j(\mathbf{x})}{1 - \tau_m(\mathbf{x})} \right] = 1.$$

The right and left eigenvectors of $\mathbf{Q}(\mathbf{0})$ (or equivalently $\mathbf{R}(\mathbf{0})$) in assumption (13) are

$$\mathbf{v} = \mathbf{v}(\mathbf{0}) > \mathbf{0}$$

and

$$\mathbf{0} \neq \mathbf{w} = \begin{bmatrix} \beta_1(\mathbf{0}) \\ \vdots \\ \beta_i(\mathbf{0}) \\ \vdots \\ \beta_m(\mathbf{0}) \end{bmatrix} \geq 0.$$

Moreover, the bifurcating continuum of equilibrium pairs is unbounded in $R_+ \times R_+$, and all nontrivial equilibria lying on the continuum are positive.

It is atypical but possible for more than one positive equilibrium to be associated with a value for n . In this case, the bifurcation graph has “turns” in it, as drawn in Figure 2. (Moreover, the theorem does not claim that all positive equilibria must lie on the bifurcating continuum.) More is said about this possibility below.

Stability of Equilibria

The “linearization principle” is valid for equation (10). This principle states that the local stability properties of a hyperbolic equilibrium \mathbf{e} are determined by those of the linearization of equation (10) at the equilibrium. (An equilibrium is called “hyperbolic” if none of the eigenvalues of $\mathbf{J}(\mathbf{e})$, $\lambda_i = \lambda_i(\mathbf{e})$, lies on the unit circle in the complex plane; i.e., if all $|\lambda_i(\mathbf{e})| \neq 1$.) The linearization at \mathbf{e} is the linear matrix equation whose projection matrix is the Jacobian of the right-hand side of equation (10) evaluated at \mathbf{e} . If we denote the right-hand side of (10) by $\mathbf{f}(\mathbf{x}) = [f_i(\mathbf{x})]$, the Jacobian is the matrix $\mathbf{J}(\mathbf{x}) = [\partial f_i(\mathbf{x})/\partial x_j]$. The linearization principle implies that \mathbf{e} is (locally asymptotically) stable if all of the eigenvalues $\lambda_i(\mathbf{e})$ lie inside the unit circle (i.e., $|\lambda_i(\mathbf{e})| < 1$ for all i) and that \mathbf{e} is unstable if at least one of the eigenvalues lies outside the unit circle (i.e., $|\lambda_i(\mathbf{e})| > 1$ for at least one i).

“Locally asymptotically stable” means that \mathbf{e} is stable and also that orbits that start close enough to \mathbf{e} actually approach \mathbf{e} as $t \rightarrow +\infty$. “Stable” means that when $\varepsilon > 0$, there is a δ greater than 0 such that $|\mathbf{x}(0)| < \delta$, implying that $|\mathbf{x}(t)| < \varepsilon$ ($t > 0$). “Unstable” means “not stable.”

Suppose that assumptions (11), (12), and (13) apply for equation (10) written in form (15), and consider the equilibrium $\mathbf{e} = \mathbf{0}$, for which the Jacobian matrix is $\mathbf{J}(\mathbf{0}) = \mathbf{A}(\mathbf{0})$. Following the preceding section, the equilibrium $\mathbf{e} = \mathbf{0}$ is (locally asymptotically) stable if $n < 1$ and is unstable if $n > 1$.

We say that the equilibrium $\mathbf{e} = \mathbf{0}$ “loses stability” as n increases through the critical value $n = 1$. This fact has the same biological interpretation here, at least at low population densities, as it does for linear equations. Namely, if the expected number of offspring per individual over its lifetime is less than one (less than replacement), when population densities are low, then populations that are initially at a low level will become extinct. If this expected number is larger than one, however, then low-level populations will survive. Unlike the linear case, however, it may *not* be true when $n < 1$ that *all* populations decline to extinction.

Notice that in view of Theorem 1, the point $n = 1$ at which the equilibrium $\mathbf{e} = \mathbf{0}$ loses stability is a bifurcation point for nonzero equilibria. At this point the equilibrium $\mathbf{e} = \mathbf{0}$ is nonhyperbolic. The parameter values that yield nonhyperbolic equilibria are important because qualitative changes in asymptotic dynamics can occur at (and only at) such parameter values, often resulting in the appearance of new asymptotic states.

It was easy to see how the (local) stability of equilibrium $\mathbf{e} = \mathbf{0}$ depends on the inherent net reproductive number, n . In contrast, the stability properties of positive equilibria, especially those on the bifurcating continuum (as guaranteed by Theorem 1) are much more difficult to ascertain. These properties depend closely on the nonlinearities in the equation. However, one general result can be proved under the assumption that

$$1 \text{ is a strictly dominant eigenvalue of } \mathbf{N}(\mathbf{0}) + \mathbf{T}(\mathbf{0}). \quad (20)$$

Note that $\mathbf{N}(\mathbf{0}) + \mathbf{T}(\mathbf{0})$ is just the projection matrix of (15) evaluated at the bifurcation point $(n, \mathbf{e}) = (1, \mathbf{0})$. That $n = 1$ is an eigenvalue of $\mathbf{N}(\mathbf{0}) + \mathbf{T}(\mathbf{0})$ follows from assumption (14).

With the addition of assumption (20), it can be shown that the stability properties of the positive equilibria lying on the bifurcating continuum depend, at least in the neighborhood of the bifurcation point $(n, \mathbf{e}) = (1, \mathbf{0})$, on the “direction of bifurcation” (Cushing 1995). Specifically, if the bifurcating pairs (n, \mathbf{e}) near $(1, \mathbf{0})$ exist when $n > 1$, then the equilibria $\mathbf{e} > \mathbf{0}$ are (locally asymptotically) stable; on the other hand, if these pairs exist when $n < 1$, then the equilibria $\mathbf{e} > \mathbf{0}$ are unstable. In the first case the bifurcation is said to be “to the right” (or “supercritical” or “stable”), and in the second case it is said to be “to the left” (or “subcritical” or “unstable”). See Figure 2.

Furthermore, the direction of bifurcation can be determined by a formula derived from so-called Liapunov-Schmidt expansions of

the equilibrium branch. The result is that

$$\left\{ \begin{array}{l} \text{the bifurcation is to the left (i.e., stable or supercritical)} \\ \text{if } n_1 > 0, \\ \text{the bifurcation is to the right (subcritical or unstable)} \\ \text{if } n_1 < 0, \end{array} \right.$$

where

$$n_1 = - \langle \mathbf{w}, [\nabla_{\mathbf{x}} \langle a_{ij}(0, 1), \mathbf{v} \rangle] \mathbf{v} \rangle, \\ \nabla_{\mathbf{x}} a_{ij}(\mathbf{x}, n) = \begin{bmatrix} \partial a_{ij}(\mathbf{x}, n) / \partial x_1 \\ \vdots \\ \partial a_{ij}(\mathbf{x}, n) / \partial x_m \end{bmatrix}$$

and \mathbf{v} and \mathbf{w} are the right and left eigenvectors of $\mathbf{R}(\mathbf{0})$ (see eq. 13). This formula allows the direction of bifurcation, and hence the local stability properties of the positive equilibria near the bifurcation point, to be calculated from the nonlinear entries in the projection matrix $\mathbf{A}(\mathbf{x}, n)$, at least “generically” (i.e., in most cases) when $n_1 \neq 0$. Note that for the linear case, when \mathbf{A} is independent of \mathbf{x} and the bifurcation is vertical (i.e., is neither to the left nor to the right), n_1 is zero.

A simplified formula holds when all newborns belong to the same class, say, to class $i = 1$ (without loss in generality). Then, there is a positive constant c such that

$$n_1 = -c \langle \nabla_{\mathbf{x}} q(\mathbf{0}), \mathbf{v} \rangle, \quad (21)$$

where $q(\mathbf{x})$ is given by equation (19) (Cushing 1988a, 1995).

This simplified formula is valid, for example, for the nonlinear model (18). The nonlinear Leslie model satisfies requirement (20), sufficient for stability to be determined by the direction of bifurcation, if 1 is strictly dominant as an eigenvalue of the constant Leslie matrix

$$\mathbf{N}(\mathbf{0}) + \mathbf{T}(\mathbf{0}) = \begin{bmatrix} \beta_1(\mathbf{0}) & \beta_2(\mathbf{0}) & \cdots & \beta_{m-1}(\mathbf{0}) & \beta_m(\mathbf{0}) \\ \tau_1(\mathbf{0}) & 0 & \cdots & 0 & 0 \\ 0 & \tau_2(\mathbf{0}) & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & \tau_{m-1}(\mathbf{0}) & \tau_m(\mathbf{0}) \end{bmatrix}.$$

Necessary and sufficient conditions for this to hold are known (Impagliazzo 1980). A simple sufficient condition is that there are two adjacent age classes that are fertile. For example, $\beta_{m-1}(\mathbf{0}) > 0$ is sufficient, since it has been assumed all along that $\beta_m(\mathbf{0}) > 0$.

In the general case, since

$$\frac{\partial a_{ij}(\mathbf{0}, 1)}{\partial x_k} = \frac{\partial \beta_{ij}(\mathbf{0})}{\partial x_k} + \frac{\partial \tau_{ij}(\mathbf{0})}{\partial x_k},$$

it is the nonlinear dependence of the fertilities β_{ij} (or, equivalently, f_{ij}) and the transition probabilities τ_{ij} that determine the direction of bifurcation and hence the local equilibrium stability near the point of bifurcation. The most common modeling assumptions in population-dynamics models, that fertility and survival are adversely affected by increased population density (and consequently that both β_{ij} and τ_{ij} , and hence a_{ij} , are decreasing in each component x_k), imply that $n_1 > 0$. Thus, the usual situation is that a stable (supercritical) bifurcation of positive equilibria occurs as n increases through 1.

There are interesting cases, however, when unstable bifurcations to the left occur. Necessary for such an occurrence is that not all of the partial derivatives $\partial \beta_{ij}(\mathbf{0}, 1)/\partial x_k$, $\partial \tau_{ij}(\mathbf{0}, 1)/\partial x_k$ be non-negative. One case is that of a so-called "Allee effect" (or "depensation"). Such an effect is present when the opposite of the usual regulatory density effects occurs on at least one of the vital rates, usually at low population densities only. Thus, at low population densities, birthrates might *increase* and/or death rates might *decrease* with increased population density for at least some age classes (see the application below; Allee 1931; Cushing 1988*b*; Dennis 1993). If these reversed effects are significant enough at *low* population densities, then n_1 can be negative and the bifurcating positive equilibria will be unstable, at least near the bifurcation point.

Normally it is assumed, however, that such Allee effects on the vital rates do not persist at *high* population densities, at which the usual adverse effects of density on the vital rates are assumed to hold. It turns out that this causes the bifurcating branch to "turn around" as in Figure 2*b*. Usually in this case, although not always, the "top" of the branch (i.e., the positive equilibria of larger magnitude) consists of stable equilibria. There are several things to note in this case. First of all, stable positive equilibria exist for values of the inherent net reproductive number, n , less than 1. This is in marked contrast to linear models, in which the population always becomes extinct when $n < 1$. Second, there are multiple equilibria and multiple stable equilibria when $n < 1$. Third, there is the potential for a *sudden* collapse of the population as n decreases (unlike the case of a stable bifurcation when there is a continuous

decrease to the trivial solution as n decreases). Finally, a hysteresis effect is caused by the existence of multiple stable equilibria.

Another interesting case that can result in an unstable bifurcation is that of cannibalism (see Cushing 1991a; for an example of unstable bifurcation due to complicated nonlinear interactions and stage structure, see Cushing 1988a).

In a general setting, the loss of stability of the trivial equilibrium at a critical value, $n = 1$, results in the bifurcation of a global continuum of positive equilibria from the trivial equilibrium. Under suitable assumptions, the stability properties of these bifurcating equilibria near the bifurcation point are determined by the direction of bifurcation. However, it is not true that the stability properties of the positive equilibria near the bifurcation point necessarily persist globally along the continuum. Stable equilibria that result from a supercritical bifurcation can lose their stability farther along the continuum. Unstable equilibria that result from a subcritical bifurcation can gain stability farther along the continuum. Such changes in stability often result in the bifurcation of other kinds of stable attractors. The “generic” possibilities are described in the next subsection.

Loss of Stability of a Positive Equilibrium

The stability of a positive equilibrium, $\mathbf{x} = \mathbf{e} > \mathbf{0}$, of the nonlinear matrix equation (10) is determined by the eigenvalues $\lambda(\mathbf{e})$ of the Jacobian matrix. Loss of stability occurs if a change in a model parameter causes one or more of these eigenvalues to move outside of the unit circle. A critical parameter value, then, is one that places an eigenvalue exactly on the unit circle, that is, that causes $|\lambda(\mathbf{e})|$ to be equal to 1 for at least one eigenvalue. Such an eigenvalue has the complex form $\lambda_i(\mathbf{e}) = \exp[i\theta(\mathbf{e})]$ for some polar angle $\theta(\mathbf{e}) \in [0, 2\pi)$. Conversely, if the equilibrium \mathbf{e} is unstable because an eigenvalue is outside the unit circle and a change in a model parameter causes this eigenvalue (and all other eigenvalues) to be inside the unit circle, then the equilibrium has been stabilized. Once again the critical parameter value is the one that places the eigenvalue exactly on the unit circle.

It turns out that the nature of the bifurcation that takes place at a critical parameter value, where a change in equilibrium stability occurs, depends on this polar angle $\theta(\mathbf{e})$ of the eigenvalue lying on the unit circle, that is, on exactly where the eigenvalue crosses the unit circle as it moves from the inside to the outside (or vice versa). The simplest occurrences, and the ones best understood,

are those in which there is either a single real eigenvalue at ± 1 with the remaining $n - 1$ eigenvalues lying inside the unit circle or a single complex conjugate pair lying on the unit circle with the remaining $n - 2$ eigenvalues lying inside. Described below are only the most commonly occurring types of bifurcations that can occur in population models in these simplest cases (for a more complete discussion, see Lauwerier 1986; Wiggins 1990). Relevant discussions appear in the chapters by Caswell (2), Nisbet (4), and de Roos (5).

Eigenvalue +1. Consider the case when an eigenvalue associated with the linearization at an equilibrium \mathbf{e} assumes the value $+1$ at a critical value of n in the nonlinear matrix equation (15). The bifurcation that occurs at such a critical point is associated, in one way or another, with the existence of multiple equilibria.

For example, an eigenvalue of 1 occurs in the linearization of equation (15) at $\mathbf{e} = \mathbf{0}$ when $n = 1$. This is an example of a “transcritical bifurcation.” Transcritical bifurcations involve the intersection of two different branches of equilibria in such a way that two equilibria exist for values of n on both sides of the critical value 1. For equation (15), at the point $(\mathbf{0}, 1)$, the branch consisting of the trivial equilibria (which exists for all n) intersects a branch of nontrivial equilibria (\mathbf{e}, n) that exists for n greater than and n less than 1. Only one side, however, consists of positive equilibria, $\mathbf{e} > \mathbf{0}$ (the side where $n > 1$ in the case of a stable supercritical bifurcation and the side where $n < 1$ in the case of an unstable subcritical bifurcation), and therefore the equilibria from the other side of the intersecting branch in the discussion above are ignored. It typically happens at a transcritical bifurcation that an “exchange of stability” occurs, by which is meant that the branch containing the stable equilibria for n less than 1 contains unstable equilibria for n greater than 1, and vice versa (the stability having been passed from one branch to the other as n passes through 1).

As seen above, general nonlinear matrix models of the form (10) possess a transcritical bifurcation and an exchange of stability at the trivial equilibrium when the inherent net reproductive rate increases through the critical value $n = 1$. Positive equilibria of equation (15) can also experience bifurcations as n changes. Besides transcritical bifurcations (which are not common for positive equilibria of models of the form in eq. 15), “saddle-node” bifurcations can occur at positive equilibria when an eigenvalue of the linearization equals $+1$ at a critical value of n . In a saddle-node bifurcation, two different positive equilibria exist for n on one side

of the critical value, move together as n equals the critical value, and then disappear for n on the other side of the critical value.

An example is illustrated in Figure 2*b*, where a subcritically bifurcating branch of positive equilibria “turns around” at the critical value when $n < 1$; a saddle-node bifurcation occurs at the “turn-around” point (the “nose” of the graph in Fig. 2*b*). Generally, in a saddle-node bifurcation one of the equilibria is stable (a node) and the other unstable (a saddle).

Another type of equilibrium bifurcation that can occur is called a “pitchfork” bifurcation. In this case a positive equilibrium loses stability at a critical value of n on one side of which there exist two more positive equilibria. An exchange of stability takes place between these two equilibrium branches.

It is not always easy to determine, analytically, the kind of equilibrium bifurcation that occurs at an eigenvalue of $+1$. Formulas sufficient to determine the types above are known for two-dimensional models (see Wiggins 1990). For higher-dimensional cases, however, an additional complicated calculation (called a “center manifold calculation”) is required in order to use these formulas. Numerical computer simulations are often useful in determining the kinds of bifurcations that occur.

Eigenvalue -1 . Suppose that a positive equilibrium of equation (15) loses stability at a critical value of n where the linearization has an eigenvalue equal to -1 (all remaining $n - 1$ eigenvalues remaining inside of the complex unit circle). In this case there exist, for n on one side of the critical value or the other, non-equilibrium periodic solutions of equation (15) of period 2, so-called “2-cycles.” The amplitude of these cycles grows from zero at the critical value of n ; the 2-cycles either “pop out of” or “shrink into” the equilibrium as n increases through the critical bifurcation value. This kind of bifurcation is called a “period-doubling” bifurcation.

When a period-doubling bifurcation occurs, there exist both a positive equilibrium and a 2-cycle (actually two 2-cycles, since a shift of a 2-cycle is still a 2-cycle) for n on one side of the critical value or the other. However, the equilibria and the 2-cycles do not possess the same stability properties; if one is stable, the other is unstable (so another exchange of stability can be said to occur). In this sense the stability of the bifurcating 2-cycles is determined by the direction of bifurcation.

For example, if the positive equilibrium loses stability as n increases through the critical value, then the 2-cycles are unstable if they exist for n less than the critical value (a subcritical bi-

furcation) and stable if they exist for n greater than the critical value (a supercritical bifurcation). Formulas exist for the calculation of a constant whose sign determines the direction of bifurcation and the stability of the 2-cycles; however, this calculation is notoriously complicated and not useful for examining parameter changes. Again, evidence of stable 2-cycles is usually gained through numerical simulations.

Complex pair of eigenvalues of magnitude 1. For one-dimensional difference equations, loss of stability can occur only in one of the two cases above. For higher-dimensional models, which are central to structured-population dynamics, other possibilities arise because the linearization at an equilibrium can possess complex eigenvalues, which leave the unit circle at points other than ± 1 .

In the simplest case, at the critical value of n there is a pair of complex conjugate eigenvalues of magnitude 1,

$$\lambda(\mathbf{e}) = e^{\pm i\theta(\mathbf{e})}, \quad \theta(\mathbf{e}) \neq 0 \text{ or } \pi,$$

while all the remaining eigenvalues lie inside the unit circle. For technical reasons, we assume that

$$\theta(\mathbf{e}) \neq 2\pi/3, 4\pi/3, \pi/4, 3\pi/4.$$

That is to say, we assume that

$$\lambda^k \neq 1 \quad \text{for } k = 1, 2, 3, 4.$$

When these equalities hold, the eigenvalues are said to satisfy a “resonance” condition, and the resulting bifurcations are not well understood (Lauwerier 1986; Wiggins 1990). We exclude resonances because they are not “generic” (typical).

The result of a complex pair moving across the unit circle (but not at one of the first four roots of unity) is a “Naimark-Sacker” bifurcation to an invariant loop (sometimes called a “Hopf bifurcation”). An “invariant loop” is a closed curve L in m -dimensional space with the property that if an orbit starts on L then it forever stays on L . That is, if $x(0)$ lies on L , then the solution $x(t)$ of equation (15) lies on L for all nonnegative t . This theorem states that such invariant loops exist for values of n on one side of the critical value or the other. They “pop out of” the positive equilibrium at the critical value of n , in the sense that their amplitude shrinks to zero as n passes through the critical value. Moreover, as in the case of a period doubling, the positive equilibrium and the loop are not “stable” at the same time, and hence, the “stability” of the bifurcating loops depends on the direction of bifurcation.

(The loop is called “stable” if all nearby orbits tend to the loop in m -dimensional space as $t \rightarrow +\infty$.) The direction of a bifurcation can in principle be determined by the calculation of a certain quantity, but in practice this is tedious and often intractable. The plotting of two components of $x(t)$ by means of computer simulations can usually indicate the presence of stable invariant loops.

The use of the word “stable” with regard to the bifurcating invariant loops must be properly understood. Unlike the bifurcation results of the preceding subsections, the Naimark-Sacker bifurcation to an invariant loop says something about the geometry of the orbits (plots of solutions $x(t)$ in m -dimensional space) but nothing about the dynamics of solutions around the loop, which can be exactly periodic or, more typically, totally aperiodic. In the latter case, time series (i.e., plots of components of solutions $x(t)$) oscillate in a nearly periodic fashion, although their oscillation often looks irregular or “chaos-like” (but they are not technically chaotic in the sense of being sensitively dependent upon initial conditions; Wiggins 1990).

So far, the focus has been on the bifurcations that can occur when positive equilibrium states of equation (15) lose stability as the inherent net reproductive number, n , increases. We have seen that, when this happens, new kinds of “stable” entities come into existence, namely, new positive equilibria or oscillatory solutions (2-cycles or those on an invariant loop). This is certainly not the end of the story, however. As n increases farther, these nonequilibrium states can lose their stability, and new kinds of bifurcations can occur. Probably the most familiar is the well-known period-doubling sequence of bifurcations that occurs when 2-cycles lose stability and stable 4-cycles come into existence, which then lose stability to stable 8-cycles, and so on. Often this cascade occurs until n increases past a critical value, after which “chaos” occurs. The famous one-dimensional discrete logistic equation is the prototypical example. Stable invariant circles can lose their stability to chaos as n increases as well. In this case, chaos is often preceded, however, by regions of “period locking,” in which cycles of certain periods occur (and often period double).

The implications of complicated bifurcations and dynamics in discrete (and continuous) models and their relevance to biological populations are controversial. For example, claims that certain population data can be explained by the dynamics of simple difference-equation models are often poorly supported. Problems here include inaccurate or insufficient data sets, inadequate sta-

tistical tests for parameter estimation and model verification, use of simplistic models with little biological relevance, and neglect of stochastic effects. However, these issues are increasingly being addressed by more-careful studies, for which a thorough understanding of the deterministic dynamics of the model is certainly prerequisite.

3 Some Examples

This section presents some applications that illustrate how the analysis of nonlinear models can be carried out from the point of view of bifurcation theory.

The first application illustrates a typical, supercritical bifurcation of stable positive equilibria as n increases through $n = 1$. In this example, as n increases, the bifurcating continuum of positive equilibria ultimately loses stability, leading either to a bifurcation to stable 2-cycles or to a stable invariant loop, depending upon model parameter values.

The second application illustrates the possibility of a subcritical (unstable) bifurcation of positive equilibria where $n = 1$. This example also illustrates a saddle-node bifurcation at a subcritical value of the inherent net reproductive rate. This leads to an interval of n values in which multiple stable equilibrium states exist and hysteresis effects occur.

The last application provides an example in which the fundamental result relating the direction of bifurcation to the stability of the bifurcating positive equilibria fails to hold. This example illustrates the necessity of assumption (20) for relating the direction of bifurcation to stability. It also shows that even when our general results fail, the bifurcation-theory viewpoint remains helpful. The manner in which the assumptions fail to hold often provides a clue as to what is happening at the bifurcation point and thus what analytical steps to take next. In this application, this clue ultimately leads to a full understanding of the dynamics at the primary bifurcation point.

A Model for Flour Beetle Dynamics

Discrete models have been extensively used to help understand the complicated population dynamics of flour beetles of the genus *Tribolium* (Sokoloff 1974; Costantino & Desharnais 1991). The simplified model below tries to capture one important behavior of most

species of *Tribolium*, the cannibalism of eggs and pupae by adults and larvae (see also the discussion by Botsford, Chapter 12). It is a simplification and precursor of a more complicated model used by Costantino et al. (1995) and Dennis et al. (1995).

In this model are two classes, adults and immatures. The fertility and transition matrices are given by

$$\mathbf{F} = \mathbf{F}(x_1, x_2) = \begin{bmatrix} 0 & be^{-c_E x_2} \\ 0 & 0 \end{bmatrix},$$

$$\mathbf{T} = \mathbf{T}(x_1, x_2) = \begin{bmatrix} 0 & 0 \\ e^{-c_P x_2} & 1 - \mu \end{bmatrix}.$$

Here the exponentials account for losses due to cannibalism, with the nonnegative coefficients c_E and c_P (not both 0) corresponding to cannibalism on eggs and pupae, respectively. The parameter b is the immature recruitment rate in the absence of cannibalism, and μ is the adult mortality rate; $\mu \in (0, 1)$. The unit of time equals the maturation period.

Clearly, basic properties (11) hold on the whole (x_1, x_2) plane where $D = \mathbb{R}^2$, and the inverse exists for all x_1 and x_2 :

$$\mathbf{E}(x_1, x_2) = \begin{bmatrix} 1 & 0 \\ e^{-c_P x_2} / \mu & 1 / \mu \end{bmatrix}.$$

The matrix

$$\mathbf{R}(0, 0) = \begin{bmatrix} 0 & b \\ 0 & b / \mu \end{bmatrix}$$

satisfies assumption (13) with

$$n = b / \mu, \quad \mathbf{v} = \begin{bmatrix} b \\ b / \mu \end{bmatrix}, \quad \mathbf{w} = \begin{bmatrix} 0 \\ \mu / b \end{bmatrix}.$$

This leads to the matrices

$$\mathbf{N}(x_1, x_2) = \begin{bmatrix} 0 & \mu e^{-c_E x_2} \\ 0 & 0 \end{bmatrix}, \quad \mathbf{Q}(x_1, x_2) = \begin{bmatrix} 0 & \mu e^{-c_E x_2} \\ 0 & e^{-(c_E + c_P)x_2} \end{bmatrix},$$

and to the matrix

$$\mathbf{N}(0, 0) + \mathbf{T}(0, 0) = \begin{bmatrix} 0 & \mu \\ 1 & 1 - \mu \end{bmatrix},$$

which has 1 as its strictly dominant eigenvalue. Hence, assumption (20) also holds.

We conclude that there exists an unbounded branch of positive equilibrium pairs that bifurcates from the trivial equilibrium at

the critical value where $n = 1$ ($b/\mu = 1$). Since the nonlinearities are decreasing functions of x_2 , it follows that $n_1 > 1$ and that the bifurcation is supercritical and stable. (The quantity n_1 can also be explicitly calculated by the formula above, and whereby it is found that $n_1 = c_P b$.)

Equation (17) gives the relationship

$$n \exp[-(c_E + c_P)A_e] = 1$$

between the positive equilibria (specifically, the equilibrium adult number, $A_e > 0$) and the inherent net reproductive number, n . This scalar equation shows that the bifurcating continuum of positive equilibria is a logarithmic function of n . Thus, this fact supports the deductions that the bifurcation is supercritical, that the spectrum of n values corresponding to positive equilibria is infinite (specifically, the half-line where $n > 1$), that the magnitudes of positive equilibria are unbounded as a function of n greater than 1, and that for each n greater than 1 there is a unique positive equilibrium (the equilibrium number of immatures is $I_e = n\mu \exp(-c_E A_e)$).

Stability does not persist along the continuum of positive equilibria as n increases, however. It can be shown that a 2-cycle bifurcation can occur and an invariant loop bifurcation can occur, depending upon parameter values. The critical value of n ($n_{cr} > 1$) at which this loss of stability occurs can be calculated by computing the linearization of the equations at the positive equilibria and determining when the resulting 2×2 matrix has eigenvalues on the complex unit circle. This leads to the formula

$$n_{cr} = \begin{cases} e^{(1+1/\mu)(1+r)} & \text{when } r < r_{cr}, \\ e^{2(1-1/\mu)(1+r)/(1-r)} & \text{when } r > r_{cr}, \end{cases} \quad (22)$$

where

$$r = c_P/c_E \quad \text{and} \quad r_{cr} = (3 - \mu)/(1 + \mu).$$

A 2-cycle bifurcation occurs, where $n = n_{cr}$, when $r > r_{cr}$; and an invariant loop bifurcation occurs, where $n = n_{cr}$, when $r < r_{cr}$. See Figure 3 for a numerical example of the latter case.

A Model with Allee Effect

We have previously pointed out that when increased population density reduces vital rates (as in the preceding example), we obtain a supercritical stable bifurcation at $n = 1$ in the model (10). A reversal of this relationship between population density and at

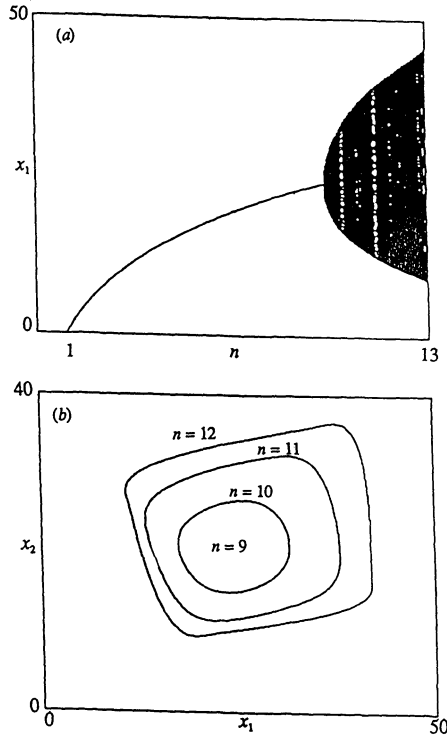


FIGURE 3. (a) The bifurcation diagram for the Tribolium model when $c_e = 0.10$, $c_p = 0.01$, and $\mu = 0.95$. The (positive) asymptotic attractor is shown plotted against the inherent net reproductive number, n . The supercritical (and hence stable) bifurcation of equilibria is clearly seen occurring when $n = 1$. The loss of stability of these positive equilibria followed by a bifurcation to stable invariant loops is also seen to occur at larger values of n . (b) The attractors are shown in the phase plane generated when $n = 9$, at which a stable equilibrium occurs, and at $n = 10, 11$, and 12 , at which stable invariant loops are seen. According to equation (22), a Naimark-Sacker bifurcation occurs at n_{cr} , just above 9.56.

least one vital rate (fertility, survival, growth rates, etc.), at low population densities, may lead to a subcritical and unstable bifurcation. Allee effects or “depensation” effects are of this type (Allee 1931; Clark 1976; Dennis 1989).

To illustrate, consider an age-structured population, equation (18), in which fertility rates are density-dependent but survival rates are not. The fertility rates are assumed to be proportional to the rate u at which a limited resource is consumed, and this consumption or uptake rate u depends on population density. Specifically,

$$u = u[W(t)] > 0,$$

where

$$W(t) = \sum_{i=1}^m w_i x_i(t)$$

is a weighted total population size, $\sum_{i=1}^m w_i = 1$, and $w_i \geq 0$. The Allee effect is modeled by the assumption that

$$u'(0) > 0. \tag{23}$$

This means that as low population levels *increase* (i.e., as the weighted total population size W increases from near zero), per capita resource consumption, and hence fertility, *also increases*.

However, we also assume that for high population densities, per capita resource consumption decreases with increased population density; specifically,

$$\lim_{W \rightarrow +\infty} u(W) = 0. \tag{24}$$

In the nonlinear Leslie matrix model (18), write

$$\beta_i(W) = b_i u(W)$$

(i.e., $f_i = n\beta_i(W) = nb_i u(W)$), yielding

$$q = q(W) = u(W) \left(b_1 + \sum_{i=2}^{m-1} b_i \prod_{j=1}^{i-1} \tau_j + b_m \frac{\prod_{j=1}^{m-1} \tau_j}{1 - \tau_m} \right).$$

Assuming that $u(W)$ and the coefficients b_i are normalized by $u(0) = 1$,

$$b_1 + \sum_{i=2}^{m-1} b_i \prod_{j=1}^{i-1} \tau_j + b_m \frac{\prod_{j=1}^{m-1} \tau_j}{1 - \tau_m} = 1,$$

such that $q(0) = 1$ (i.e., in the model, n really equals the inherent

net reproductive number). Thus, equation (17) becomes

$$nu(W) = 1. \tag{25}$$

From the general results, if $b_m > 0$, a global, unbounded continuum of positive equilibrium pairs (n, \mathbf{x}) bifurcates from $(1, \mathbf{0})$. The direction of bifurcation is determined by the sign of n_1 (if it is nonzero). Using (21) and the expression for \mathbf{v} given after (18), the sign of n_1 is the same as the sign of

$$\begin{aligned} -\nabla_{\mathbf{x}}q(\mathbf{0})\mathbf{v} &= -u'(0) \sum_{i=1}^m \mathbf{w}_i \mathbf{v}_i \\ &= -u'(0) \left(w_1 + \sum_{i=2}^{m-1} w_i \prod_{j=1}^{i-1} \tau_j + w_m \frac{\prod_{j=1}^{m-1} \tau_j}{1 - \tau_m} \right). \end{aligned}$$

In other words, n_1 has the opposite sign from $u'(0) > 0$, and consequently, the direction of bifurcation is to the left (subcritical).

Under the added assumption that 1 is a strictly dominant eigenvalue of the Leslie matrix

$$\mathbf{N}(0) + \mathbf{T}(0) = \begin{bmatrix} b_1 & b_2 & \cdots & b_{m-1} & b_m \\ \tau_1 & 0 & \cdots & 0 & 0 \\ 0 & \tau_2 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & \tau_{m-1} & \tau_m \end{bmatrix},$$

the stability of the positive bifurcating equilibria near the bifurcation point is determined by the direction of bifurcation.

This example illustrates how the Allee assumption, inequality (23), causes an unstable primary bifurcation of equilibria at the critical value where $n = 1$.

An easier way to see that the bifurcation in this example is subcritical is to note that the bifurcating continuum of positive equilibria can be described mathematically by the pairs (n, W) , where $W > 0$, satisfying equation (25). Clearly, as W increases from 0, $u'(0) > 0$, implying that n must decrease. Moreover, as $W \rightarrow +\infty$ and hence $u(W) \rightarrow 0$, it follows from equation (25) that n must also tend to $+\infty$. This means, among other things, that the bifurcating branch “turns around,” as shown in Figure 2*b*. At this turning point there occurs a saddle-node bifurcation of positive equilibria, and one can usually expect that the “larger” equilibria lying on the upper part of the branch are stable, while those on

the lower are unstable. This does not always occur, however, but when it does, one sees an interval of inherent net reproductive numbers less than 1 for which there exist two stable equilibrium states, the stable positive equilibrium and the trivial or extinction equilibrium. This in turn leads to hysteresis effects. (For a simple model displaying these phenomena, see Cushing 1988*b*.)

A Size-Structured Model for Density-Dependent Growth

The following example (from Cushing & Li 1992) shows the importance of assumption (20) in drawing the conclusion that stability is related to the direction of bifurcation. In this example, this assumption fails to hold, although assumptions (11), (12), and (13) do hold and hence the existence of the bifurcation continuum of positive equilibria is ensured. In fact, in this example a supercritical but *unstable* bifurcation can occur. One point of this example is that even when the assumptions and conclusions of our bifurcation theorem fail to hold, this approach can give insights into the dynamics and suggest other avenues of analysis.

One question concerning intraspecific competition that has received considerable attention deals with competition between juvenile and adult members of a single population and whether such an interaction is a “stabilizing” or “destabilizing” influence on the population’s dynamics. Generally, such competition of juveniles versus adults is considered destabilizing, although there can be exceptions and a great deal depends on how the notion of “destabilization” is measured. (Studies of this problem based upon discrete dynamic model equations can be found in Ebenman 1987, 1988*a,b*; Cushing & Li 1989, 1992; Loreau 1990. Studies using continuous models appear in May et al. 1974; Tschumy 1982; Cushing 1991*b*; Cushing & Li 1991.)

There are many ways of modeling competition between juveniles and adults. Most published models assume that competition reduces age-class survival rates and/or adult fertility rate. Many contributors to the book by Ebenman and Persson (1988) argued that body size, rather than chronological age, is the key individual variable. In this case, competition can significantly affect an individual’s growth rate, size at maturation, etc.

Ebenman (1988*b*) studied a size-structured model for juvenile-versus-adult competition. His model is not analytically tractable, however, and he relied heavily on computer simulations. A simpler

model is considered here that focuses on competition effects on the size at maturation and hence on adult fertility rates (Cushing & Li 1992).

Consider a population of juveniles and two adult size classes, one consisting of smaller and less fertile adults and the other of larger and more-fertile adults. It is assumed that after one unit of time a juvenile matures but that its size at maturity depends on the amount of competition (for, say, a limited food resource) that it experienced as a juvenile. Adults do not change size after maturity. The amount or intensity of competition experienced during maturation is assumed to be a function of the weighted population size,

$$W = x_1 + \gamma_1 x_2 + \gamma_2 x_3,$$

where the coefficients γ_i measure the competitive effects of the adults on juvenile growth (relative to the self effects of juveniles). Density effects on survival and on adult fertility (except through adult size at maturation as described above) are ignored. If x_1 denotes the density of juveniles and x_2 and x_3 denote the densities of the smaller and larger adult classes, respectively, then the model is described by the difference equations

$$\begin{aligned} x_1(t+1) &= b_1 x_2(t) + b_2 x_3(t), \\ x_2(t+1) &= \varphi[W(t)] x_1(t), \\ x_3(t+1) &= \{1 - \varphi[W(t)]\} x_1(t), \end{aligned}$$

where $b_2 > b_1 > 0$, $\varphi \in C(R_+, [0, 1))$, and $\varphi'(W) > 0$ (Cushing & Li 1992). The inequalities $b_2 > b_1 > 0$ express the fact that larger individuals are more fertile. The function $\varphi(W)$, the fraction of juveniles growing to smaller size, incorporates the density dependence of juvenile growth. The mathematical assumption that this fraction is monotonically increasing as a function of W reflects the biological assumption that, as the population density W increases, a larger fraction of juveniles grow to the smaller adult size. (Here, in order to reduce the number of model parameters, juveniles are measured in units required to produce adults, considering a constant survivability over one unit of time. Thus, no mortality coefficient is needed in the equations for x_2 and x_3 .)

This model has the form of equation (15) with

$$\mathbf{F} = \mathbf{F}(W) = \begin{bmatrix} 0 & b_1 & b_2 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix},$$

$$\mathbf{T} = \mathbf{T}(W) = \begin{bmatrix} 0 & 0 & 0 \\ \varphi(W) & 0 & 0 \\ 1 - \varphi(W) & 0 & 0 \end{bmatrix}.$$

Assumptions (11) are fulfilled. There is an inverse,

$$\mathbf{E}(W) = [\mathbf{I} - \mathbf{T}(W)]^{-1} = \begin{bmatrix} 1 & 0 & 0 \\ \varphi(W) & 1 & 0 \\ 1 - \varphi(W) & 0 & 1 \end{bmatrix};$$

so assumption (12) is met. Regarding the final remaining assumption required for Theorem 1, the matrix

$$\mathbf{R}(0) = \mathbf{E}(0)\mathbf{F}(0) = \begin{bmatrix} 0 & b_1 & b_2 \\ 0 & b_1\varphi(0) & b_2\varphi(0) \\ 0 & b_1[1 - \varphi(0)] & b_2[1 - \varphi(0)] \end{bmatrix}$$

is seen to have a double eigenvalue 0 and the dominant simple eigenvalue

$$n = b_1\varphi(0) + b_2[1 - \varphi(0)].$$

Writing the model equations in form (15) with

$$\mathbf{N}(W) = \begin{bmatrix} 0 & \beta_1 & \beta_2 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}, \quad \mathbf{T}(W) = \begin{bmatrix} 0 & 0 & 0 \\ \varphi(W) & 0 & 0 \\ 1 - \varphi(W) & 0 & 0 \end{bmatrix},$$

where $\beta_i = b_i/[b_1\varphi(0) + b_2(1 - \varphi(0))]$, and applying Theorem 1, leads to an unbounded continuum of positive equilibria that bifurcates from the trivial equilibria at $n = 1$.

Moreover, a calculation shows that the quantity n_1 is a positive constant multiple of $\varphi'(0)(b_2 - b_1)$, and therefore, a supercritical bifurcation of positive equilibria occurs in this model system. For this to imply that the bifurcating positive equilibria are stable, requirement (20) must hold. However, the matrix

$$n\mathbf{N}(0) + \mathbf{T}(0) = \begin{bmatrix} 0 & n\beta_1 & n\beta_2 \\ \varphi(0) & 0 & 0 \\ 1 - \varphi(0) & 0 & 0 \end{bmatrix}$$

has eigenvalues 0, $-n$, and $+n$; consequently, $n = 1$ is not a dominant eigenvalue. As a result, assumption (20) fails to hold. This, of course, does not mean that the bifurcating equilibria are necessarily unstable, only that we do not know if the direction of bifurcation determines stability.

Since the eigenvalues of $n\mathbf{N}(0) + \mathbf{T}(0)$ lie inside the complex unit circle when $n < 1$ and outside the circle when $n > 1$, it follows that the trivial equilibrium loses stability at the bifurcation

point $(n, W) = (1, 0)$. However, when $n = 1$, this matrix has eigenvalue -1 in addition to $+1$, which suggests that in addition to a (transcritical) bifurcation of the equilibrium branches there might also occur a bifurcation of 2-cycles at $n = 1$! This is, in fact, true (Cushing & Li 1992). When $n = 1$, there also bifurcates a global branch of nonnegative “synchronous” 2-cycles (nonnegative, nontrivial 2-cycles in which juvenile and adult populations are never simultaneously present).

Thus, when $n > 1$, there exists both a unique positive equilibrium and a unique nonnegative synchronous 2-cycle. At least near the bifurcation point, one of these branches is stable and the other is unstable, depending upon a “competition coefficient” defined by

$$\sigma = \gamma_1 \varphi(0) + \gamma_2 [1 - \varphi(0)]$$

(Cushing & Li 1992). If $\sigma < 1$, then the positive equilibrium branch is stable and the synchronous 2-cycle branch is unstable; if $\sigma > 1$, then the opposite is true.

It is interesting to note that in this model strong juvenile-versus-adult competition implies that the population will stabilize into a dynamic situation (a 2-cycle) in which adults and juveniles never appear together. Thus, the population structure evolves, purely as a result of the dynamic assumptions, to a state in which competition is altogether avoided, a kind of temporal niche.

4 Concluding Remarks

The familiar properties of linear matrix equations can be viewed from the point of view of bifurcation theory using the net reproductive number, n , of the population as a bifurcation parameter. From this perspective, the facts that the population dies out exponentially when $n < 1$, grows exponentially without bound when $n > 1$, and possesses equilibrium states if and only if $n = 1$ can be viewed as a continuum of (neutrally stable) equilibria vertically bifurcating from the trivial equilibrium $\mathbf{x} = \mathbf{0}$ at the critical value, $n = 1$, where the trivial equilibrium loses stability. Under rather general circumstances, nonlinear matrix equations can in the same way possess a continuum of equilibria that bifurcates from the equilibrium $\mathbf{x} = \mathbf{0}$ when $n = 1$, where n is the inherent net reproductive number. For nonlinear equations, the bifurcation is usually not vertical, and consequently, in contrast to linear equations, equilibria exist for values of n other than 1. Near the bifurcation point the

stability of the bifurcating equation depends on the direction of bifurcation.

The approach taken above to nonlinear matrix equations can also be applied to coupled systems of matrix equations as models for several interacting structured species. For such systems, the projection matrix for one species can depend on the density of the other species. General existence and stability results for equilibrium states can be obtained by techniques from bifurcation theory, by defining and using the inherent net reproductive number of one species, when its density is low and the remaining community is at equilibrium, as a bifurcation parameter. Stability results again depend on the direction of bifurcation. This approach can be viewed as the study of conditions under which a species can be added to or invade a community of other species as a function of its inherent net reproductive number. (For details, see Cushing 1995.) Moreover, the same approach can also be applied when the underlying community is not at a stable equilibrium but in a stable cycle. In this case, a bifurcating branch of stable cycles can be proved to exist, with stability again depending on the direction of bifurcation. These results have been used, for example, to show the cyclic coexistence of competing species under circumstances in which the principle of competitive exclusion (which is based upon equilibrium dynamics) would imply otherwise (Crowe 1991).

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