

NONLINEAR MATRIX MODELS AND POPULATION DYNAMICS ¹

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ABSTRACT. Nonlinear matrix difference equations are studied as models for the discrete time dynamics of a population whose individual members have been categorized into a finite number of classes. The equations are treated with sufficient generality so as to include virtually any type of structuring of the population (the sole constraint is that all newborns lie in the same class) and any types of nonlinearities which arise from the density dependence of fertility rates, survival rates and transition probabilities between classes. The existence and stability of equilibrium class distribution vectors are studied by means of bifurcation theory techniques using a single composite, biologically meaningful quantity as a bifurcation parameter, namely the inherent net reproductive rate r . It is shown that, just as in the case of linear matrix equations, a global continuum of positive equilibria exists which bifurcates as a function of r from the zero equilibrium state at and only at $r = 1$. Furthermore the zero equilibrium loses stability as r is increased through 1. Unlike the linear case however, for which the bifurcation is "vertical" (i.e., equilibria exist only for $r = 1$), the nonlinear equation in general has positive equilibria for an interval of r values. Methods for studying the geometry of the continuum based upon the density dependence of the net reproductive rate at equilibrium are developed. With regard to stability, it is shown that in general the positive equilibria near the bifurcation point are stable if the bifurcation is to the right and unstable if it is to the left. Some further results and conjectures concerning stability are also given. The methods are illustrated by several examples involving nonlinear models of various types taken from the literature.

KEY WORDS: structured population dynamics, nonlinear matrix difference equations, density dependence, equilibria, stability, bifurcation theory.

1. Introduction. It is becoming widely recognized that an adequate description of the growth dynamics of most biological populations must take into account internal structuring of the population based upon

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physiological differences between individuals. This recognition can be found in a wide diversity of disciplines, including population dynamics, population ecology, epidemiology, genetics, cell dynamics, renewable resource, bioeconomics, pest control, fisheries management and many others (Metz and Diekmann [1986]). This is in stark contrast to the vast majority of models in population dynamics and theoretical ecology in which all individuals are implicitly treated as identical and only gross statistics at the population level (such as total population size, dry weight, biomass, etc.) are followed dynamically.

The use of matrix difference equations in models of age structured population growth was introduced several decades ago by Lewis [1942] and Leslie [1945, 1948] and is now quite commonplace. The same type of models are useful in describing growth dynamics of populations in which vital parameters, such as birth and death rates, depend significantly on other physiological differences between individuals as well. By tracking a vector of densities of subclasses of individuals, matrix models provide one way of relating population level dynamics to physiological properties of individual members of the population. Thus population level phenomena such as total population growth rates, equilibration and stability, periodic fluctuations or other oscillatory properties, can be related to individual properties such as resource uptake and growth rates, metabolic and conversion rates, birth and survival rates, any or all of which can vary significantly from individual to individual due to such differences as age, weight, body size, etc.

The early developers of matrix model methods were primarily interested in human demography and the dynamics of age class distributions. Moreover, the emphasis in both theory and application was primarily (although not exclusively) on linear models. This linear theory is a beautiful application of the mathematical theory of nonnegative matrices and as a result it is very well developed and quite general (see the book by Impagliazzo [1980]).

It often has been pointed out that age may not be (some would say, rarely is) the important structuring variable affecting the growth dynamics of most biological populations. Other physical attributes of individuals which may not correlate well with chronological age such as size, weight, physiological development or reproductive stage may play the determining role. Moreover, the age of an individual is often difficult if not impossible to measure in either natural or laboratory

populations. As will be pointed out in more detail below, the theory of linear matrix equations developed for age structure is in no way restricted to age structure models (i.e., to Leslie matrices), but applies equally well to models based on other structuring variables as well.

The simplicity of linear matrix models, the ease with which they can be set up and analyzed and their susceptibility to numerical use and analysis by computers have all contributed to their popularity. Linear models, however, yield exponential total population growth. In early recognition of this fact Leslie [1948] investigated some nonlinear versions of his age structured models in an attempt to include density effects and obtain "limited" or what would now be termed "logistic-like" total population growth. Since this seminal work of Leslie on age-structured population dynamics many nonlinear (or "density dependent") matrix models have appeared in the literature. Some references, which include applications to populations structured by variables other than age structure, are Barclay [1986], Buongiorno and Michie [1980], Caswell [1985], Caswell and Werner [1978], Desharnais and Cohen [1986], Ek [1974], Ek and Monserud [1979], Fisher and Goh [1984], Guckenheimer et.al. [1976], Hassell and Comins [1976], Horwood and Shepherd [1981], Levin and Goodyear [1980], Lewis [1942], Liu and Cohen [1987], North [1985], Pennycuick [1969], Pennycuick et al., [1968], Pollard [1973], Smouse and Weiss [1975], Travis et al. [1980], Usher [1972], Watt [1960, 1968], Werner and Caswell [1977] and this list is in no way complete.

To date the treatment of nonlinear matrix models has been very *ad hoc*, with methods and results specialized to particular types of matrix equations and applications and with the analysis often restricted to numerical simulations. No broadly based, unifying theory, such as one finds for linear models, emerges from the existing literature. The main purpose of this paper is to offer one such theory.

The intent is to consider as general a class of models as possible so that the theory is not dependent upon the specifics of particular equations, to special types of nonlinearities nor to particular types of structuring. One major restriction will be made however; namely, whatever the classification scheme for individuals is, it will be assumed that all newborn members of the population lie in the same class. This restriction is met by virtually all applications in the literature, although not by all (e.g., some stage models for plant dynamics take

into account both seed and vegetative reproduction). Undoubtedly the approach taken in this paper can be extended to an arbitrary number of newborn classes since the analytic methods are quite general. The restriction to only one newborn class is made primarily for simplicity and since it is the most common case.

The development below is based on the ideas and methods of bifurcation theory. Besides providing a very general theory of population equilibria and stability for general nonlinear matrix equation models, this approach makes available the powerful techniques of bifurcation theory for the analysis of specific models in considerable detail.

The type of general matrix equations to be considered are described in Section 2. Some preliminary matters are given in Section 3 and the necessary linear theory is presented in Section 4. Nonlinear equations are treated in Sections 5, 6, and 7 and some examples are given in Section 8.

2. Matrix Models. Throughout this paper lower case bold face letters will denote column vectors and a superscript "*" will denote transpose. Thus \mathbf{x}^* is a row vector. Bold face capital letters will denote square matrices. The juxtaposition of vectors and matrices such as $\mathbf{A}\mathbf{x}$ implies the usual matrix multiplication. Thus the product $\mathbf{w}^*\mathbf{x}$ denotes the usual scalar or dot product of two vectors. If $\mathbf{1} = (1, 1, \dots, 1)^*$ then $\mathbf{1}^*\mathbf{x}$ is the sum of the components of \mathbf{x} . The symbol $\mathbf{0}$ denotes the zero vector. The inequality $\mathbf{A} \geq 0$ (> 0) for a matrix \mathbf{A} means that all entries are nonnegative (positive). The identity matrix is \mathbf{I} .

Suppose that the individuals of a population are categorized by means of $m + 1$ classes, $m \in J_+ = \{0, 1, 2, 3, \dots\}$. In discrete time dynamical models the numbers or densities $x_k(i)$ in each class at a time i are placed in a *class distribution* $(m + 1)$ -vector $\mathbf{x}(i) = (x_k(i))^*$ and this distribution vector at an arbitrary time $i + 1$ is related in some deterministic manner to the class distribution vector at time i (and possibly earlier times as well). The model equations are simply bookkeeping devices which keep track, during one unit of time, of the movement of individuals into and out of classes which can occur because of births and deaths, transitions between classes (such as might be due, for example, to aging or growth), emigrations and/or immigrations, harvesting, etc.

Let p_k be the probability that an individual in class k at any time will survive one unit of time. If p_{jk} is the probability that an individual in class k at any time i will be in class j at time $i + 1$, given that it survives one unit of time, then the fraction of individuals in class k expected to transfer to class j during one unit of time is the product $t_{jk} = p_k p_{jk} \in [0, 1]$. Let \mathbf{T} denote the $(m+1) \times (m+1)$ transition matrix $\mathbf{T} = (t_{jk}) \geq 0$. The individuals distributed at time i according to the vector $\mathbf{x}(i)$ who survive to time $i + 1$ will be redistributed according to the vector $\mathbf{T}\mathbf{x}(i)$.

To account for births let b_{jk} be the expected number of j -class offspring produced per k -class individual during one unit of time. If s_{jk} is the probability that a j -class offspring born during any time interval to a k -class parent will survive to the end of that time interval, then $f_{jk} = s_{jk} b_{jk}$ equals the expected number of j -class newborns per k -class individual alive at time $i + 1$ due to births during the time interval $(i, i + 1)$. Let \mathbf{F} be the $(m + 1) \times (m + 1)$ fertility matrix $\mathbf{F} = (f_{jk}) \geq 0$. The distribution vector of new individuals at time $i + 1$ due to births from individuals from the class distribution vector $\mathbf{x}(i)$ at time i is then $\mathbf{F}\mathbf{x}(i)$.

Only populations closed to immigration and emigration will be considered here. Thus the class distribution vector at time $i + 1$ is given by the matrix difference equation

$$(1) \quad \mathbf{x}(i + 1) = \mathbf{A}\mathbf{x}(i), \quad i \in J_+, \mathbf{x}(0) \geq 0$$

where the nonnegative coefficient matrix \mathbf{A} is given by

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

The matrix \mathbf{A} is usually referred to as the *projection matrix*. Clearly $\mathbf{x}(i)$ is uniquely determined for all $i \geq 1$ by this recursive formula once the initial distribution vector $\mathbf{x}(0)$ is given. If \mathbf{A} remains constant in time, then (1) is a linear autonomous system. If \mathbf{A} depends on time i only through a dependency on the distribution vector $\mathbf{x}(i)$ then (1) is autonomous and nonlinear.

Besides an appropriate choice of class structure and discrete time unit, the construction of a reasonable model involves the specification of submodels for the class specific survival rates p_k , s_{jk} and birth rates b_{jk} . These in turn can be based on fundamental individual physiological

and behavioral processes such as resource preferences and availabilities; resource uptake rates and conversion factors; growth, fertility, and metabolic rates; resource allocation strategies among growth, fertility and maintenance processes; etc.

If the population is structured by age classes (of length equal to the dynamical time unit chosen for i) then the only possible transitions are from class k to $k + 1$, assuming no individual lives beyond age $m + 1$. The transition matrix \mathbf{T} is then subdiagonal, that is, all entries are zero except the entries along the diagonal immediately below the main diagonal which are the probabilities of survival from one age class to the next in one unit of time. The fertility matrix \mathbf{F} has nonzero entries only in its first row since births can occur, by definition, only in the first age class. The resulting matrix \mathbf{A} is usually referred to as a *Leslie matrix*.

Another example is provided by so-called *Usher-type matrices* which are Leslie matrices modified by the occurrence of nonzero probabilities along the main diagonal of the transition matrix \mathbf{T} . Such matrices have been used in size structured population dynamics in which the size classes are so configured as to allow, during one unit of time, two possibilities: either an individual advances to the next larger size class or remains in its current size class. Matrix equations of this type, both linear and nonlinear, have been extensively used in studying the dynamics of forests, the member trees of which are classified according to trunk diameter (Ek [1974], Ek and Monserud [1979], Usher [1966, 1969a, 1969b]).

Normally the class structure is chosen and ordered so that the usual course of events is for an individual to progress in time through the classes in the designated order. Any nonzero entry in the transition matrix \mathbf{T} lying above the main diagonal would then imply a nonzero probability of a "regression." In an age class model this is impossible (there are no fountains of youth), but in a model built on size classes such an entry would allow for the possibility of shrinkage. Such a case can also arise in models based on life or reproductive stages in which regression to an "earlier" stage is possible. Plants categorized on the basis of seeds, non-flowering rosettes and flowering rosettes are an explicit example. Furthermore, classes may be described according to more than one variable so that life cycle stages can be further broken down into age or size or weight subclasses. See Caswell [1985] for many

references to applications in plant biology. Also see Lefkovich [1969] and Desharnais and Cohen [1986]. Such non-Leslie matrix models also arise if the distribution vector contains class densities of several different interacting species (Barclay [1986], Travis and Post [1979], Travis et al. [1980]) or if class categories are based upon sex (Caswell and Weeks [1986], Pollard [1973]). Models of this type for energy and nutrient flow in ecosystems have also been proposed by Usher [1972].

Thus there is a need in the theory of matrix models (1) to allow for some generality and not to restrict the projection matrix \mathbf{A} unnecessarily by, for example, an assumption that \mathbf{A} is a Leslie matrix or that no nonzero entries appear above the main diagonal.

If all the entries in the projection matrix \mathbf{A} are assumed constant, i.e., independent of time i both explicitly and implicitly, then the equation (1) is linear autonomous. The resulting linear equation falls under the purview of the mathematical theory of nonnegative matrices and in particular the famous Perron-Frobenius theory. This theory is well known to students of demography and Leslie matrices (see Impagliazzo [1980]), but it applies equally well to any linear nonnegative projection matrix model (for a summary see Caswell [1985]). The elements of this theory required here will be presented in Section 3.

Our interest in this paper will be, on the other hand, with nonlinear models (1) which arise because entries in the projection matrix depend in some manner on the distribution vector \mathbf{x} or some of its components. Density dependent effects in survival, fertility and growth rates, the basic ingredients in the matrix \mathbf{A} , have long been recognized as important in population dynamics and ecology. Their incorporation into the matrix model (1) result, under the assumption that \mathbf{A} is otherwise independent of time i , in a nonlinear matrix difference equation

$$(2) \quad \mathbf{x}(i+1) = \mathbf{A}(\mathbf{x}(i))\mathbf{x}(i), \quad i \in J_+, \quad \mathbf{x}(0) \geq 0.$$

Clearly the density vector $\mathbf{x}(i)$ is uniquely determined for all times $i \geq 1$ by (2) once an initial vector $\mathbf{x}(0) \geq 0$ is given.

The linear theory of nonnegative matrices, based primarily on the Perron-Frobenius theorem, describes the long time asymptotic behavior of solutions of the linear matrix equation (1) (under certain technical assumptions on the projection matrix \mathbf{A} which rarely interfere with biological applications); see Section 3. This paper will be concerned, on

the other hand, with the asymptotic behavior of solutions of the non-linear matrix equation (2).

3. Linear Matrix Equations. The solution of the linear equation (1) is given by $\mathbf{x}(i) = \mathbf{A}^i \mathbf{x}(0)$ and hence the long time behavior of solutions is determined by the eigenvalues λ_j of \mathbf{A} , of which there are of course $m + 1$, counting complex eigenvalues and multiplicities. This is most easily seen in the case that there is a basis of eigenvector \mathbf{e}_j (i.e. \mathbf{A} is diagonalizable). Expand the initial distribution, which we assume is nonnegative and not zero, in terms of these eigenvectors and write $\mathbf{x}(0) = \sum_j c_j \mathbf{e}_j$ for some scalar coefficients c_j . Then the solution of (1) can be written

$$(3) \quad \mathbf{x}(i) = \sum_{j=0}^m \lambda_j^i c_j \mathbf{e}_j.$$

Thus if all eigenvalues of \mathbf{A} are less than one in modulus then all solutions of (1) tend exponentially to 0 as $i \rightarrow +\infty$, while if \mathbf{A} has at least one eigenvalue of modulus greater than one then not all solutions will tend to 0 and at least one solution will exponentially increase without bound as $i \rightarrow +\infty$. In the former case the zero distribution vector is called *stable* (globally asymptotically stable) and in the latter case *unstable*. This also holds when \mathbf{A} is not diagonalizable.

Clearly the eigenvalue of \mathbf{A} of largest modulus is of interest. Since \mathbf{A} is nonnegative, it is known that it has a nonnegative (real) eigenvalue $\lambda_0 \geq 0$, to which there corresponds a nonnegative eigenvector $\mathbf{e}_0 \geq 0$, such that the moduli of all other eigenvalues do not exceed λ_0 [cf. Gantmacher [1959], Theorem 3, page 66]. Perron's famous theorem places strict inequalities in the preceding statement; namely if \mathbf{A} is positive then it has a positive (algebraically simple) eigenvalue $\lambda_0 > 0$, to which there corresponds a positive eigenvector, such that λ_0 strictly exceeds the moduli of all other eigenvalues of \mathbf{A} . In applications to population dynamics, however, \mathbf{A} usually has some zero entries. Consequently the generalization of Perron's theorem due to Frobenius is relevant. Frobenius' theorem replaces the positivity of \mathbf{A} in Perron's theorem with the nonnegativity and irreducibility of \mathbf{A} .

A matrix $\mathbf{A} = (a_{jk})$ is *reducible* if the index set $I = \{0, \dots, m\}$ can be partitioned into two nonempty, disjoint subsets $I_1 = \{i_1, \dots, i_\alpha\}$ and

$I_2 = \{i_1, \dots, i_\beta\}$, $I = I_1 \cup I_2$, such that $a_{jk} = 0$ for all $j \in I_1, k \in I_2$. In other words a permutation of \mathbf{A} can be performed (i.e., a permutation of rows together with the same permutation of columns) which places \mathbf{A} in the block form

$$(4) \quad \mathbf{A} = \begin{pmatrix} \mathbf{B} & \mathbf{0} \\ \mathbf{C} & \mathbf{D} \end{pmatrix}, \quad \mathbf{B} = \alpha \times \alpha, \quad \mathbf{C} = \beta \times \alpha, \quad \mathbf{D} = \beta \times \beta.$$

Such a permutation corresponds in the models above to a re-ordering of the classes. From this form of a reducible matrix \mathbf{A} it can be seen that its reducibility means that there exists a subset of classes (those with subscripts from I_1 , or after the permutation the first α classes) which are unreachable from the remaining classes, either by transitions or by births.

Frobenius' theorem states that if \mathbf{A} is nonnegative and irreducible then it has a positive, algebraically simple eigenvalue $\lambda_0 > 0$, to which there corresponds a positive eigenvector $\mathbf{e}_0 > 0$, and the moduli of all other eigenvalues of \mathbf{A} do not exceed λ_0 . Moreover no other eigenvector of any other eigenvalue is nonnegative (Gantmacher [1959]).

Also relevant to the asymptotic dynamics of the linear equation (1) is the notion of primitivity. A nonnegative, reducible matrix \mathbf{A} is called *primitive* if no other eigenvalue has modulus equal to λ_0 . This condition will be used below in the study of the stability of bifurcating equilibria for the nonlinear equation (2). A test for primitivity of \mathbf{A} can be based upon the exponents n_j of the nonzero terms in its monic, $(m+1)^{\text{st}}$ order characteristic polynomial. Suppose the exponents n_j ($j = 1, \dots, \nu$) are arranged in decreasing order. \mathbf{A} is primitive if (and only if) the greatest common divisor of the differences $m+1 - n_1, n_1 - n_2, n_2 - n_3, \dots, n_{\nu-1} - n_\nu$ is one.

Primitivity is also of fundamental importance in the linear theory with regard to *ergodicity*. If \mathbf{A} is nonnegative and irreducible and if the initial class distribution vector $\mathbf{x}(0)$ is nonnegative and nonzero, then the leading coefficient in the eigenvector expansion (3) is positive, $c_0 = \mathbf{x}(0) \cdot \mathbf{e}_0 > 0$. It is not difficult to see from the expansion (3) that if \mathbf{A} is also primitive then the *normalized class distribution* $\mathbf{x}(i)/p(i)$, where $p(i) = \mathbf{1} \cdot \mathbf{x}(i)$ is the *total population size*, tends as time $i \rightarrow +\infty$ to the so-called *stable class distribution*

$$\mathbf{x}(i)/p(i) \rightarrow \mathbf{e}_0/\mathbf{1} \cdot \mathbf{e}_0 \text{ as } i \rightarrow \infty.$$

For the special case of Leslie matrices \mathbf{A} , i.e., for the age structured case, this result is known as the *fundamental theorem of demography*. Note that this holds regardless of whether the total population size decreases or increases exponentially.

4. Linear Class Structured Models. Consider the linear equation (1) under the assumption that $\mathbf{A} = \mathbf{F} + \mathbf{T}$ where the $(m+1) \times (m+1)$ matrices $\mathbf{T} = (t_{jk})$ and $\mathbf{F} = (f_{jk})$ satisfy

$$0 \leq t_{jk} < 1, \sum_{j=0}^{m+1} t_{jk} < 1$$

$$f_{jk} = 0 \text{ if } j \geq 1 \text{ and } f_{0k} \geq 0, \sum_{k=0}^{m+1} f_{0k} \neq 0.$$

The entries in the transition matrix \mathbf{T} are all probabilities and the column sum restraint means that there is always some loss (e.g., due to deaths) from each class in each unit of time so that survival is never one hundred percent.

The constraint on the fertility matrix $\mathbf{F} \geq 0$ means that all newborns are in the same class, namely class $k = 0$. Thus the only nonzero entries in \mathbf{F} lie in its first row, which is denoted by

$$\mathbf{f}_0^* = \text{first row of } \mathbf{F} = (f_{00}, \dots, f_{0m}) \geq (\neq 0).$$

It will also be assumed that the projection matrix $\mathbf{A} = \mathbf{F} + \mathbf{T}$ is irreducible.

The matrix of probabilities involving transitions between all class except the newborn class $k = 0$ will be important in the development below. This $m \times m$ matrix will be denoted by \mathbf{Q} ; that is

$$\mathbf{Q} = (t_{jk})_{j,k=1}^m.$$

Clearly \mathbf{Q} satisfies the same constraints as does \mathbf{T} , that is all entries lie in the interval $[0, 1]$ and the column sums are strictly less than one. Some needed facts about such matrices are contained in the following lemma.

LEMMA. Suppose that \mathbf{M} is a square matrix all of whose entries lie in the interval $[0, 1]$ and all of whose column sums are less than one. Then $\mathbf{I} - \mathbf{M}$ is nonsingular and all of the eigenvalues of \mathbf{M} are less than 1 in magnitude. Moreover $(\mathbf{I} - \mathbf{M})^{-1} \geq 0$ and

$$\det(\mathbf{I} - \mathbf{M})^{-1} > 0.$$

Notice that if all transition probabilities $t_{j0} = 0$ for $j \geq 1$ then \mathbf{A} would be reducible because no transitions from the 0-class to any other class would be possible; or, in other words, \mathbf{A} could then be placed in the form (4) by simply listing the newborn class last. Since this contradicts our assumption that \mathbf{A} is irreducible we see that

$$(t_{10}, \dots, t_{m0}) \geq 0 \text{ and } \neq 0.$$

The diagonal entries in $(\mathbf{I} - \mathbf{Q})^{-1} = \mathbf{I} + \mathbf{Q} + \mathbf{Q}^2 + \dots$ are all positive (in fact greater than or equal to one) and consequently

$$(e_1, \dots, e_m)^* = (\mathbf{I} - \mathbf{Q})^{-1}(t_{10}, \dots, t_{m0})^* > 0.$$

Let $\mathbf{e} = (1, e_1, \dots, e_m)^*$. Then $\mathbf{e} > 0$.

Consider now the existence of a nontrivial equilibrium solution $\mathbf{x}(i) = \mathbf{x} = (x_k)^* \neq 0$ of (1). The vector equation $\mathbf{x} = \mathbf{A}\mathbf{x}$ consists of $m + 1$ equations for the $m + 1$ unknowns x_k . Solving the last m of these equations for the last m unknowns $x_k, k = 1, \dots, m$, one obtains

$$(5) \quad (x_1, \dots, x_m) = (e_1, \dots, e_m)x_0.$$

With use of the notation

$$\mathbf{t}_0^* = \text{first row of } \mathbf{T} = (t_{00}, \dots, t_{0m}) \geq 0$$

this equation, when substituted into the first equation, results in the single scalar equation

$$x_0 = (\mathbf{f}_0 + \mathbf{t}_0)^* \mathbf{e} x_0$$

for the first component x_0 . In order to introduce an important biologically meaningful parameter into the analysis we rewrite this equation as

$$(6) \quad x_0 = r x_0$$

where

$$(7) \quad r = \frac{\mathbf{f}_0^* \mathbf{e}}{1 - \mathbf{t}_0^* \mathbf{e}}.$$

The expression $\mathbf{t}_0^* \mathbf{e}$ can be shown to be less than one (it is in fact the probability of a following a path from class 0 which returns to class 0 exactly once)

$$0 \leq \mathbf{t}_0^* \mathbf{e} < 1.$$

The expression r defined by (7) turns out to be the expected number of offspring per individual per lifetime, taking into account the possibility of rejuvenation (i.e., of all returns to class 0) and is accordingly called the *inherent net reproductive rate*. The term "inherent" is used because r is the reproductive rate of the population in the absence of density (nonlinear) effects.

From (5)-(7) it follows that (1) has a nontrivial equilibrium if and only if

$$(8) \quad r = 1$$

in which case all nontrivial equilibria are multiples of $\mathbf{e} > 0$. This has a clear biological meaning, namely that the inherent net reproductive rate r must equal one at equilibrium.

The asymptotic dynamics of any model depend, of course, on the parameter values in the model. One of the difficulties in population dynamical models is very often the annoyingly large number of model parameters. Explicit in the linear equation (1) are the numerous parameters t_{jk}, f_{0k} , to say nothing of implicit parameters which may make up these entries in the projection matrix \mathbf{A} in specific applications. The inherent net reproductive rate r is a single composite, biologically meaningful parameter which turns out to be crucial in describing the asymptotic dynamics of both linear and nonlinear model equations. It is this parameter upon which we will focus in the nonlinear theory below.

In order to introduce the inherent net reproductive rate r explicitly into the equation (1), the fertility matrix \mathbf{F} can be written $\mathbf{F} = r\mathbf{N}$ where $\mathbf{N} = (n_{jk})$ is a matrix normalized so that its first row $\mathbf{n}_0 = (n_{00}, \dots, n_{0m})$ satisfies the constraint

$$(9) \quad \frac{\mathbf{n}_0^* \mathbf{e}}{1 - \mathbf{t}_0^* \mathbf{e}} = 1.$$

In summary, we make the following assumption concerning the projection matrix in the linear matrix equation (1).

H1 : $\mathbf{A} = r\mathbf{N} + \mathbf{T}$ is irreducible for $r > 0$ where $\mathbf{N} \geq 0$ has nonzero entries only in its first row \mathbf{n}_0 which satisfies the normalization (9) and where $\mathbf{T} = (t_{jk}) \neq 0$ with $t_{jk} \in [0, 1]$ has column sums strictly less than one.

Consider the linear matrix equation

$$(10) \quad \mathbf{x}(i + 1) = (r\mathbf{N} + \mathbf{T})\mathbf{x}(i), i \in J_+, \mathbf{x}(0) \geq 0.$$

We are interested in the maximal positive eigenvalue λ_0 of the projection matrix $r\mathbf{N} + \mathbf{T}$ as a function of the inherent net reproductive rate r . Let $p(\lambda, r) = \det(\lambda\mathbf{I} - r\mathbf{N} - \mathbf{T})$. The eigenvalue $\lambda_0 = \lambda_0(r)$ is continuously differential (in fact analytic) in r and satisfies $\lambda_0(1) = 1$.

The first thing to observe is that by the Lemma all eigenvalues of \mathbf{T} are less than 1 in magnitude. As a result $\lambda_0(0) < 1$.

Secondly we note that since an eigenvector corresponding to the eigenvalue 1 is an equilibrium, it follows from manipulations above that $r = 1$ is the *only* value of r for which $\lambda_0 = 1$. It follows that the derivative $\lambda'_0(1) \geq 0$.

Finally we will argue that in fact $\lambda'_0(1) > 0$. Suppose to the contrary that $\lambda'_0(1) = 0$. A differentiation of $p(\lambda_0(r), r) = 0$ with respect to the r shows that $\partial_r p(1, 1) = 0$. On the other hand, $\partial_r p(\lambda, r) = \partial_r \det(\lambda\mathbf{I} - r\mathbf{N} - \mathbf{T})$ which yields

$$0 = \partial_r p(1, 1) = \begin{pmatrix} -n_{00} & -n_{01} & -n_{02} & \cdots & -n_{1m} \\ -p_{10} & 1 - p_{11} & -p_{12} & \cdots & -p_{1m} \\ \vdots & \vdots & \vdots & & \vdots \\ -p_{m0} & -p_{m1} & -p_{m2} & \cdots & 1 - p_{mm} \end{pmatrix}.$$

An expansion of this determinant by minors across the first row in turn yields

$$0 = -\det(\mathbf{I} - \mathbf{Q})\mathbf{n}_0^* \mathbf{e},$$

and hence to a contradiction to the Lemma, namely that $\det(\mathbf{I} - \mathbf{Q}) \neq 0$.

These facts together imply that $\lambda_0(r) < 1$ for $r < 1$ and $\lambda_0(r) > 1$ for $r > 1$. We have proved the following result.

THEOREM 1. *Assume hypothesis H1 holds. There exists a nontrivial equilibrium solution of the linear equation (10) if and only if $r = 1$ in which case all equilibria are scalar multiples of the positive equilibrium e . Moreover, if $r < 1$ then all solutions of (10) tend to the zero vector, while if $r > 1$ then all positive solutions are unbounded as $i \rightarrow +\infty$.*

This general mathematical result has an extremely simple biological meaning. If the inherent net reproductive rate is less than one the population will die out, while if the inherent net reproductive rate is greater than one then the population will grow without bound. Only at the point of exact replacement when the inherent net reproductive rate is one will there exist an equilibrium population level. This is graphically illustrated in Figure 1a in which a vector norm $|x|$ of the equilibria are plotted against r .

5. Equilibria and Nonlinear Matrix Models. The main result of this section (Theorem 2) can be readily understood graphically with reference to Figure 1. The result states that, under only the mildest of smoothness conditions on the nonlinearities, there exists a graph of nontrivial equilibria of the *nonlinear* system (2) as a function of the inherent net reproductive rate r which has the same basic topological properties as that for the *linear* system (10), namely the graph of pairs (r, x) bifurcates from the trivial equilibrium $x = 0$ at the critical value $r = 1$ and extends globally as a continuum in $R \times R^{m+1}$ Euclidean space.

From this point of view the linear theory is a highly special case which results in a "vertical" bifurcation or a "point spectrum." On the other hand, the nonlinear system has in general a continuous "spectrum" of r values corresponding to positive equilibria.

In specific applications the bifurcation diagram may not be as simple as appears in Figure 1b. While it follows from the bifurcation theoretical methods below that the graph never intersects the r -axis at any point other than $(r, x) = (1, 0)$, the graph can have other branches and loops. There can also exist nontrivial equilibria which do not lie on the bifurcating branch.

Nonetheless, it is a fact that for any nonlinear matrix model of the form (2) one can be assured of the existence of a global, bifurcating branch of nontrivial equilibria as pictured in Figure 1b and as is

described in Theorem 2 below.

To see the precise mathematical result, assume that the projection matrix $\mathbf{A} = \mathbf{A}(\mathbf{x})$ depends on the class distribution vector \mathbf{x} in the following general way.

H2: Assume the projection matrix has the form $\mathbf{A}(\mathbf{x}) = r\mathbf{N}(\mathbf{x}) + \mathbf{T}(\mathbf{x})$ where $r > 0$ is a positive real. Assume that the only nonzero entries in the normalized fertility matrix \mathbf{N} appear in the first row $\mathbf{n}_0^*(\mathbf{x}) = (n_{00}(\mathbf{x}), \dots, n_{0m}(\mathbf{x}))$ where each $n_{0j} : R^{m+1} \rightarrow [0, +\infty)$ is continuously differentiable. Assume that the entries $t_{jk} : R^{m+1} \rightarrow [0, 1)$ in the transition matrix \mathbf{T} are also continuously differentiable. Finally assume that $\mathbf{A} = \mathbf{A}(\mathbf{0})$, $\mathbf{N} = \mathbf{N}(\mathbf{0})$, $\mathbf{T} = \mathbf{T}(\mathbf{0})$ satisfy H1 and that $\mathbf{N} = \mathbf{N}(\mathbf{0})$ satisfies the normalization (9).

Under H2 the projection matrix has the same form as in the linear theory of Section 3 (in particular newborns all lie in class $k = 0$), but now we allow any or all entries to depend on class densities in the distribution vector \mathbf{x} . This density dependence is completely general and requires only that mild smoothness condition of continuous differentiability. If \mathbf{x} is set to $\mathbf{0}$ in the projection matrix \mathbf{A} of (2), then the linear theory of Section 3 is obtained. The constant r thus represents the *inherent net reproductive rate* of the population in the sense that r is the net reproductive rate at zero (or "at low") density levels.

The equilibrium matrix equation associated with the nonlinear equation (2) under H2, i.e., with the equation

$$(11) \quad \mathbf{x}(i + 1) = [r\mathbf{N}(\mathbf{x}(i)) + \mathbf{T}(\mathbf{x}(i))]\mathbf{x}(i), \quad i \in J_+, \quad \mathbf{x}(0) \geq 0$$

is

$$(12) \quad \mathbf{x} = [r\mathbf{N}(\mathbf{x}) + \mathbf{T}(\mathbf{x})]\mathbf{x}.$$

This equation, which consists of $m + 1$ equations in $m + 1$ unknowns, can be rewritten in an equivalent form using the same manipulations as were used to obtain (5)-(6) in the linear theory of Section 4. This results in the equilibrium equations

$$\begin{aligned} x_0 &= [r\mathbf{n}_0(\mathbf{x}) + \mathbf{t}_0(\mathbf{x})]^* \mathbf{e}(\mathbf{x})x_0 \\ (x_1, \dots, x_m) &= (e_1(\mathbf{x}), \dots, e_m(\mathbf{x}))x_0 \end{aligned}$$

where

$$\begin{aligned} \mathbf{e}(\mathbf{x}) &= (1, e_1(\mathbf{x}), \dots, e_m(\mathbf{x}))^*, \\ (e_1(\mathbf{x}), \dots, e_m(\mathbf{x}))^* &= (\mathbf{I} - \mathbf{Q}(\mathbf{x}))^{-1}(t_{10}(\mathbf{x}), \dots, t_{m0}(\mathbf{x}))^*. \end{aligned}$$

The former of these two equilibrium equations can be rewritten as

$$x_0 = rn(\mathbf{x})x_0$$

with

$$n(x) = \frac{\mathbf{n}(\mathbf{x})^* \mathbf{e}(\mathbf{x})}{1 - \mathbf{t}_0(\mathbf{x})^* \mathbf{e}(\mathbf{x})}.$$

By H2 and the normalization (9)

$$n(\mathbf{0}) = 1.$$

Finally the equilibrium equations reduce to

$$(13) \quad x_0 = rn(\mathbf{x})x_0$$

$$(14) \quad (x_1, \dots, x_m) = (e_1(\mathbf{x}), \dots, e_m(\mathbf{x}))x_0.$$

Note that the linear eigenvector in the linear theory of Section 3 with $\mathbf{A} = \mathbf{A}(\mathbf{0}) = r\mathbf{N}(\mathbf{0}) + \mathbf{T}(\mathbf{0})$ and $r = 1$ is $\mathbf{e}_0 = \mathbf{e} = \mathbf{e}(\mathbf{0})$ by H2.

For all values of r the equilibrium equations (13)-(14) have the trivial solution $\mathbf{x} = \mathbf{0}$. The question is: for what values of the parameter r do these equations have a positive solution $\mathbf{x} > 0$? In the linear case we saw that the answer was: only for $r = 1$. An answer (but not necessarily the complete answer) in the nonlinear case can be obtained from an application of global results from bifurcation theory. The following theorem is proved in the Appendix.

THEOREM 2. *Under the assumptions in H2 the nonlinear matrix equation (11) has a continuum $\mathcal{C} \subset R \times R^{m+1}$ of equilibrium pairs (r, \mathbf{x}) with the following properties:*

- (a) \mathcal{C} is unbounded in $R \times R^{m+1}$;
- (b) $(1, \mathbf{0}) \in \mathcal{C}$
- (c) $(1, \mathbf{0}) \neq (r, \mathbf{x}) \in \mathcal{C} \Rightarrow r > 0$ and $\mathbf{x} > 0$.

The unbounded continuum of equilibria \mathcal{C} is said to bifurcate from the critical point $(r, \mathbf{x}) = (1, \mathbf{0})$ since it is at this point that it intersects the set of trivial equilibria $(r, \mathbf{x}) = (r, \mathbf{0})$.

Any nontrivial equilibrium, whether on the bifurcating branch \mathcal{C} or not, must have a nonzero first component $x_0 \neq 0$ since (14) implies that $\mathbf{x} = \mathbf{0}$ if $x_0 = 0$. Thus, by (13), any nontrivial equilibrium (and hence any positive equilibrium from \mathcal{C}) must satisfy

$$(15) \quad 1 = rn(\mathbf{x}).$$

The right hand side of this identity is the *net reproductive rate at equilibrium* \mathbf{x} (not to be confused with r , the *inherent* net reproductive rate at low, technically zero, density). This identity expresses the expected result that in a population at equilibrium each individual exactly replaces itself by reproduction. The expression n will be referred to as the *normalized density factor*.

Graphically the result of Theorem 2 is represented in Figure 1b. This so-called bifurcation diagram and particular properties of the graph can often be obtained by methods of analytic geometry from the scalar equation (15). Properties of the graph which are of interest include the "spectrum" of r values corresponding to positive equilibria (the projection of the graph onto the r -axis), the "direction of bifurcation" (i.e., the left or right bend in the graph near the point of bifurcation $(r, \mathbf{x}) = (1, \mathbf{0})$), folds in the graph which give rise to multiple equilibrium states for a given r value, boundedness or unboundedness of the graph in the \mathbf{x} component, etc.

One particularly important and simple case is when density dependence in the model equations is through a dependency on total population size $p(i)$, or more generally on a *weighted population size*

$$(16) \quad w(i) = \mathbf{w}^* \mathbf{x}(i), \mathbf{w} \geq 0, \mathbf{w} \neq \mathbf{0}.$$

That is, $\mathbf{N} = \mathbf{N}(w)$, $\mathbf{T} = \mathbf{T}(w)$ so that $n = n(w)$.

Then (15) becomes the scalar equation

$$(17) \quad 1 = rn(w)$$

which determines a relation between r and w whose graph in the r, w -plane describes the equilibria and the global bifurcating branch in Theorem 2. Examples can be found in Section 8.

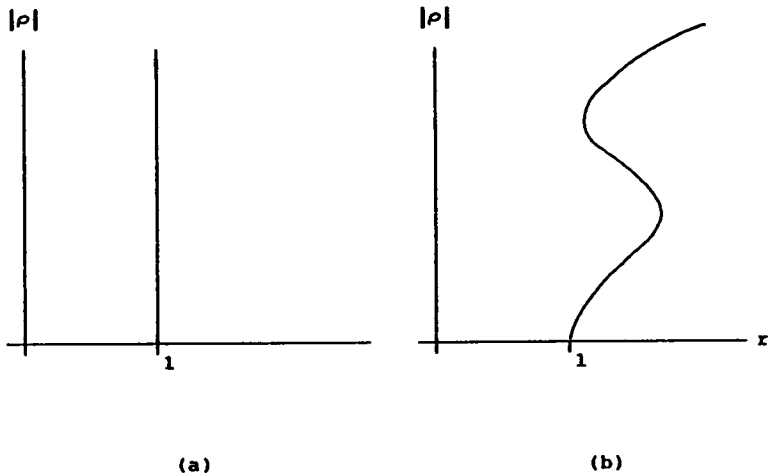


Figure 1. A plot of the norms of positive equilibria \mathbf{x} against the corresponding value r of the inherent net reproductive rate for the linear equation (10) yields the vertical diagram in (a) with the resulting "point spectrum" at $r = 1$. In graph (b) for the nonlinear equation (11) the global continuum of positive equilibria which bifurcates from the trivial $\mathbf{x} = 0$ equilibrium at the critical value of $r = 1$ is not in general vertical and as a result has a "continuous spectrum".

While the graph of the branch of equilibria in Figure 1b can have a complicated global geometry, near the bifurcation point $(1, 0)$ the nature of the branch can readily be studied by simple analytical methods. The classical method for doing this (called the Lyapunov-Schmidt or regular perturbation method) is to parameterize the branch of nontrivial equilibria (r, \mathbf{x}) by means of an auxiliary small parameter ϵ and to compute ϵ expansions, or at least the lower order terms of ϵ expansions, of the equilibria (see Vainberg and Trenogin [1962]). Under the smoothness assumptions in H2 such Taylor expansions have the

form

$$\begin{aligned} r &= r(\varepsilon) = 1 + r'(0)\varepsilon + 0(\varepsilon^2) \\ \mathbf{x} &= \mathbf{x}(\varepsilon) = \mathbf{x}_1\varepsilon + \mathbf{x}_2\varepsilon^2 + 0(\varepsilon^3). \end{aligned}$$

Coefficients $r'(0)$, \mathbf{x}_1 in these expansions can be found in a routine way by substituting the expansions into (11) and equating the resulting coefficients of the first and second powers of ε . The first order terms lead to the linearized equation (10) for \mathbf{x}_1 with $r = 1$ and hence $\mathbf{x}_1 = \mathbf{e}$. The second order terms in ε lead to a nonhomogeneous version of (10) for \mathbf{x}_2 whose nonhomogeneous term must, by the Fredholm alternative, be orthogonal to the null space of the adjoint equation. This "orthogonality condition" imposes a constraint in the form of an equation for the coefficient $r'(0)$. With this determination of $r'(0)$ the equation for \mathbf{x}_2 is solvable (uniquely in the space orthogonal to \mathbf{e}).

In view of the alternative formulation of the equilibrium equations given by (13) and (15) it is easier to proceed slightly differently. We choose x_0 as the branch expansion parameter ε and treat equations (13) and (15) as $m + 1$ equations to be solved for the $m + 1$ unknowns r, x_1, \dots, x_m in terms of the remaining component x_0 . A solution can be obtained by solving (14) for x_1, \dots, x_m by the implicit function theorem, which yields local solutions (i.e., solutions for small x_0) which are as smooth as the terms in (14) and (15) are as functions of their arguments. These solutions can then be substituted into (15) and the result solved for $r = 1/n(x_0, x_1(x_0), \dots, x_m(x_0))$. This leads to the formulas

$$(18) \quad \begin{aligned} r &= 1 - \nabla n(\mathbf{0})^* \mathbf{e}x_0 + 0(x_0^2) \\ \mathbf{x} &= \mathbf{e}x_0 + \mathbf{J}(\mathbf{0})\mathbf{e}x_0^2 + 0(x_0^3) \end{aligned}$$

where

$\mathbf{J}(\mathbf{x}) =$ the Jacobian matrix of $\mathbf{e}(\mathbf{x})$ with respect to \mathbf{x}

$\nabla n(\mathbf{x}) =$ the gradient of $n(\mathbf{x})$ with respect to \mathbf{x} .

These expansions can be used to study the effects, to lowest order, that the nonlinearities have on both the equilibrium class distribution vector and the corresponding inherent net reproductive rate.

For example, consider the normalized class distribution \mathbf{x}/p at equilibrium. From (18) it follows, ignoring terms of order two or higher in

x_0 , that

$$x/p \approx \left[\mathbf{I} + \frac{(\mathbf{1}^* \mathbf{e} \mathbf{J}(\mathbf{0}) - \mathbf{1}^* \mathbf{J}(\mathbf{0}) \mathbf{e} \mathbf{I})}{\mathbf{1}^* \mathbf{e}} x_0 \right] \mathbf{e} / \mathbf{1}^* \mathbf{e}$$

where $x_0 \approx (1-r)/\nabla n(\mathbf{0})^* \mathbf{e}$. This shows the effect of the nonlinearities on the normalized class distribution at equilibrium for a population whose inherent net reproductive rate r is not greatly different from the replacement value $r = 1$. In this formula the nonlinear normalized class distribution is a perturbation of the linear "stable class distribution" $\mathbf{e}/\mathbf{1}^* \mathbf{e}$, the perturbation being determined by the Jacobian $\mathbf{J}(\mathbf{x})$.

The first order term in the expansion of r in (18) determines the "direction of bifurcation"; i.e., whether small magnitude equilibria exist for $r > 1$ (*supercritical bifurcation* or bifurcation to the right) or for $r < 1$ (*subcritical bifurcation* or bifurcation to the left):

$$(19) \quad \begin{aligned} \nabla n(\mathbf{0})^* \mathbf{e} < 0 &\Rightarrow \text{supercritical bifurcation} \\ \nabla n^*(\mathbf{0})^* \mathbf{e} > 0 &\Rightarrow \text{subcritical bifurcation.} \end{aligned}$$

See the bifurcation diagrams in Figure 2.

The first implication says roughly that if the effects of increased (low level) density are detrimental in the sense that they result in a smaller net reproductive rate at equilibrium, then the bifurcation is supercritical and results in the existence of positive equilibria (which, as will be seen in the next Section 6, turn out to be stable), at least for inherent net reproductive rates r slightly greater than one. See Figure 2. This is by far the most frequently occurring case in nonlinear models found in the literature. It generally occurs under common modeling assumptions that survival rates decrease (i.e., death rates increase) and fertility rates decrease with increases in population density.

If on the other hand increases in low level population densities act to increase the net reproductive rate (specifically the normalized density factor n), then the bifurcation is subcritical (and, as it turns out, unstable; see Figure 2b). Such can be the case in the presence of a so-called "Allee effect" (Allee [1931]) under which survivability and/or fertility is enhanced by density increases (Cushing [1988]). Another possible cause of subcritical bifurcation which seems not to have been previously recognized is the presence of certain types of nonlinearities in the transition probabilities contained in the Matrix \mathbf{T} . An example in Section 8 will illustrate this point.

In the important special case when density dependence is through a density on a weighted total population size (16) then $n = n(w)$ and $\nabla n(0)^*e = n'(0)w^*e$. Since $w^*e > 0$ the criteria (19) for the direction of bifurcation reduce to

$$(20) \quad \begin{aligned} n'(0) < 0 &\Rightarrow \text{supercritical bifurcation} \\ n'(0) > 0 &\Rightarrow \text{subcritical bifurcation.} \end{aligned}$$

6. Stability of Equilibria. As with ordinary differential equations, there are two fundamental methods for determining the stability of an equilibrium solution of a nonlinear matrix equation: a linearized stability analysis and methods based upon Lyapunov functions. In a linearized stability analysis the model equations are linearized at the equilibrium point and the eigenvalues of the resulting projection matrix are investigated. As described in the linear theory of Section 3, the linearized equation is stable if all eigenvalues of its projection matrix are less than one in magnitude while it is unstable if at least one eigenvalue has magnitude larger than one. Fundamental stability theorems show that the equilibrium of the original nonlinear equation is also correspondingly (locally) stable or unstable.

The theory of Lyapunov functions for difference equations is well developed (LaSalle [1976]) and they have been used to investigate some nonlinear matrix equation models (e.g., see Desharnais and Cohen [1986] and Fisher and Goh [1984]). Their use has not been extensive, however, a fact which undoubtedly reflects the usual difficulty of constructing Lyapunov functions even for relatively simple models.

Whereas one can obtain very general results concerning the existence of equilibria for quite general nonlinear matrix equations (Section 5) it is more difficult to obtain stability results of wide generality for positive equilibria. Stability depends considerably on the specifics of particular model equations, the nature of the nonlinearities and the model parameter values.

Nonetheless, it turns out one can say a great deal about the linearized stability of two types of equilibria in a completely general setting. These are the trivial equilibria $(r, \mathbf{x}) = (r, \mathbf{0})$ and the small magnitude positive equilibria on the bifurcating continuum \mathcal{C} of positive equilibria in a neighborhood of the bifurcation point $(1, \mathbf{0})$.

The linearization of (11) at a trivial equilibrium $(1, \mathbf{0})$ yields the linear equation (10) with $\mathbf{N} = \mathbf{N}(\mathbf{0})$ and $\mathbf{T} = \mathbf{T}(\mathbf{0})$ and consequently by

Theorem 1 we find that $(r, \mathbf{0})$ is stable if and only if $r < 1$. Thus we see that the trivial equilibrium $\mathbf{x} = \mathbf{0}$ of the nonlinear equation (11) (just as with the linear equation (10)) loses stability as the inherent net reproductive rate r is increased through the critical value $r = 1$.

The Lyapunov-Schmidt expansions (18) for the nontrivial equilibria along \mathcal{C} can be used to investigate the stability of the positive bifurcating equilibria near $(1, \mathbf{0})$, i.e., for $x_0 > 0$ small. First the linearization of (11) is computed at an equilibrium. This results in a linear matrix equation whose projection matrix depends upon the equilibrium at which the linearization is computed and hence, for equilibrium from the branch \mathcal{C} near the bifurcation point, depends upon the branch parameter x_0 used in the expansions (18). The stability determining eigenvalues of this matrix are consequently functions of x_0 . At criticality, when $x_0 = 0$ this linearized projection matrix reduces to $\mathbf{N}(\mathbf{0}) + \mathbf{T}(\mathbf{0})$ which has a maximal eigenvalue equal to one. The eigenvalues of the linearized projection matrix are smooth functions of x_0 and hence have expansions in x_0 which can be used to study their location. The eigenvalue of obvious interest, which we will denote by $\lambda = \lambda(x_0)$, is that which at $x_0 = 0$ is equal to one.

If it is assumed, in addition to the irreducibility assumption in H1, that $r\mathbf{N}(\mathbf{0}) + \mathbf{T}(\mathbf{0})$ is primitive at criticality $r = 1$ so that not only does this projection matrix have a maximal eigenvalue of one but all other eigenvalues have modulus strictly less than one, then for small x_0 all eigenvalues, except possibly $\lambda(x_0)$, have modulus strictly less than one. As a result for small x_0 the stability of the bifurcating positive equilibria (18) is determined by $\lambda = \lambda(x_0)$, more specifically by whether $\lambda(x_0)$ is less than or greater than one for small positive x_0 .

This stability criterion can be determined from the sign of $\lambda'(0)$ which in turn can be determined by another application of the regular perturbation method of substituting expansions

$$\lambda = \lambda(x_0) = 1 + \lambda'(0)x_0 + 0(x_0^2) \text{ and } \mathbf{v} = \mathbf{v}(x_0) = \mathbf{v}_0 + 0(x_0)$$

for the linearized eigenvalue and eigenvector into both sides of the linearized equations and equating the resulting coefficients of like powers of x_0 . The lowest order terms yield the eigenvalue problem for the linearization which, because $\lambda(0) = 1$ is an eigenvalue, implies $\mathbf{v}_0 = \mathbf{e}$. The first order terms lead to a corresponding nonhomogeneous system whose solution requires an orthogonality condition which determines

the coefficient $\lambda'(0)$. The tedious details of this procedure lead to a formula for $\lambda'(0)$ which shows that it is a negative constant multiple of $r'(0) = \nabla n(\mathbf{0})^* \mathbf{e}$, the very term which as we have seen determines the direction of bifurcation. Thus we have the following result.

THEOREM 3. *Under hypothesis H2 the trivial equilibrium $\mathbf{x} = 0$ of (11) is (locally) stable if $r < 1$ and unstable if $r > 1$. Under the additional assumption that the projection matrix $r\mathbf{N}(\mathbf{x}) + \mathbf{T}(\mathbf{x})$ is primitive at the critical point $(r, \mathbf{x}) = (1, \mathbf{0})$, the small amplitude positive equilibria from the bifurcating branch \mathcal{C} near the critical point are stable if the bifurcation is supercritical and unstable if the bifurcation is subcritical.*

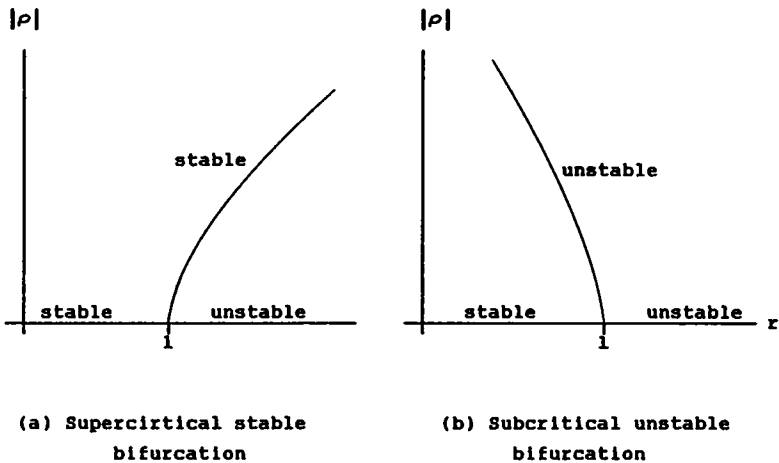


Figure 2. The trivial equilibrium $\mathbf{x} = 0$ loses its stability as the inherent net reproductive rate r increases through one. Locally near the bifurcation point $(r, \mathbf{x}) = (1, \mathbf{0})$ the stability of the positive equilibria on the bifurcation branch depends upon the direction of bifurcation.

7. Global Properties of the Equilibrium Branch. Although there is always an exchange of stability in the supercritical bifurcation case for the general nonlinear matrix equation (11) as the inherent net reproductive rate r is increased through the critical value $r = 1$, the resulting stability along the bifurcating branch of positive equilibria may not persist globally. As is widely known, particularly for the simple scalar ($m = 0$) case for an unstructured population, stability along the positive branch can be lost with further increases of r . Bifurcations to limit cycles can occur and with even further increases in r repeated bifurcations to period doubled cycles can result. More complicated global dynamics involving features of much current interest such as "chaos" and "strange attractors" can occur for larger values of r , although the relevance of such exotic model dynamics to population dynamics is still a subject of debate and research. Hassell et al. [1976] suggest that values of r are rarely large enough in natural or laboratory populations to imply chaotic dynamics. Others have challenged this conclusion, particularly for structured populations since higher order matrix models seem to have a greater propensity for instability (Guckenheimer et al. [1976]).

Similarly the instability of a subcritically bifurcating branch of equilibria may not persist and the branch equilibria may become stable at some point. As pointed out at the end of Section 6, the subcritical case arises from an Allee effect under which a reversal of the usual density effects occurs at low population densities. In general, however, one does not expect such reversed density effects on survivability and fertility to hold for high population densities. The usual effects of suppressed survivability and fertility with increased levels of high density imply that the components of $\nabla n(\mathbf{x})$ are negative and that the subcritically bifurcating branch in Figure 2 "turns around" (cf. (15)). This results in multiple equilibrium states for values of r less than one and one might conjecture that the "upper" branch consists of stable equilibria, although this need not always be the case (Cushing [1988]). See Figure 3.

Locally near the bifurcation point stability is determined by the effects that changes in population density have on the net reproductive rate as measured by the gradient $\nabla n(\mathbf{x})$ of the normalized density factor at $\mathbf{x} = \mathbf{0}$ (or, in the special case when density dependence is through a dependence on total population size w , by the derivative $n'(w)$ at $w = 0$). It is natural to inquire about the possibly more general

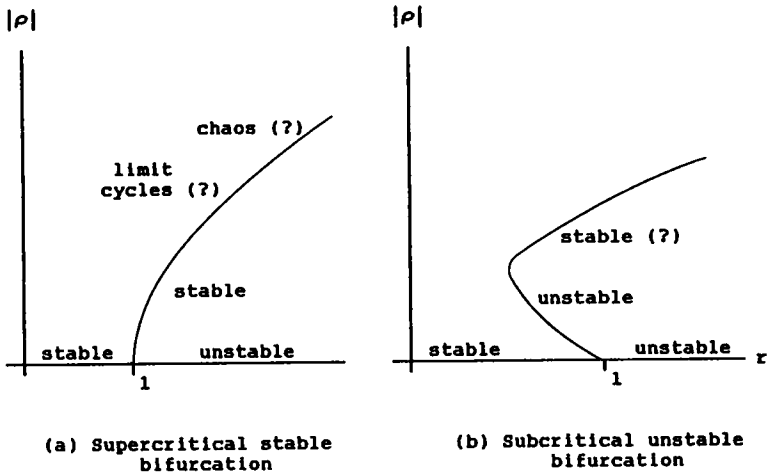


Figure 3. The stability properties possessed by the bifurcating branch of positive equilibria locally near the bifurcation point $(r, \mathbf{x}) = (1, \mathbf{0})$ may not persist globally. Changes in equilibrium stability, Hopf bifurcation to limit cycles, period doubling bifurcations and chaos can occur as r increases. In the subcritical case reasonable biological assumptions usually cause the branch to “turn around”, creating multiple positive equilibrium states and the possibility of hysteresis type phenomena.

relationship between these derivatives $\nabla n(\mathbf{x})$ or $n'(w)$ at a nontrivial equilibrium and the stability of that equilibrium. Simple examples show that the negativity of these derivatives cannot in general imply stability as it does locally near the bifurcation point according to (19) and (20) (indeed a supercritical stable bifurcating branch can lose stability, for example, by means of a Hopf bifurcation to a stable limit cycle). *An unproved conjecture is that negativity is necessary for stability, i.e., the positivity of $\nabla n(\mathbf{x})$ or $n'(w)$ at an equilibrium implies its instability.* This conjecture is based upon evidence from many examples as well as some results of Rorres [1979a,b] for some special continuous age

structure models with nonlinear fertility rates. Graphically, for the case $n = n(w)$, this means that decreasing portions of the bifurcation diagram correspond to unstable equilibria.

This conjecture can be proved for the special case of age structured populations, i.e., for nonlinear Leslie matrix equations, when the density dependence is through a weighted total population size $w(i)$ given by (16). Suppose (r, \mathbf{x}) is a positive equilibrium pair of (11) with corresponding weighted total population size $w > 0$ and suppose that the linearization of (11) at this equilibrium has projection matrix $\mathbf{B}(w)$. By a straightforward calculation of $\mathbf{B}(w)$ for the Leslie matrix case it can be shown by using appropriate fundamental row operations that

$$\det(\mathbf{I} - \mathbf{B}(w)) = -rn'(w)w.$$

If $n'(w) > 0$ then the characteristic polynomial $\det(\lambda\mathbf{I} - \mathbf{B}(w))$ is negative at $\lambda = 1$ and hence, because it is obviously positive for large $\lambda > 0$, must have a positive real root. Consequently $n'(w) > 0$ implies that the equilibrium is unstable.

Although $\nabla n(\mathbf{x}) < 0$ does not in general imply stability an interesting question is: what additional conditions will insure stability? Some clues might be provided by Rorres' results for the continuous age structure case.

Another intriguing question concerns the possibility of a connection between the density dependent net reproductive rate at equilibrium $rn(\mathbf{x})$ and Lyapunov functions. This is suggested by the idea that when $\nabla n(\mathbf{x}) < 0$ holds $rn(\mathbf{x})$ acts as a kind of "restoring force" in that an increase (decrease) in density above (below) equilibrium level decreases (increases) the net reproductive rate which in turn forces population densities back down (up) to equilibrium levels. If Lyapunov functions could be constructed from this expression for the density dependent net reproductive rate, and this has not been done to date, then one would not only have available a powerful analytical tool for global dynamics but one would have, unlike with the few *ad hoc* applications of Lyapunov function theory which have been made in the literature, a biological motivated and meaningful Lyapunov or "energy" functional.

Thus there remain many unsolved and interesting questions concerning the global dynamics of nonlinear matrix models of the sort being considered here. There is, however, one special but rather general (and historically important) case for which global results are available. This

is a case originally introduced by Leslie [1948] for an age structured population in which the nonlinearities arising because of density dependence are of a special type.

Specifically Leslie considered the case when fertility is density independent and only survivability is density dependent, but is density dependent in such a way that all age classes are equally affected. That is to say the survival probabilities p_k and s_{jk} are all multiples of a common scalar density dependent factor $h = h(\mathbf{x}), h : R^{m+1} \rightarrow (0, 1], h(0) = 1$. In this case the nonlinear model (12) takes the form

$$(21) \quad \begin{aligned} \mathbf{x}(i + 1) &= h(\mathbf{x})\mathbf{A}\mathbf{x}(i), i \in J_+, \mathbf{x}(0) \geq 0 \\ \mathbf{A} &= r\mathbf{N} + \mathbf{T} \end{aligned}$$

where the nonnegative matrices \mathbf{N} and \mathbf{T} are constant and satisfy the conditions in H1 in the linear theory of Section 3.

Let $\mathbf{y}(i) = \mathbf{x}(i)/p(i)$. It is easy to see that $p(i)$ satisfies the difference equation

$$(22) \quad p(i + 1) = 1^* \mathbf{A} \mathbf{y}(i) h(p(i) \mathbf{y}(i)) p(i).$$

A division of both sides of (21) by $p(i)$ shows that $\mathbf{y}(i)$ satisfies the equations

$$\begin{aligned} \mathbf{y}(i + 1) &= \mathbf{A} \mathbf{y}(i + 1) / 1^* \mathbf{y}(i + 1), 1^* \mathbf{y}(i) = 1 \text{ for } i \in J_+ \\ \mathbf{y}(0) &= \mathbf{x}(0) / p(0) \end{aligned}$$

which can without much difficulty be shown to have as their unique solution $\mathbf{y}(i) = \mathbf{z}(i) / 1^* \mathbf{z}(i)$ where $\mathbf{z}(i)$ solves the *linear* equation (1) with $\mathbf{z}(0) = \mathbf{x}(0)$. Thus by the strong ergodic result for (1) described at the end of Section 3 we find that for the *nonlinear* equation (21) the ergodic property still holds

$$(23) \quad \frac{\mathbf{x}(i)}{p(i)} \rightarrow \frac{\mathbf{e}}{1^* \mathbf{e}} \text{ as } i \rightarrow \infty$$

regardless of the dynamics of the total population size $p(i)$ which are governed by the nonautonomous, scalar difference equation (22). Recall that $\mathbf{e} > 0$ is an eigenvector associated with the dominant eigenvalue $\lambda_0 > 0$ of $\mathbf{A} = r\mathbf{N} + \mathbf{T}$. Although this scalar difference equation for

$p(i)$ is nonautonomous, it is by (23) "asymptotically equivalent" to the limiting equation

$$(24) \quad q(i+1) = \lambda_0 h(q(i) \frac{e}{\mathbf{1}^* e}) q(i),$$

which is a type of scalar autonomous difference equation about whose dynamics so much has been learned in recent years.

The question naturally arises as to the relationship between the asymptotic dynamics of the equation (22), particularly the global dynamics of (22), and that of its limiting equation (24). One anticipates that an understanding of the dynamics of (24) will lead to an understanding of the dynamics of (22) and to a large extent this has been shown to be true (LaSalle [1976], Cushing [1987]), although it is obvious that the asymptotic state of a particular solution may not be predictable from the corresponding solution of (24) with the same initial state since large deviations between (22) and (24) can occur initially.

It can be shown that if the limiting equation has in any compact interval at most a finite number of equilibria, all of which are hyperbolic (i.e., their linearizations do not have an eigenvalue of magnitude one) and if it is known that all bounded solutions of the limiting equation tend asymptotically to an equilibrium, then every bounded solution of (22) tends to an equilibrium of the limiting equation. (A similar statement is true for k -cycles.)

It is not true in general, however, that a solution of (22) which approaches an equilibrium must tend to a *stable* equilibrium of (24). However, if *both* the initial total population size and the initial class distribution vector are sufficiently close to a stable equilibrium of the limit equation and to its corresponding class density equilibrium respectively, then the total population size will tend asymptotically to this stable equilibrium (Cushing [1987]). The same is true for k -cycles, $k \geq 2$.

It is also not necessarily true that if the total population size starts near a stable equilibrium of (24) that it will tend asymptotically to this equilibrium. This fact illustrates the important result that the total population size of a class structured population cannot be expected to tend to a stable equilibrium by starting close to that stable equilibrium unless the initial class distribution is also sufficiently close to the stable distribution. Thus a small disturbance in the class

distribution from equilibrium can alone (even without a disturbance in total population size from an equilibrium state) lead to instability. This illustrates one danger in relying on classical unstructured models for total population size for a description of the dynamics of a strongly structured population.

In any case, whatever the dynamics of total population size for a population governed by the matrix model equation (21) with Leslie-type nonlinearity, the strong ergodicity property (23) holds.

8. Examples. (a) *A size structured model with growth and survival density dependence.* Consider a population structured by some measurement of size into $m + 1 \geq 3$ ordered classes in such a way that all newborns are in the class 0 of smallest individuals. Assume that during one unit of time an individual in a class i either dies, remains in the same size class i or grows into the next larger size class $i + 1$. Thus no individual can regress to a smaller size class nor grow so fast as to advance two or more size classes in one unit of time. The transition matrix T is then an Usher-type matrix with nonzero entries possible only along the main diagonal and main subdiagonal:

$$(25) \quad T = \begin{pmatrix} t_{00} & 0 & \cdots & 0 & 0 \\ t_{10} & t_{11} & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & t_{m,m-1} & t_{mm} \end{pmatrix}, t_{jk} = p_k p_{jk}.$$

Assume that the probability of survival p_k over one unit of time of a class k individual is a decreasing function of a weighted total population size w which drops to zero as w increases without bound. Mathematically

$$0 \leq p_k(w) < 1, p'_k(w) \leq 0, p_k(+\infty) = 0, p_k(0) > 0.$$

Examples include (Leslie [1948])

$$p_k = \pi_k \frac{1}{1 + a_k w}, \quad 0 < \pi_k < 1, a_k > 0$$

and (Desharnais and Cohen [1986], Lui and Cohen [1987], Smouse and Weiss [1975])

$$p_k = \pi_k \exp(-a_k w), \quad 0 < \pi_k < 1, a_k > 0.$$

The conditional probability $p_{jj} = p_{jj}(w)$ that an individual in class j does *not* grow into the next larger size class $j + 1$ after one unit of time, given that it survives, will be assumed to be an increasing function of weighted population size w . Moreover this probability of “no-growth” will be very small when population levels are very small and it will be nearly equal to one when population levels are very large. Mathematically,

$$0 \leq p_{jj}(w) \leq 1, p'_{jj}(w) \geq 0, p_{jj}(0) = 0, p_{jj}(+\infty) = 1.$$

A simple example is given by the Michaelas-Menton (or Holling type II) form

$$p_{jj} = b_{jj}w / (1 + b_{jj}w), b_{jj} > 0.$$

These assumptions lead to a transition matrix (25) with

$$t_{jj} = t_{jj}(w) = p_j(w)p_{jj}(w)$$

$$t_{j,j-1} = t_{j,j-1}(w) = p_{j-1}(w)(1 - p_{j-1,j-1}(w)).$$

For simplicity in this example it will be assumed that fertility is density independent so that the fertility matrix F does not depend on w . Under these assumptions the projection matrix is

$$A(w) = F + T(w) = \begin{pmatrix} f_0 + t_{00}(w) & f_1 & \cdots & f_{m-1} & f_m \\ t_{10}(w) & t_{11}(w) & \cdots & 0 & 0 \\ 0 & t_{21}(w) & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & t_{m-1,m-1}(w) & t_{mm}(w) \end{pmatrix}.$$

The normalization $F = rN$ will be made explicit below.

At $w = 0$ the projection matrix $A(w)$ reduces to a constant Leslie matrix because $p_{jj}(0) = 0$, namely to

$$F + T(0) = \begin{pmatrix} f_0 & f_1 & \cdots & f_{m-1} & f_m \\ \pi_0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & \pi_{m-1} & 0 \end{pmatrix}, \pi_k = p_k(0)$$

which is irreducible and primitive if $f_m > 0$ and if there are at least two consecutive fertile size classes which we assume true (Impaglizzao [1980]).

It is easy to show that

$$e(w) = (1, q_1(w), \dots, q_m(w))^*$$

$$q_k(w) = \prod_{j=1}^k \frac{t_{j,j-1}(w)}{1 - t_{j,j}(w)}, k = 1, \dots, m.$$

Normalizing the fertility rates $f_i = rn_i$ in accordance with (9) we have

$$n_0 + \sum_{k=1}^m n_k q_k(0) = n_0 + \sum_{k=1}^m n_k \prod_{j=1}^k \pi_{j-1} = 1$$

and the normalized density factor in identity (17), whose graph determines the bifurcation diagram in the r, w -plane for nontrivial equation, is given by

$$n(w) = \frac{n_0 + \sum_{k=1}^m n_k q_k(w)}{1 - p_{00}(w)p_0(w)}.$$

A study of this function of $w > 0$ together with the general existence and stability results described above allow several conclusions to be easily drawn about this model.

First of all $p_k(+\infty) = 0$ implies $n(+\infty) = 0$ and it follows from (17) and Theorem 2 that there exists a positive equilibrium for (at least) all inherent net reproductive rates $r > 1$.

Secondly if $n'(0) > 0$ then the equilibria (r, w) near $(1, 0)$ bifurcate subcritically and are unstable. If $n'(0) < 0$ then these local equilibria bifurcate supercritically and are stable. The stability of other equilibria satisfying $n'(w) > 0$ is an open question for this model.

It is interesting to note that subcritical bifurcation can occur in this model. Subcritical bifurcations can be caused by density effects which reflect enhanced fertility and survivability with increase low level densities (often referred to as the "Allee effect" or "strict decompensation"). A discussion of this phenomenon can be found in Cushing [1988]. The model above demonstrates the theoretical possibility of a subcritical bifurcation, under certain conditions, in a size structured population which has none of these properties. Subcritical bifurcation results in this case from an interplay between the nonlinear effects on survivability and the growth rate.

By way of illustration consider the case when

$$p_k = \pi_k \exp(-aw), \quad a > 0, \quad p_{jj}(w) = \phi(w) \text{ for all } j \text{ and } k$$

where

$$0 \leq \phi(w) \leq 1, \quad \phi'(w) \geq 0, \quad \phi(0) = 0, \quad \phi(+\infty) = 1,$$

which postulates that the effects of density on survivability and on growth are the same for all size classes. A straightforward calculation shows that

$$(26) \quad n'(0) = \phi'(0) \left(\pi_0 + \sum_{i=1}^m n_i (-i + \sum_{j=1}^i \pi_j) \prod_{k=1}^i \pi_{k-1} \right) - a \left(\sum_{i=1}^m i n_i \sum_{k=1}^i \pi_{k-1} \right).$$

We will not be concerned with this complicated expression here except to observe that it can be positive under certain circumstances.

For example, a large value of $\phi'(0)$ (implying that the deleterious effects on growth of increased density increase rapidly as total population size w increases), larger values of π_i (implying high survivability over one unit of time) and relatively low fertility at larger size all contribute to the positivity of $n'(0)$ and the occurrence of a subcritical unstable bifurcation.

One can see this more clearly in the case of three size categories ($m = 2$), the first of which is immature: $n_0 = 0$. Then

$$n'(0) = \phi'(0) (\pi_0 + \pi_1 - 1 - n_2 \pi_0 \pi_1 (1 - \pi_2)) - a (1 - n_2 \pi_0 \pi_1 + 2 \pi_0 \pi_1 \pi_2)$$

and $n'(0) > 0$ if $\pi_0 + \pi_1 - 1 > 0$, n_2 is small and if $\phi'(0)$ is large enough.

In the event of a subcritical bifurcation, since $n(+\infty) = 0$ the bifurcation branch "turns around" as in Figure 3b. Although we have no proof, one anticipates that the upper branch consists of stable equilibria. Such a case results in multiple equilibria and the possibility hysteresis effects.

An opposite case is when the density effects on growth are small in comparison to those on survivability. In the extreme case one can set $p_{jj} = 0$. Not only will this result in a stable supercritical bifurcation (see (26) with $\phi'(0) = 0$) but in a matrix model with a Leslie-type

nonlinearity, namely in one of the form (21) with a projection matrix of the form

$$(27) \quad \mathbf{A}(w) = h(w)(r\mathbf{N} + \mathbf{T}) = \exp(-aw) \begin{pmatrix} rn_0 & rn_1 & \cdots & rn_{m-1} & rn_m \\ \pi_0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & \pi_{m-1} & 0 \end{pmatrix}.$$

The total population size $p(i)$ is governed by the equation (22) whose dynamics can be predicted (in many cases) by those of the limiting equation (24), which in this case is

$$(28) \quad q(i + 1) = \lambda q(i) \exp(-aw^*eq(i)/1^*e)$$

where \mathbf{e} is the positive eigenvector associated with the maximal positive eigenvalue λ of the constant Leslie matrix $r\mathbf{N} + \mathbf{T}$ above.

A great deal is known about the dynamics of this simple difference equation (which can, however, be far from simple). See Guckenheimer et al. [1976]. Known facts lead to the following conclusions: if $0 < \lambda < 1$ then all initially positive total population sizes $p(i)$ tend to zero as $i \rightarrow +\infty$. For $1 < \lambda < e^2$ all such $p(i)$ tend to a unique equilibrium $(aw^*\mathbf{e}/1^*\mathbf{e})^{-1} \ln \lambda$. For $\lambda > e^2$, but $\lambda < \lambda_1 = e^{2.6934\dots} \approx 14.767\dots$, $p(i)$ tends to a positive k -cycle for some $k \geq 1$ and any population whose total population size $p(i)$ starts initially close to a stable k -cycle with an initial class distribution sufficiently close to that of the stable k -cycle will tend to that k -cycle as $i \rightarrow +\infty$. Similar statements are obviously true for the weighted total population size $w(i)$.

For $\lambda > \lambda_1$ the limiting equation can exhibit chaotic dynamics. In this case the dynamics of $x(i)$ and $p(i)$ are not known, although one suspects that in all likelihood they are also subject to chaotic behavior in this case. A numerical example is given by Cushing [1987].

In any case, the normalized class distribution satisfies the strong ergodic property (23), regardless of the dynamics of the total population size $p(i)$.

(b) *An age structured model with density dependent fertility and survivability.* In the example above the fertility rates of all classes are density independent. It is widely recognized however that fertility often is

density dependent and a variety of nonlinear matrix models which allow for this possibility appear in the literature (e.g., see Desharnais and Cohen [1986], Ek and Monserud [1979], Fisher and Goh [1984], Leslie [1948], Levin and Goodyear [1980], Usher [1972]). The projection matrix for an age-structured model with density dependent fertility and survival rates is of the general form

$$(29) \quad \mathbf{A}(w) = \mathbf{F}(w) + \mathbf{T}(w) = \begin{pmatrix} f_0(w) & f_1(w) & \cdots & f_{m-1}(w) & f_m(w) \\ p_0(w) & 0 & \cdots & 0 & 0 \\ 0 & p_1(w) & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & p_{m-1}(w) & p_m(w) \end{pmatrix}.$$

In this case the normalized density factor $n(w)$ in identity (17) is

$$n(w) = n_0(w) + \sum_{j=1}^{m-1} n_j(w) \prod_{k=0}^{j-1} p_k(w) + n_m \prod_{k=0}^{m-1} p_k(w) / (1 - p_m(w))$$

where $f_j = rn_j$ with the normalization

$$1 = n_0(0) + \sum_{j=1}^{m-1} n_j(0) \prod_{k=1}^{j-1} p_k(0) + n_m(0) \prod_{k=0}^{m-1} p_k(0) / (1 - p_m(0)).$$

Clearly the assumption that all fertility and survivability rates decrease with increasing population size w (i.e., $n'_i(w) < 0$ and $p'_k(w) < 0$) imply $n'(w) < 0$ and consequently a supercritical bifurcation. Furthermore from (17) we see that if either of these vital rates tend to zero as w increases without bound or approaches a finite upper limit then the spectrum of net reproductive rate values r for which there exist positive equilibrium states contains half line $(1, +\infty)$.

Thus under these typical modelling assumptions there exists at least one positive equilibrium state for every $r > 1$ and at least those small amplitude equilibria corresponding to inherent net reproductive values r near 1 are stable.

A specific example is provided by a matrix equation model used by Pennycuick et al. [1968]. With an elimination of nonfertile older age

classes, the projection matrix (29) in their model takes the form

$$A(w) = \begin{pmatrix} 0 & 0.1\phi & 1.2\phi & 1.0\phi & 0.8\phi & 0.6\phi & 0.1\phi \\ 0.3\psi & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.95\psi & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.9\psi & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.8\psi & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.8\psi & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.7\psi & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0.65\psi \end{pmatrix}$$

$$\phi = 15000/(2500 + w), \quad \psi = 1/(1 + \exp(-5 + w/1389)).$$

Here $r \approx 3.66 > 1$ and hence there exists a positive equilibrium class distribution vector. From computed numerical solutions the positive equilibrium appears stable (see Usher [1972]).

The nonlinear dependencies of survivability and fertility expressed by ϕ and ψ are qualitatively similar in this example. If in the general model with projection matrix (29) these nonlinear dependencies are in fact taken to be identical, say of the form of ϕ in the model above, then (29) has a Leslie-type nonlinearity and a projection matrix

$$(30) \quad A(w) = \frac{1}{1 + aw} \begin{pmatrix} rn_0 & rn_1 & \cdots & rn_{m-1} & rn_m \\ p_0 & 0 & \cdots & 0 & 0 \\ 0 & p_1 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & \cdots & p_{m-1} & p_m \end{pmatrix}.$$

This model is, in fact, one of those studied by Leslie [1948].

The dynamics of $w(i)$ are governed by the limiting equation

$$q(i + 1) = \lambda q(i)/(1 + aw^*eq(i)/1^*e)$$

which, unlike the limiting equation (28), has only equilibrium dynamics.

For this nonlinear model all positive weighted population sizes tend to zero if $\lambda < 1$ and to the positive equilibrium $(\lambda - 1)^{-1} \mathbf{e}/a\mathbf{e}^* \mathbf{w}$ if $\lambda > 1$ where λ is the maximal eigenvalue of the constant Leslie matrix in (30) and \mathbf{e} is its associated positive eigenvector. Moreover the class distribution vector satisfies the strong ergodic property.

(c) *Density enhanced fertility.* In example (b) the common assumption that fertility is suppressed by increases in population density was made. This assumption is not always warranted, at least at low population levels. A diversity of plants and animal species have been found to show enhanced per capita fertility rates in the presence of increased population density (Allee [1931], Parise [1976], Sarukhan and Harper [1973], Sarukhan [1974], Sarukhan and Gadil [1974], Silvertown [1982], Watt [1968]). In a model for such a case the density dependence in the fertility rates f_j would not be a decreasing function of w but instead would increase for at least small population sizes w before decreasing to larger values of w .

An example can be found in Watt [1968] where a model for an age-structured population consisting of a nonfertile newborn class and two older fertile age classes is studied (also see Usher [1972]) with a projection matrix of the form

$$\mathbf{A} = \begin{pmatrix} 0 & rn_1\phi(w) & rn_2\phi(w) \\ p_0 & 0 & 0 \\ 0 & p_1 & 0 \end{pmatrix}$$

where

$$0 < p_k < 1, \quad n_j > 0, \quad n_1p_0 + n_2p_0p_1 = 1.$$

Consider a density factor

$$\phi = (1 + bw)e^{-aw}, \quad b > a > 0$$

which is qualitatively similar to the complicated expression used by Watt [1968]. Then ϕ , and hence both age-specific fertility rates, increase with population size from $w = 0$ to $w = (b - a)/ab > 0$ after which they decrease monotonically to zero as $w \rightarrow +\infty$.

This model has a subcritical unstable bifurcation. The equilibrium branch is described by the identity (17) which reduces to

$$1 = r\phi(w) = r(1 + bw)e^{-aw}$$

and has a bifurcation diagram as appears in Figure 3b. As a result the small magnitude equilibria for r less than one, specifically for

$$\frac{a}{b} \exp\left(\frac{b}{a} - 1\right) < r < 1,$$

are unstable. Numerical results suggest that the upper branch of large magnitude equilibria are stable. This has not been proved analytically however; nor has the dynamics been investigated for the possibility of cycles and/or chaotic behavior for large values of r .

9. Concluding Remarks. In the 1940's Lewis [1942] and Leslie [1945, 1948] introduced matrix equation models which predicted the age structure of a population for future times given age specific fertility and survivability rates and given the initial age distribution. Subsequently the use of these types of models has become widespread for modeling the dynamics of age-structured populations as well as (more recently) of populations structured by other physiological parameters such as size, weight, reproductive stage, etc.

This popularity seems to be due to several factors. The simplicity of the building and analysis of the matrix models in comparison to calculus based models is appealing to many users. Certainly the algebraic techniques required for an analysis of such models are more likely to be understood by those with limited mathematical backgrounds. Even for those with considerable mathematical expertise the mathematical difficulties associated with continuous models for structured populations can be formidable. See Metz and Diekmann [1986]. Indeed, in some cases, even the most fundamental questions concerning the well-posedness of such problems have not been answered, while for matrix models these questions pose no difficulties whatsoever. This is the case, for example, when regressions to earlier classes are permitted. Furthermore, the appropriateness of a discrete time model is apparent in many applications in which biological processes occur in discrete periods and are not continuous in their action. Finally, the ease of computer simulations when using matrix models in comparison to continuous models is obvious.

While the linear theory of discrete matrix models has reached a high level of development (as a beautiful application of the mathematical theory of nonnegative matrices), the nonlinear theory of density dependent population growth has received only *ad hoc* analytical treatments.

Much of the analysis of nonlinear models appearing in the literature has been restricted to numerical studies.

The primary purpose of this paper is to suggest one possible approach to the theory of equilibrium states of nonlinear matrix models for the dynamics of arbitrarily structured populations and to do so in a quite general setting. It is hoped that the bifurcation theory approach taken here will provide a useful, instructive and unifying conceptual context in which to understand and organize one's thinking about the dynamics of such models.

APPENDIX

To prove Theorem 2 we first rewrite the equilibrium equations (13)-(14) in the equivalent form

$$\begin{aligned}x_0 &= rn(\mathbf{x})x_0 \\(x_1, \dots, x_m) &= r(e_1(\mathbf{x}), \dots, e_m(\mathbf{x}))n(\mathbf{x})x_0\end{aligned}$$

obtained by substituting equation (13) for x_0 into the right hand side of equation (14). Using a Taylor's expansions with remainder we can rewrite these equations in the form

$$(A1) \quad \mathbf{x} = r\mathbf{L}\mathbf{x} + r\mathbf{h}(\mathbf{x})$$

where $\mathbf{h}(\mathbf{x}) = o(|\mathbf{x}|)$ as $|\mathbf{x}| \rightarrow 0$ and

$$(A2) \quad \mathbf{L} = \begin{pmatrix} 1 & 0 & 0 & \cdots & 0 \\ e_1 & 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & & \vdots \\ e_m & 0 & 0 & \cdots & 0 \end{pmatrix}.$$

The global bifurcation result described below (called the Rabinowitz's Alternative) applies directly to the formulation (A1) of the equilibrium equations.

Suppose $L : B \rightarrow B$ is a compact linear operator on a real Banach space B and suppose $H : R \times B \rightarrow B$ is compact and continuous and satisfies $H = H(r, u) = o(|u|)$ for u near 0 uniformly on bounded r intervals. A *characteristic value* μ of L is a real for which there

exists a $u \in B, u \neq 0$, such that $u = \mu Lu$, i.e., μ is the reciprocal of nonzero eigenvalues of L . By the multiplicity of μ here is meant *geometric* multiplicity, i.e., the dimension of $\cup_{i=1}^{\infty} \ker(\mu L - I)^i$ where "ker" denotes kernel or nullspace. This dimension is finite because L is compact.

Let S be the closure of the set of nontrivial solution pairs $(r, u) \neq (r, 0)$ of the equation

$$u = rLu + H(r, u), (r, u) \in R \times B.$$

A connected set is one which cannot be written as the union of two disjoint closed sets. A continuum is a closed and connected set.

Rabinowitz's Alternative (Rabinowitz [1971], Theorem 1.3) states that if r' is a characteristic value of L of odd multiplicity then S contains a (maximal) subcontinuum $C_{r'}$ such that $(r', 0) \in C_{r'}$ and $C_{r'}$ is either unbounded or contains a point $(r'', 0)$ where $r'' \neq r'$ is also a characteristic value of L .

The continuum $C_{r'}$ is said to bifurcate from $(r', 0)$ because it intersects the set of *trivial solutions* $(r, 0)$ at this point. It is a fundamental principle of bifurcation theory that only characteristic values r' of L can be bifurcation points (e.g., see Pimbley [1969]).

To apply Rabinowitz's Alternative to the equation (A1) we need to investigate the characteristic values of the matrix L given by (A2).

Clearly $r' = 1$ is the only characteristic value of L . Moreover $I - L$ is easily seen to be a projection (i.e., $(I - L)^2 = (I - L)$) and hence $r' = 1$ has multiplicity one, or in other words is a *simple* characteristic value of L . Since $r' = 1$ is the only characteristic value in this case the second alternative is ruled out and we conclude that the set of nontrivial equilibrium pairs (r, \mathbf{x}) contains an unbounded continuum $C_{r'}$.

Furthermore since $r' = 1$ is simple, a stronger result of Rabinowitz applies to (A1). Theorem 1.40 of Rabinowitz [1971] implies that $C_{r'}$ contains an unbounded subcontinuum C which in a neighborhood of the "bifurcation point" $(1, \mathbf{0})$ consists of positive equilibria (r, \mathbf{x}) , $\mathbf{x} > 0$. In the general case this "locally positive" continuum C need not consist entirely of positive solutions, but in the application to the equilibrium equations (A1) this is easily seen to be the case. For if this were not so then C would (since it is a continuum) have to contain a pair (r_0, \mathbf{x}_0) ,

other than $(1, 0)$, for which \mathbf{x}_0 is on the boundary of the positive cone, i.e., $\mathbf{x}_0 \geq 0$ and at least one component of \mathbf{x}_0 vanishes. By (13)-(14) it follows then that in fact x_0 must vanish which in turn implies $\mathbf{x}_0 = \mathbf{0}$. Since only characteristic values of L can be bifurcation values it follows that $r_0 = 1$ and we have the contradiction $(r_0, \mathbf{x}_0) = (1, \mathbf{0})$.

We conclude that $(r, \mathbf{x}) \in C\{(1, \mathbf{0})\}$ implies that $\mathbf{x} > 0$. Finally we note that $(0, \mathbf{x})$ cannot lie in C for any \mathbf{x} . This is because $r = 0$ in (13) implies $\mathbf{x} = \mathbf{0}$ and $(0, \mathbf{0})$ cannot lie in C since $r = 0$ is not a characteristic value of L . This proves Theorem 2.

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