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Chapter 26  
Nonlinear Matrix Models for Structured Populations

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ABSTRACT: Leslie matrix models for the dynamics of age-structured populations become nonlinear if fertility and survival rates are density dependent. More general matrix equations can model the nonlinear dynamics of populations structured in other ways as well, e.g. by size classes, life cycle stages, etc. It is shown how simple bifurcation theory techniques can be used to obtain information about the existence and stability of equilibria for such nonlinear matrix equations. The method is very general and works under only mild conditions on the equations. A single bifurcation parameter is used, namely, the inherent net reproductive number. It is also shown how the method can be extended to models for interacting structured species. Applications to some single species and multi-species models are given.

KEY WORDS: Structured population dynamics, equilibria, stability, bifurcation

## 1. Introduction

The utilization of matrix methods for the description of the the dynamics of structured populations (i.e. populations in which the dynamics of sub-classes of individuals are of interest) was popularized by several influential papers of Lewis (1942) and Leslie (1945, 1948). In these early papers, age-structured populations were of primary interest and the methods developed there have become fundamental tools for demographers ever since. Lefkovich (1965) was among the first to point out that the methods of Lewis and Leslie quite easily generalize to populations structured in other ways as well (such as populations structured by individual body size, life cycles stages, DNA content, etc.); also see Usher (1966, 1972) and Woodward (1982). The recent book by Caswell (1989) is the latest comprehensive exposition of matrix methods for structured populations.

Matrix methods are used to describe the evolution through discrete time steps of populations whose individuals are placed into a finite number of categories. The dynamics of structured populations can also be described, of course, by continuous models, i.e. models in which time is continuous and the population is described by means of a density distribution with respect to a continuous structuring variable; see Metz & Diekmann (1986). The relative merits of these two modeling procedures will not be discussed here nor will discrete models necessarily be advocated over continuous models. Suffice it to say that matrix methods have been widely utilized in population dynamics and that one of the reasons for this is undoubtedly that the derivation and analysis of discrete matrix models are often considerably easier for many researchers who, because of their mathematical background, find it considerably more difficult to deal with the partial differential equations that are used in continuous models. In addition, from a mathematical point-of-view matrix models do not suffer from many difficult and technical problems associated with continuous models, such as well-posedness (existence and uniqueness of solutions), the rigorous justification of linearization methods for stability, and so on. Moreover, models involving matrix equations are eminently suited for use on computers, unlike partial differential equations whose numerical integration involves problems concerning appropriate discretation procedures, stability, and convergence (and, in the end, utilize matrix difference equations anyway). Although some relatively simple relationships between the discrete and continuous types of models have been pointed out, namely how certain discretations of the

partial differential equations of the continuous models lead to the matrix equations of the discrete models (e.g. see Liu & Cohen (1987) for the age-structured case involving the McKendrick/von Foerster equations and Leslie matrices), these relationships have not been thoroughly and rigorously studied with regard to consistency, stability, and convergence (exceptions are Uribe (1992) and the unpublished paper of Saints (1987)). It is known that one has to be careful how such discretations are carried out in order to obtain convergence and hence that the discrete and continuous models approximate each other. For example, some discretations of the age-structured McKendrick/von Foerster equation mentioned in the literature that lead to the classical Leslie matrix model are in fact not convergent (Uribe (1992), Saints (1987)). For an interesting modeling methodology that encompasses the spectrum from discrete to continuous time see De Roos et al. (1992).

Most of the early literature that utilized matrix methods for structured populations focused on the nature of the evolution in time of the age class distribution in linear models. When density effects are ignored the model populations, of course, grow or die out geometrically. However, the inclusion of density effects for "self regulating" populations or for multi-species interactions leads to nonlinear matrix equations and the possible asymptotic dynamics of the model population becomes considerably more varied and complicated. The first step in the analysis of such nonlinear matrix models involves gaining an understanding of the existence and stability of possible equilibrium states. The goal of this paper is to present one general approach to this problem for "closed" populations, i.e. for populations that are not subject to immigration or emigration.

The approach taken here is based upon bifurcation theory methods, i.e. on methods that study how equilibrium states depend upon and change as a function of model parameters. Specifically, the existence and stability of nontrivial equilibrium states will be studied as a function of an "inherent net reproductive number" as defined below. Certainly other approaches are possible, particularly in specific applications, where other methods and/or other bifurcation parameters might be more useful. However, one of the main advantages of the approach taken here is the generality of its applicability. It provides one way of gaining an overview of any particular application. Moreover, our approach provides analytic techniques and formulas that can yield nontrivial information about equilibrium states in specific applications that might be otherwise quite analytically intractable.

The results and methods will be illustrated by means of several



applications, taken mostly from the literature. Furthermore, some of these applications will show that even when the methods developed here fail to apply, because of the failure of one theoretical hypothesis or another, the approach often still provides valuable insights into the dynamics and suggests fruitful avenues to explore.

The paper is organized as follows. In Sec. 2 a general class of nonlinear matrix models for the dynamics of a single structured population is described and in Secs. 3 and 4 some general results concerning the existence and stability of nontrivial equilibrium states are given. These single species results are a generalization of those obtained for discrete models by Cushing (1988a). The bifurcation approach taken for single species models is extended to multi-species interactions in Sec. 6. This extension is done along the lines of that done for continuous age-structured models by Cushing (1987). Applications to a variety of model populations are given in Sec. 5 and Sec. 7 in order to illustrate the approach and results. Some applications to which the results do not apply will also be given. From these examples it will be seen how the method can nonetheless provide insights into the dynamics. The applications will not be studied in any depth and their biological implications will be only briefly touched upon, if at all. Further details about these particular applications can be found in the cited literature.

## 2. Nonlinear Matrix Models: Single Species.

Consider a population in which each individual is placed into one and only one of  $m$  different stages or classes and let  $X = \text{col}(x_i)$  denote the column  $m$ -vector of class abundances or densities  $x_i$ . The case of a population closed to immigration and emigration that is sampled at discrete times  $t = 0, 1, 2, \dots$  will be considered. At any time  $t$  there is a (transition) probability  $t_{ij}$  that an individual in class  $j$  will survive to time  $t + 1$  and move to class  $i$  and there are a certain number  $f_{ij}$  of offspring of class  $i$  borne to an individual of class  $j$  that survive to time  $t + 1$ . If the  $m \times m$  "fertility" matrix is denoted by  $F = [f_{ij}] \geq 0$  and the  $m \times m$  "transition" matrix by  $T = [t_{ij}] \geq 0$ , then the class density vector  $X(t+1)$  at time  $t + 1$  is given by

$$X(t+1) = AX(t) \tag{1}$$

where  $A = F + T$  is the so called  $m \times m$  "projection" matrix. (By non-negative or positive matrices or vectors is meant that all entries are

non-negative or positive.)

Perhaps the most famous example of a population projection matrix  $A$  is the Leslie matrix in which only the first row of  $F$  and only the sub-diagonal of  $T$  contain nonzero entries. In this case the classes represent age classes of one unit of time in length. Another example is the Usher matrix which is a Leslie matrix with added positive elements along the main diagonal (Usher (1966)). This is a simple "standard" size class model in which individuals either grow one size class or remain in the same size class after one unit of time (Caswell (1989)).

Mathematically the solutions of the linear equation (1) are trivial, namely  $X(t) = A^t X(0)$ , and the study of the population dynamics reduces to a study of the sequence of powers  $A^t$ . In this linear case the population "generically" grows geometrically without bound or dies out geometrically.

In a more realistic model for the long term (asymptotic) dynamics of a growing population, densities must be regulated in some way in order to prevent unlimited population numbers. Of interest here is the case of self regulation through a dependency of the transition and fertility matrices (i.e. of the class specific fertility rates and survival and the transition probabilities) on population density. The assumption that  $T = T(X)$  and  $F = F(X)$  depend on  $X$  leads to the mathematically more difficult and interesting case of nonlinear matrix equations

$$X(t+1) = A(X(t))X(t) \tag{2}$$

where  $A(X) = T(X) + F(X)$ .

Assume that  $t_{ij}: \mathbb{R}_+^n \rightarrow [0,1]$  and  $f_{ij}: \mathbb{R}_+^n \rightarrow [0,\infty)$  are twice continuously differentiable functions where  $\mathbb{R}_+ = [0,\infty)$ . For fixed  $j$  the set of probabilities  $t_{ij}$  represent the fractions of  $j$  class individuals distributed to all  $m$  classes in one unit of time. Thus the sum of these probabilities over  $i$  must be less than or equal to one. It will be assumed here that there is always some loss due to mortality from every class over any unit of time and hence that

$$0 \leq \sum_{i=1}^m t_{ij}(X) < 1 \text{ for all } j \text{ and } X \in \mathbb{R}_+^n. \tag{3}$$

Note that any initial density distribution  $X(0) \geq 0$  obviously determines a unique solution  $X(t)$  of Eq.(2) and that, because the projection matrix  $A(X)$  has non-negative entries, this unique solution is non-negative for all time  $t > 0$ .

### 3. Equilibria for Single Species Models.

The first step in understanding the dynamics of a model population described by the nonlinear Eq.(2) is to determine the equilibrium solutions  $X(t) = X \geq 0$ . Clearly  $X(t) = 0$  is a trivial equilibrium. Other non-negative equilibria are solutions of the  $m$  nonlinear equilibrium equations

$$X = \left( F(X) + T(X) \right) X, X \geq 0, X \neq 0 \quad (4)$$

Our approach will be to treat the existence and stability of nontrivial equilibria by means of bifurcation theory methods. Of course, any parameter in a specific model of the form of Eq.(2) can serve as a "bifurcation parameter". In the general setting to be considered here, a biologically important parameter common to all population models will be utilized, namely the "inherent net reproductive number", i.e. the expected number of offspring from an individual over its life time in the absence of density regulation (in other words at low population densities). This parameter is mathematically defined and introduced into our model equations as follows.

Because of assumption (3) the inverse of  $E(X) = I - T(X)$  exists for all  $X \geq 0$ . That  $E(X)$  is non-negative can be seen by

$$E(X) = \left[ e_{ij}(X) \right] = \left( I - T(X) \right)^{-1} = \left( I + T(X) + T^2(X) + \dots \right) \geq 0.$$

The entry  $e_{ij}$  of  $E$  is the expected fraction of time spent in class  $i$  by an individual starting in class  $j$ . The equilibrium equations (4) can be rewritten equivalently as  $X = \left( I - T(X) \right)^{-1} F(X) X$  or as  $X = R(X) X$  where  $R(X) = E(X) F(X) \geq 0$ . We now make the assumption

$$A1: \begin{cases} R(0) \text{ has a strictly dominant, simple real eigenvalue} \\ r > 0 \text{ with positive right and left eigenvectors} \\ v^0 > 0 \text{ and } w^0 > 0 \text{ respectively.} \end{cases}$$

Without loss in generality the eigenvectors can be normalized so that  $w^0 \cdot v^0 = 1$ . The eigenvalue  $r$  is called the "inherent net reproductive number". In applications the Perron-Frobenius theory can be used to check this assumption (Gantmacher (1960), Caswell (1989)). It holds, for example, if  $R(0)$  is irreducible and primitive.

In order to introduce  $r$  explicitly into our model equations the fertility matrix can be rewritten as  $F(X) = rN(X)$ . In other words, the entry  $n_{ij}$  of the matrix  $N$  is the class specific fertility measured relative to the

inherent net reproductive number  $r$ , i.e.  $f_{ij} = rn_{ij}$ .

If  $Q(X) = E(X)N(X)$ , then it is easy to see that  $R(0)$  satisfies A1 if and only if  $Q(0)$  satisfies A1 with  $r = 1$ .

Eq.(2) becomes

$$X(t+1) = (rN(X(t)) + T(X(t)))X(t) \quad (5)$$

and the equilibrium equation (4) can be equivalently written as

$$X = rQ(X)X = rQ(0)X + \Omega(r,X) \quad (6)$$

where  $\Omega = O(|X|^2)$  near  $X = 0$  (uniformly on finite  $r$  intervals). To this form of the equilibrium equation the global bifurcation theorems of Rabinowitz (1971) can be applied to obtain the follow general equilibrium existence result for Eq.(2).

**THEOREM 1 (Equilibrium existence).** Under assumption A1, there exists a "global" continuum (i.e. closed connected set) in  $R \times R_+^n$  of nontrivial equilibria pairs  $(r,X)$  for Eq.(5) that bifurcates from (i.e. contains) the trivial pair  $(1,0)$  and that consists of positive equilibria  $X > 0$  at least locally near  $(1,0)$ .

By "global" is meant that the continuum is either unbounded in  $R \times R_+^n$  or contains a pair  $(r^*,0)$  where  $r^* \neq 1$  is a characteristic value of  $Q(0)$  other than 1. This is referred to as "Rabinowitz's alternative". (The characteristic values of  $Q(0)$  are the reciprocals of its nonzero eigenvalues.) Note that 0 cannot be a characteristic value of  $Q(0)$  and hence the continuum cannot contain  $(0,0)$ . It follows from Eq.(6) that the only equilibrium associated with  $r = 0$  is the trivial equilibrium  $X = 0$  and consequently the continuum in Theorem 1 contains only pairs  $(r,X)$  with  $r > 0$ . Incidentally,  $r^*$  must be of odd geometric multiplicity.

Of course, in our model only non-negative equilibria are relevant and it is of interest to know whether all the nontrivial equilibria from the continuum are non-negative, i.e. whether the continuum leaves the positive cone and consequently contains non-relevant equilibria with at least one negative component. To do so the continuum would have to contain a pair  $(r,X)$  with  $r > 0$  and with a non-negative, nontrivial equilibrium  $X$  which contains at least one zero component. This can often be easily ruled out in specific applications from the special nature of the projection matrix  $A$ .

For example, in most applications it turns out that the only non-negative nontrivial equilibria are in fact positive.

Furthermore, it often is the case that the second Rabinowitz alternative (that the branch contains a different trivial equilibrium pair  $(r^*, 0)$ ) can also be ruled out. Such is the case, for example, if  $Q(0)$  has no other positive real characteristic value  $r^* \neq 1$  at all or if it does then all non-negative nontrivial equilibria are necessarily positive and eigenvectors associated with any other characteristic value not non-negative (which is true if  $Q(0)$  is irreducible; see Gantmacher (1960, p.63)).

An important special case is provided by models in which all newborns lie in the same class. This is the case studied in Cushing (1988a). It includes the classical Leslie age-structure models. Without loss in generality, suppose all newborns lie in the first class so that

$$F(X) = \begin{bmatrix} f_{11}(X) & \dots & f_{1m}(X) \\ 0 & \dots & 0 \\ \vdots & & \vdots \\ 0 & \dots & 0 \end{bmatrix}$$

and hence

$$R(X) = \begin{bmatrix} e_{11}(X)f_{11}(X) & \dots & e_{11}(X)f_{1m}(X) \\ e_{21}(X)f_{11}(X) & \dots & e_{21}(X)f_{1m}(X) \\ \vdots & & \vdots \\ e_{m1}(X)f_{11}(X) & \dots & e_{m1}(X)f_{1m}(X) \end{bmatrix},$$

a matrix whose eigenvalues are 0, with multiplicity  $m - 1$ , and the simple eigenvalue

$$\text{Trace}(R(X)) = \sum_{i=1}^m e_{i1}(X)f_{1i}(X) \geq 0.$$

If  $e_{i1}(0) > 0$  for at least one fertile class  $f_{1i}(0) > 0$ , that is to say, if a newborn is inherently (i.e. at low population densities in the absence of density effects) expected to spend nonzero time in at least one fertile class during its lifetime, then  $R(0)$  satisfies A1 with  $r = \text{Trace}(R(0)) > 0$ . Moreover, this  $r$  is the only characteristic value of  $R(0)$  in this case and hence the second Rabinowitz alternative is ruled out which implies that the continuum of nontrivial equilibrium must be unbounded. This means that either there exist nontrivial equilibria of arbitrarily large magnitude or for arbitrarily large  $r$  (or both).

To pursue this example a bit further, note that

$$N(X) = \begin{bmatrix} n_{11}(X) & n_{12}(X) & \dots & n_{1m}(X) \\ 0 & 0 & \dots & 0 \\ \vdots & \vdots & \dots & \vdots \\ 0 & 0 & \dots & 0 \end{bmatrix}, \quad n_{1i}(X) = \frac{f_{1i}(X)}{\sum_1^m e_{i1}(0) f_{1i}(0)}$$

and that the eigenvalues of

$$Q(X) = \begin{bmatrix} e_{11}(X)n_{11}(X) & \dots & e_{11}(X)n_{1m}(X) \\ e_{21}(X)n_{11}(X) & \dots & e_{21}(X)n_{1m}(X) \\ \vdots & & \vdots \\ e_{m1}(X)n_{11}(X) & \dots & e_{m1}(X)n_{1m}(X) \end{bmatrix}$$

are 0, with multiplicity  $m - 1$ , and the simple eigenvalue

$$n(X) = \sum_{i=1}^m e_{i1}(X)n_{1i}(X), \quad n(0) = 1.$$

Now the equivalent formulation of the equilibrium equations given by Eq.(6) for any nontrivial equilibrium pair  $(r, X)$  implies that this pair is a characteristic pair of the matrix  $Q(X)$  and hence

$$rn(X) = 1. \quad (7)$$

Suppose that  $e_{i1}(X) > 0$  for all  $i$  and all  $X \in \mathbb{R}_+^n$ ; that is to say, suppose that a newborn always has a nonzero probability of reaching each class. This is guaranteed, for example, if in the ordering of classes it happens that there is a nonzero probability of moving from any class to the subsequent class in one unit of time, or in other words that  $t_{i+1,i}(X) > 0$  for all  $i = 1, \dots, m - 1$  and  $X \in \mathbb{R}_+^n$ . Under this assumption, it follows from Eq.(6), i.e. from  $x_i = re_{i1}(X) \sum_{j=1}^m n_{1j}(X)$ , that if at least one component of a non-negative equilibrium is zero then in fact all components are zero. This means the the continuum in Theorem 1 consists entirely of positive equilibria. The results for this special case are summarized in the next theorem.

**THEOREM 2 (One newborn class).** Suppose that all newborns lie in one class, namely (without loss in generality) in class  $i = 1$  so that  $f_{ij}(X) \equiv 0$  for  $i \geq 2$ . Suppose further that each newborn always has a nonzero probability of reaching every class, i.e.

$t_{i-1,i}(X) > 0$  for  $i \leq m - 1$ . If there is at least one,

inherently fertile class,  $f_{1i}(0) > 0$  for some  $i$ , then the

continuum bifurcating from  $(r, X) = (1, 0)$  guaranteed by Theorem 1

is unbounded in  $\mathbb{R}_+^n \times (0, \infty)$  and consists, except for the trivial

equilibrium at  $r = 1$ , entirely of positive equilibria  $X > 0$ .

Eq. (7) says that the quantity  $rn(X)$  is invariant along the continuum of nontrivial equilibrium. Biologically this is not surprising in that  $rn(X)$  is the expected number of offspring born to an individual over its lifetime, i.e. the net reproductive number, when the population is held at equilibrium level  $X$ . Eq. (7) means simply that at equilibrium each member of the population must exactly replace itself. Mathematically, Eq. (7) provides an alternative equation for the nontrivial equilibria  $X$  and provides an algebraic means of studying  $X$  as a function of  $r$ . In particular, Eq. (7) can often be of use in drawing bifurcation diagrams.

For example, it is quite often the case that model assumptions concerning the effects of population density on fertility and class transition rates (survival rates, growth rates, etc.) imply that  $n(X) \rightarrow 0$  as  $\|X\| \rightarrow \infty$ . This occurs, for example, if fertility or newborn survival rates  $f_{1i}(X) \rightarrow 0$  or the expectations  $e_{i1}(X) \rightarrow 0$  as  $\|X\| \rightarrow \infty$ . For such model populations (which, incidentally, do not require monotonic dependencies on  $X$  and thus allow such phenomena as Allee effects) it follows from Theorem 2 and Eq. (7) that the set of  $r$  values obtained from the continuum  $(r, X)$ , i.e. the "spectrum" associated with the continuum of positive equilibria, is an unbounded sub-interval of  $(0, +\infty)$  which contains  $r = 1$  in its closure.

An important special case is the age-structured model where  $A(X) = rN(X) + T(X)$  is a Leslie matrix:

$$N = \begin{bmatrix} n_1(X) & n_2(X) & \dots & n_m(X) \\ 0 & 0 & \dots & 0 \\ 0 & 0 & \dots & 0 \\ \vdots & \vdots & & \vdots \\ 0 & 0 & \dots & 0 \end{bmatrix} \quad T = \begin{bmatrix} 0 & 0 & \dots & 0 & 0 \\ p_2(X) & 0 & \dots & 0 & 0 \\ 0 & p_3(X) & \dots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \dots & p_m(X) & p_{m+1}(X) \end{bmatrix}.$$

Here

$$p_i: \mathbb{R}_+^n \rightarrow (1, 0), \quad p_{m+1}: \mathbb{R}_+^n \rightarrow [0, 1), \quad n_i: \mathbb{R}_+^n \rightarrow [0, \infty), \quad n_m(0) > 0.$$

Notice that the oldest age class  $i = m$  has been assumed to be fertile at low densities and that individuals in all age classes always have a nonzero probability of surviving one unit of time. Then for  $X \in \mathbb{R}_+^n$

$$0 < E = \left[ V(X) \ V(X) \ \dots \ V(X) \right]$$

where

$$V(X) = \text{col} \left( 1, p_2(X), \dots, \prod_{j=2}^{m-1} p_j(X), (1-p_{m+1}(X))^{-1} \prod_{j=2}^m p_j(X) \right), \quad V(0) = V^0$$



and

$$n(X) = \left( n_1(X) + \sum_{i=2}^{m-1} n_i(X) \prod_{j=2}^{m-1} p_j(X) + \frac{n_m(X)}{1 - \prod_{j=2}^m p_j(X)} \right) > 0.$$

Theorem 2 implies that such nonlinear, Leslie age-structured models have a continuum of positive equilibria for an unbounded spectrum of positive inherent net reproductive numbers  $r$  that bifurcates from the trivial equilibrium at  $r = 1$ .

#### 4. Equilibrium Stability.

Study of the stability properties of equilibria as a function of the parameter  $r$  entails a return to the dynamical equation (5). Consider first  $X = 0$  which is a trivial equilibrium for all  $r$ . Linearization of Eq.(5) at  $X = 0$  yields the linear equation  $Y(t+1) = (rN(0) + T(0))Y(t)$ . Under assumption A1,  $Q(0) = (I - T(0))^{-1}N(0)$  has an eigenvalue 1 with positive right and left eigenvectors  $V^0 > 0$  and  $W^0 > 0$ . This implies that the same is true of  $N(0) + T(0)$ . Let  $\lambda(r)$  denote the eigenvalue of  $rN(0) + T(0)$  such that  $\lambda(1) = 1$ . A straightforward calculation shows that  $d\lambda(1)/dr = W^0 \cdot N(0) V^0 > 0$ . (Note that  $N(0) \geq 0$  cannot be the zero matrix if A1 holds.) Thus, if it is assumed that

A2: 1 is a strictly dominant eigenvalue of  $N(0) + T(0)$

then the trivial equilibrium  $X = 0$  loses (local asymptotic) stability as  $r$  is increased through 1.

In general a stability analysis of the positive equilibria guaranteed by Theorem 1 is difficult. However, near the bifurcation point  $(r, X) = (1, 0)$  it is possible to make some quite general assertions. If a parameterization of the bifurcating branch of equilibria by means of a small auxiliary parameter  $\epsilon$  is analyzed using regular perturbation (Liapunov-Schmidt) techniques and the expansions

$$X = V^0 \epsilon + O(\epsilon^2), \quad r = 1 + \rho \epsilon + O(\epsilon^2) \tag{8}$$

straightforward calculations show that

$$\rho = - W^0 \cdot \left[ \nabla_X q_{ij}(0) \cdot V^0 \right] V^0, \quad Q(X) = [q_{ij}(X)].$$

This means that  $\rho > 0$  implies a "right bifurcation" in that the positive equilibria on the bifurcating branch near  $(1, 0)$  exist for  $r > 1$ . The opposite case  $\rho < 0$  is called a "left bifurcation". When  $\rho \neq 0$  there is a



so-called "transcritical" bifurcation of the trivial and nontrivial equilibrium branches (including negative equilibria for  $\epsilon < 0$ ). It is typically the case for transcritical bifurcations that stability is exchanged from one branch to the other (e.g. see Smoller (1983)). This can be rigorously verified for Eq.(5) by also expanding the maximal, stability determining eigenvalue  $\mu = 1 + \mu_1 \epsilon + O(\epsilon^2)$  of the equation linearized at the positive branch equilibria (8) in terms of  $\epsilon$ . This tedious calculation, which will not be given here, shows that the coefficient  $\mu_1$  is a negative multiple of  $\rho$ . These results are summarized in the next theorem.

**THEOREM 3 (Stability and direction of bifurcation).** Assume A1 and A2 hold. Near the bifurcation point  $(r,X) = (1,0)$  the trivial equilibrium  $X = 0$  loses stability as  $r$  increases through 1, i.e.  $X = 0$  is (locally asymptotically) stable for  $r < 1$  and unstable for  $r > 1$ . Furthermore, the positive equilibria near the bifurcation point  $(1,0)$  guaranteed by Theorem 1 are (locally asymptotically) stable if  $\rho > 0$  and unstable if  $\rho < 0$ . In other words, right bifurcating branches are stable and left bifurcating branches are unstable near  $(1,0)$ .

The two cases of stable and unstable bifurcations when  $\rho \neq 0$  are schematically shown by the bifurcation diagrams in Fig. 1a,b.

INSERT FIGURES 1a & 1b NEAR HERE

A common model assumption is that fertility, survival, and class transition rates are adversely affected by increases in population densities because of increased competition for limited resources and other deleterious effects of crowding. Thus, if  $\nabla_{X^{n_{ij}}}(0) \leq 0$  and  $\nabla_{X^{t_{ij}}}(0) \leq 0$ , but not both are 0, and hence

$$\nabla_{X^{q_{ij}}}(0) = \nabla_{X^{n_{ij}}}(0) + \nabla_{X^{t_{ij}}}(0) \leq 0 (\neq 0)$$

then  $\rho > 0$  and the bifurcation of positive equilibria at  $r = 1$  is stable.

It follows that a unstable (left) bifurcation can only occur if increases in class densities are not all deleterious at low population levels. Allee effects and cannibalism are phenomena that can result in unstable bifurcations (Cushing (1988b, 1991a)). Also see Cushing (1988a) for an example involving size dependent growth and mortality.

For the case of a single newborn class considered above the direction of

bifurcation can be determined from Eq. (7). If one moves along the bifurcating branch of positive equilibria parameterized by Eq. (8) by increasing  $\epsilon > 0$ , then Eq. (7) implies  $r(\epsilon)n(X(\epsilon)) = 1$ . A differentiation with respect to  $\epsilon$  evaluated at  $\epsilon = 0$  yields  $r'(0) = -\nabla_X n(0) \cdot V^0$ . Consequently, in this case the bifurcation is

$$\text{stable (unstable) if } \nabla_X n(0) \cdot V^0 < 0 \text{ ( } > 0 \text{)}.$$

In many cases the density dependence is through a weighted population size  $w = \sum_i w_i x_i$ ,  $w_i \geq 0$ ,  $\sum_i w_i > 0$  and hence  $n = n(w)$ . Then the bifurcation is

$$\text{stable (unstable) if } n'(0) < 0 \text{ ( } > 0 \text{)}.$$

## 5. Some Applications.

In this section several single species models will be examined from the point of view described in the preceding sections. These applications will illustrate the methods developed there and how they can provide basic results concerning the dynamics of the model equations.

The first application in Sec. 5.1 is to a simple model for the dynamics of a beetle population; it illustrates the simplest case of a typical (global) stable bifurcation to the right. The second example in Sec. 5.2 deals with a model of a cannibalistic population and illustrates both possibilities of left and right bifurcations as well as multiple positive equilibrium states. Sec. 5.3 shows how an Allee effect always leads to an unstable, left bifurcation. Finally, in Sec. 5.4 an application to a size-structured population with a density dependent growth rate is given for which assumption A1 holds (and hence Theorems 1 and 2 apply), but A2 fails to hold. In this application not only is Theorem 3 inapplicable, but its conclusion can be false because a right bifurcation can be unstable.

None of the applications will be examined in depth. Our purpose is only to illustrate the bifurcation methods above and is not to discuss biological conclusions and interpretations. Most of the applications are treated elsewhere in the literature.

### 5.1. A Model for *Tribolium* Dynamics.

Discrete models have been extensively used to help understand the complicated dynamics of the flour beetles in the genus *Tribolium* (Sokoloff (1974) and Costantino & Desharnais, (1991)). The model given below is a highly simplified one that tries to capture one of the most important aspects

of the dynamics of many species of *Tribolium*, viz. the cannibalism of egg and pupa by adults and larva. It is due to Costantino (private communication).

The model distinguishes only two classes, adults and immatures. The equations are given by (4) with  $x_1$  and  $x_2$  equal to the number of immatures and adults respectively and with

$$F = F(x_2) = \begin{bmatrix} 0 & b \exp(-c_e x_2) \\ 0 & 0 \end{bmatrix}, \quad T = T(x_2) = \begin{bmatrix} 0 & 0 \\ \exp(-c_p x_2) & 1 - \mu \end{bmatrix}.$$

Here the exponentials account for losses due to cannibalism, with the non-negative coefficients  $c_e$  and  $c_p$  (not both zero) corresponding to egg and pupa cannibalism respectively. The parameter  $b$  is the per unit adult fertility and  $\mu \in (0,1)$  is the adult mortality rate. The unit of time equals the maturation period.

Theorem 2 applies immediately to this model. Specifically, the matrix

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

satisfies A1 with  $r = b/\mu$ . This leads to the matrices

$$N(x_2) = \begin{bmatrix} 0 & \mu \exp(-c_e x_2) \\ 0 & 0 \end{bmatrix}, \quad Q(x_2) = \begin{bmatrix} 0 & \mu \exp(-c_e x_2) \\ 0 & \exp(-(c_e + c_p)x_2) \end{bmatrix}$$

and to the matrix

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

which has 1 as its strictly dominant eigenvalue. Hence assumption A2 also holds. It follows that Theorems 2 and 3 apply to this model.

Inasmuch as  $n(w) = \exp(-(c_e + c_p)w)$ ,  $w = x_2$ , and  $n'(0) = -(c_e + c_p) < 0$  the bifurcation of positive equilibria at  $r = 1$  is to the right and hence stable. More specific information can be obtained from Eq. (7) which, together with the equilibrium equation  $x_1 = bx_2 \exp(-c_e x_2)$ , shows that there exists a positive equilibrium for all (and only for)  $r > 1$ , in which case the positive equilibrium is unique.

This example illustrates the typical case of a stable, right bifurcation. It also illustrates that the stability of the positive bifurcating equilibria can only be guaranteed near the bifurcation point, that is for  $r$  near 1. An analysis of the linearized stability of the positive equilibrium shows that stability is lost for sufficiently large  $r$ . This leads to a secondary bifurcation at a point  $r = r_{cr} > 1$  which can be analytically calculated.

The positive equilibrium is stable if and only if  $1 < r < r_{cr}$  where

$$r_{cr} = \begin{cases} \exp((1 + \mu^{-1})(1 + \sigma)) & \text{when } \sigma < \sigma_{cr} = (3 - \mu)/(1 + \mu) \\ \exp(2(1 - \mu^{-1})(1 + \sigma)/(1 - \sigma)) & \text{when } \sigma > \sigma_{cr} \end{cases}$$

where  $\sigma = c_p/c_e$  is the ratio cannibalism coefficients. At this critical value there bifurcates a stable 2-cycle if the ratio  $\sigma > \sigma_{cr}$  and an attracting invariant closed loop if  $\sigma < \sigma_{cr}$ . The invariant loop is, near the secondary bifurcation point, approximately an ellipse, whose basic characteristics can be analytically calculated. If the length of one axis, making an angle  $\alpha$  with the  $x_1$  co-ordinate axis, is  $a_1$  and the length of the other axis is  $a_2$ , then  $\alpha$  and the axes ratio  $a_1/a_2$  are approximately given by the formulas

$$\alpha = \frac{1}{2} \tan^{-1} \left( \frac{cd}{c^2 - 1} \right), \quad \frac{a_1}{a_2} = \left( \frac{c^2 \tan^2 \alpha - cd \tan \alpha + 1}{\tan^2 \alpha + cd \tan \alpha + c^2} \right)^{1/2}$$

$$c = \exp\left(-\left(\frac{1 + \mu}{\mu}\right)\sigma\right), \quad d = 1 - \mu - (1 + \mu)\sigma.$$

*Tribolium* populations frequently exhibit oscillations in numbers. Typical estimated cannibalism coefficients imply  $c_p/c_e \approx 1.0$  and adult mortality is roughly  $\mu \approx 0.1$  (Costantino & Desharnais (1991)). Thus  $\alpha \approx 0$  and the ratio of juveniles to adults is quite large ( $a_1/a_2 \approx 10^4$ ), as is in fact observed in *Tribolium* data. The critical value  $r_{cr}$  from this over simplified model is, however, unrealistically high.

## 5.2. A Simple Model of Cannibalism.

The *Tribolium* model above illustrates the simplest kind of primary bifurcation in population models, namely a stable right bifurcation in which a unique positive equilibrium exists for  $r > 1$ . Our next example exhibits a wider variety of bifurcation phenomena.

Fox (1975) and Polis (1981) document the widespread occurrence of cannibalism in natural populations, across many taxa. Many dynamical phenomena have been attributed to cannibalism in various species under various circumstances. While it is responsible for population regulation (i.e. stabilization) in some cases, it is held responsible for destabilization and oscillations (as a kind of intra-specific predation) in other cases. Cannibalism can serve as a "life-boat" which allows a species to survive under circumstances when it could not survive in its absence, for example when food

resources drop to drastically low levels or when available food resources are only accessible to younger (smaller) individuals who must be cannibalized in order for larger individuals to obtain them. The existence of multiple stable equilibria and the resulting possibility of hysteresis effects have also been attributed to cannibalism. Cannibalism can have dramatic effects on the internal structure of the population. For example, it can result in the periodic elimination of entire age classes and the age class dominance by older (larger) individuals.

Several models for cannibalistic populations have appeared in the literature. Continuous age-structured models have been studied by Gurtin & Levine (1982), Diekmann et al. (1986), van den Bosch et al. (1988), Hastings & Costantino (1987) and Hastings (1987). Cushing (1992) studied continuous a size-structured model. Discrete models can be found in Landahl & Hansen (1975) and Cushing (1991).

A slight generalization of the model derived by Cushing (1991) is given by the equations

$$\begin{aligned}x_1(t+1) &= \zeta R f(x_2(t)) x_2(t) + \zeta c \phi(x_1(t)) x_1(t) \Psi(x_2(t)) \\x_2(t+1) &= (1 - c \Psi(x_2(t)) \phi(x_1(t))) x_1(t) + (1 - \mu) x_2(t).\end{aligned}$$

Here adult  $x_2$  competition for an external resource  $R$ , supplied per unit time, is modeled through the decreasing function  $f(x) \geq 0$ ,  $f(0) = 1$ ,  $f(+\infty) = 0$ . Adults also obtain food resources through cannibalism of juveniles  $x_1$ . The external resource  $R$  is measured in units such that the energy obtained from one unit of  $R$  is equal to that obtained from one cannibalized juvenile. The expression  $c \phi(x_1) \Psi(x_2)$  is the probability of an individual juvenile being cannibalized, which decreases with increasing juvenile population:  $\phi'(x) < 0$ ,  $\phi(0) = 1$ , and increases (but saturates) with increasing adult population:  $\Psi'(x) > 0$ ,  $\Psi(0) = 0$ ,  $\Psi(+\infty) = 1$ . The number  $c$  is the "cannibalism coefficient" and represents the maximum probability of being cannibalized and  $\zeta$  is a resource-to-offspring conversion factor. Theorem 2 applies immediately to this model (i.e., A1 holds). It turns out that  $r = \zeta R \mu^{-1}$  and

$$T(X) = \begin{bmatrix} 0 & 0 \\ 1 - c \Psi(x_2) \phi(x_1) & 1 - \mu \end{bmatrix}, \quad N(X) = \begin{bmatrix} 0 & \mu f(x_2) + \mu R^{-1} c \phi(x_1) x_1 \Psi(x_2) / x_2 \\ 0 & 0 \end{bmatrix}$$

The matrix

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

has eigenvalues  $1, \mu < 1$ . It follows that A2 also holds and Theorem 3 applies. From  $V^0 = \text{col}(1, 1/\mu)$  and

$$n(X) = \left( f(x_2) + R^{-1}c\phi(x_1)x_1\Psi(x_2)/x_2 \right) \left( 1 - c\Psi(x_2)\phi(x_1) \right)$$

is obtained

$$\nabla n(0) \cdot V^0 = \mu^{-1} \left( f'(0) + c(R^{-1} - \mu)\Psi'(0) \right)$$

whose sign determines the direction of bifurcation.

If  $\nabla n(0) \cdot V^0 < 0$  then the bifurcation is to the right and stable. This happens, for example, when cannibalism is absent  $c = 0$  or if cannibalism is present  $c > 0$  and the resource level  $R$  is large. On the other hand if  $R$  is small and cannibalism is present, then  $\nabla n(0) \cdot V^0 > 0$  and the bifurcation is to the left and unstable. In this case, however, the assumptions made imply that  $n(X) \rightarrow 0$ , and hence Eq. (7) implies that  $r \rightarrow +\infty$ , as  $|X| \rightarrow +\infty$ , i.e. the bifurcating branch "turns around" at a point  $r = r_{cr} < 1$  (where a saddle-node bifurcation occurs); see Fig.3. Thus there exist "large" stable positive equilibria for  $r < 1$  in this case. For a further discussion of this model (at least when  $\mu = 1$ ) and how it relates to the various dynamical phenomena attributed to cannibalism see Cushing (1991a).

### 5.3. The Allee Effect.

In the previous application it was seen how the negative and positive feedback mechanisms of cannibalism can cause a left unstable bifurcation to occur under certain circumstances. Another phenomenon which leads to a left unstable bifurcation is the so-called "Allee" effect (Allee, 1931) or "strict depensation" (Clark, 1976). Unlike the usual assumption that increased population densities have deleterious effects on vital rates (growth, fertility, survival, etc), the Allee effect assumes the opposite occurs, at least at low densities. Examples of increased fertility and/or survival rates with increased, low level population densities can be found in Allee (1931) and further references cited by Cushing (1988).

As in the previous applications, consider a two stage structured model consisting of juveniles and adults. The matrices

$$F(x_2) = \begin{bmatrix} 0 & bf(w) \\ 0 & 0 \end{bmatrix}, \quad T(x_2) = \begin{bmatrix} 0 & 0 \\ p_1 & p_2 \end{bmatrix}$$

model the case of a juvenile class with survival probability  $p_1$  (during one unit of time, here taken to be the maturation period) and an adult class with survival probability  $p_2$ . Both  $p_1$  and  $p_2$  are strictly less than one so that (3) holds and  $p_1 > 0$  so that Theorem 2 will apply. Adult fertility is density dependent upon a weighted population size  $w = w_1x_1 + w_2x_2$  with a density factor  $f(w)$  as shown in Fig. 2. In particular,  $f'(w) > 0$  for

INSERT FIGURE 2 NEAR HERE

small  $w \in [0, w_0)$  expresses the Allee effect on adult fertility. Since the usual deleterious effects of increased population density are assumed to occur at larger densities,  $f(w)$  is decreasing for  $w > w_0$ . For this application

$$N(x_2) = \begin{bmatrix} 0 & (1-p_2)f(w)/p_1 \\ 0 & 0 \end{bmatrix}, \quad T(x_2) = \begin{bmatrix} 0 & 0 \\ p_1 & p_2 \end{bmatrix}, \quad r = bp_1/(1-p_2)$$

and Theorem 2 implies the existence of a global bifurcation branch of positive equilibrium pairs  $(r, X)$  which satisfies (7) with  $n = n(w) = f(w)$ . Since the Allee assumption implies  $n'(0) > 0$ , the bifurcation is unstable. This bifurcating branch can be represented by a graph in the  $(r, w)$ -plane as shown in Fig. 3.

INSERT FIGURE 3 NEAR HERE

To pursue this example a little further the stability of a positive equilibrium will be analyzed by calculating the Jacobian at such an equilibrium

$$J = \begin{bmatrix} bw_1f'(w)x_2 & bw_2f'(w)x_2 + bf(w) \\ p_1 & p_2 \end{bmatrix}.$$

The equilibrium is stable if and only if the trace  $Tr$  and the determinant  $Det$  of this matrix satisfy the Jury conditions (Murray, 1989):  $|Det| < 1$ ,  $|Tr| < 1 + Det$ . From  $Det = (w_1p_2 - w_2p_1)bf'(w)x_2 + p_2 - 1$  and  $Tr = bw_1f'(w)x_2 + p_2$  it easily follows that if  $f'(w) > 0$  then  $Tr > 1 + Det$  and the second Jury condition fails. Thus, all equilibria at which fertility is increasing as a function of the weighted population size  $w$  are unstable. In



particular the lower portion of the left bifurcating branch for  $r < 1$  consists of unstable equilibria and the local instability guaranteed by Theorem 3 is in fact global until the turning point at the minimum value  $r_{cr} = 1/f(w_0)$  is reached. See Fig. 3.

What about the upper portion of the bifurcating branch? For  $r > r_{cr}$ , but near  $r_{cr}$ , for larger equilibria  $w$  on the upper branch  $f'(w) < 0$ ,  $f'(w) \approx 0$ , in which case it is easy to see that the Jury conditions hold. Thus, the upper branch is stable at least near the turning point (but may be lost for larger  $r$ ).

In summary, an Allee effect leads to an unstable bifurcation at  $r = 1$ . For values of  $r < 1$  there exist two stable equilibrium states, the extinction state 0 and a positive survival state. Consequently, survival requires sufficiently large initial population density. Moreover, there is a critical value of  $r$  below which there occurs a sudden collapse of the population, with a hysteresis effect occurring if  $r$  is increased back above this critical value.

For further analyses of the model in the case when  $p_2 = 0$ , i.e. the case of a semelparous population, see Cushing (1988b).

#### 5.4. Density Dependent Growth Rates.

In all of the previous applications, assumptions A1 and A2 have held and Theorems 1-3 have been applicable. In this section an example when this is not the case is examined. Specifically in the following application A1 holds but A2 fails. Consequently, while the existence of a global bifurcating branch of positive equilibria is assured by Theorems 1 and 2, Theorem 3 is inapplicable. Indeed, it will be seen in this example that although the bifurcation is to the right, the positive equilibrium near the bifurcation point can be unstable.

One question concerning intra-specific competition that has received considerable attention is that that might occur between juveniles and adults and whether or not such an interaction is a "stabilizing" or "destabilizing" influence on the population's dynamics. Generally, such juvenile vs. adult competition 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 dynamical model equations can be found in the papers of Ebenman (1987, 1988a, 1988b), Loreau (1990), Cushing & Li (1989, 1992b). Studies utilizing continuous models appear in May et al



(1974), Tschumy (1982), Cushing (1991b), and Cushing & Li (1991d).

In modeling juvenile vs. adult competition, there are several different basic possibilities depending upon how the competition effects the vital rates of both classes. Most model equations appearing in the literature are based upon age classes and competition is assumed to effect class survival rates and the adult fertility rate deleteriously. The many contributors to the book edited by Ebenman & Lennart (1989) argue that body size, rather than chronological age, is more often the determining factor in an individual's interaction with its physical and biological environment. In this case there is the further complication that competition can significantly effect an individual's growth rate, size at maturation, etc. Ebenman (1988b) studies a size-structured model with regard to the juvenile vs. adult competition question. His model is not analytically tractable, however, and he relies heavily on computer simulations. Cushing & Li (1992) consider a simpler model which focuses on the competition effects on size at maturation (and hence fertility). Here their model will be considered from the point-of-view of the methodology above and Theorems 1-3.

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 will mature, but its adult size depends on the amount of competition it experienced as a juvenile. The competition experienced will be assumed to be a function of the weighted population size  $w = x_1 + \gamma_1 x_2 + \gamma_2 x_3$  where the coefficients  $\gamma_i$  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 while  $x_2$  and  $x_3$  denote the densities of the smaller and larger adults classes respectively, then

$$x_1(t+1) = r(n_1 x_2(t) + n_2 x_3(t))$$

$$x_2(t+1) = \phi(w(t))x_1(t)$$

$$x_3(t+1) = (1 - \phi(w(t)))x_1(t)$$

where the normalization

$$n_1 \phi(0) + n_2 (1 - \phi(0)) = 1$$

is required so that  $r$  is the inherent net reproductive number. From

$$Q(X) = (I - T(X))^{-1}N(X) = \begin{bmatrix} 0 & n_1 & n_2 \\ 0 & \phi(w)n_1 & \phi(w)n_2 \\ 0 & (1 - \phi(w))n_1 & (1 - \phi(w))n_2 \end{bmatrix}$$

$$N(X) = \begin{bmatrix} 0 & n_1 & n_2 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}, \quad T(X) = \begin{bmatrix} 0 & 0 & 0 \\ \phi(w) & 0 & 0 \\ 1 - \phi(w) & 0 & 0 \end{bmatrix}.$$

we find that  $Q(0)$  has a strictly dominant eigenvalue 1 (and a double eigenvalue 0). The inequalities  $n_2 > n_1 > 0$  express the fact that larger individuals are more fertile. The function  $\phi(w) \in [0,1)$  is the fraction of juveniles growing to smaller size and incorporates the density dependence of juvenile growth. As a function of  $w$ , this fraction is assumed monotonically increasing:  $\phi'(w) > 0$ , which reflects the assumption that as 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 adult, considering a constant survivability over one unit of time. Thus no mortality coefficient is needed in the equations for  $x_2$  and  $x_3$ .)

As mentioned,  $Q(0)$  has a strictly dominant eigenvalue 1 and hence A1 holds. Theorems 1 and 2 guarantee the existence of a global, bifurcating branch of positive equilibria. Since  $n(w) = n_1\phi(w) + n_2(1 - \phi(w))$  and  $n'(w) = \phi'(w)(n_1 - n_2) < 0$ , a right bifurcation is seen to occur (and, in fact, because of the monotonicity, there is a unique positive equilibrium for each  $r > 1$ ).

However, the matrix

$$rN(0) + T(0) = \begin{bmatrix} 0 & rn_1 & rn_2 \\ \phi(0) & 0 & 0 \\ 1 - \phi(0) & 0 & 0 \end{bmatrix}$$

has eigenvalues  $0, -r^{1/2}, +r^{1/2}$  and consequently when  $r = 1$  it does not have 1 as a strictly dominant eigenvalue. As a result assumption A2 fails to hold and Theorem 3 cannot be applied.

Since the eigenvalues of  $rN(0) + T(0)$  lie inside the complex unit circle when  $r < 1$  and outside the circle when  $r > 1$  it follows that the trivial equilibrium loses stability at the bifurcation point  $(X,r) = (0,1)$ .

However, at  $r = 1$  this matrix has eigenvalue  $-1$  in addition to  $+1$ , which suggests that in addition to the transcritical bifurcation of the equilibrium branches there might also occur a bifurcation of 2-cycles. This in fact shown by Cushing & Li (1992) to be the case. At  $r = 1$  there bifurcates a global branch of non-negative "synchronous" 2-cycles (non-negative, nontrivial 2-cycles in which juvenile and adult populations are never simultaneously present). Thus for  $r > 1$  there exists both a unique positive equilibrium and a unique non-negative synchronous 2-cycle. Cushing & Li show that, at least near the bifurcation point, one of these branches is stable and the other is unstable depending upon the "competition coefficient" defined by  $\sigma = \gamma_1\phi(0) + \gamma_2(1 - \phi(0))$ . If  $\sigma < 1$  then the positive equilibrium branch is stable and the synchronous 2-cycle branch is unstable while if  $\sigma > 1$  then the opposite is the case. It is interesting to note that this result implies that strong juvenile vs. adult competition in this model population implies that the population will stabilize to a dynamical situation in which adults and juveniles never appear together. Thus, the population structure evolves, purely as a result of the dynamical assumptions, to a state in which competition is altogether avoided, a kind of temporal niche.

In this application, an example has been seen, when  $\sigma > 1$ , in which the relationship described in Theorem 3 between the direction of bifurcation and the stability of the positive equilibrium branch fails because assumption A2 fails to hold.

## 6. Multi-Species Interactions

Matrix models have been used mostly for the dynamics of single structured populations. Some exceptions in which matrix models have been used to describe the dynamics of interacting structured species are Pennycuik et al. (1968), Travis et al. (1979, 1980), Crowe (1991), Cushing (1991c, 1992a). The bifurcation methods used above for studying the equilibria of the nonlinear matrix Eq. (2) can also be used for coupled systems of matrix equations that arise in modeling interactions between several structured populations. The point of view will be that of adding a species  $Y(t)$  to a community of species at equilibrium in the absence of  $Y$  and modeled by the equation

$$X(t+1) = G(X(t), Y(t)). \quad (9)$$

Here  $X(t)$  is a vector of class densities of one or more species. For example  $X(t)$  might represent a single species whose dynamics are governed by an equation like Eq. (2) whose projection matrix is affected by another species

$Y(t)$  so that  $G(X,Y) = A(X,Y)X$ . In the absence of  $Y$ , the results and methods above apply to the dynamics of  $X$  with projection matrix  $A(X)$  replaced by  $A(X,0)$ . More generally,  $X(t)$  might also incorporate the class densities of more than one structured species. This community of "resident" species is assumed to have an equilibrium state. This equilibrium state will be used as the "trivial" equilibrium for the augmented system with the new or "invading" species  $Y$  added.

An equilibrium  $X_0$  of

$$X(t+1) = G(X(t),0) \quad (10)$$

is "non-degenerate" if 1 is not an eigenvalue of the Jacobian  $J_X G(X^0,0)$ . The resident community is assumed to have a non-degenerate equilibrium:

H1: Eq. (10) has a non-degenerate equilibrium  $X^0 > 0$ .

To Eq. (9) is now added a dynamical equation for  $Y$ :

$$\begin{aligned} X(t+1) &= G(X(t),Y(t)) \\ Y(t+1) &= B(X(t),Y(t))Y(t) \end{aligned} \quad (11)$$

where as before the projection matrix  $B$  for  $Y$  is decomposed into the sum  $B(X,Y) = F(X,Y) + T(X,Y)$  of a fertility and transition matrix which, as twice continuously differentiable functions, satisfy the assumptions of Sec. 2 and 3, and in particular the inequality (3). Then  $(I - T(X,Y))^{-1}$  exists and, following the procedure in Sec. 3, the equilibrium equations

$$X = G(X,Y), \quad Y = (F(X,Y) + T(X,Y))Y$$

can be rewritten as

$$X = G(X,Y), \quad Y = rQ(X,Y)Y \quad (12)$$

where  $F(X,Y) = rN(X,Y)$  and  $Q(X,Y) = (I - T(X,Y))^{-1}N(X,Y) = [q_{ij}(X,Y)]$  satisfies

$$\text{H2: } \begin{cases} 1 \text{ is a strictly dominant eigenvalue of } Q(X^0,0) \\ \text{with positive right and left eigenvectors } v^0 > 0, \\ w^0 > 0, w^0 \cdot v^0 = 1. \end{cases}$$

The  $r$  is the "inherent net reproductive number of  $Y$  when  $X = X^0$ ".

Eq. (11) has the trivial equilibrium  $(X,Y) = (X^0,0)$  for all values of  $r$ . A branch of positive equilibria  $(X,Y) > 0$  that bifurcates from this trivial equilibrium at  $r = 1$  is sought. Let  $Z = X - X^0$  and expand the equilibrium equations (12) in the Taylor series with remainder

$$Z = J_X G(X^0, 0)Z + J_Y G(X^0, 0)Y + \text{higher order}$$

$$Y = rQ(X^0, 0)Y + \text{higher order}$$

or using H1

$$Z = (I - J_X G(X^0, 0))^{-1} J_Y G(X^0, 0)Y + \text{higher order}$$

$$Y = rQ(X^0, 0)Y + \text{higher order}$$

These equilibrium equations can equivalently be written

$$\begin{bmatrix} Z \\ Y \end{bmatrix} = r \begin{bmatrix} 0 & (I - J_X G(X^0, 0))^{-1} J_Y G(X^0, 0) Q(X^0, 0) \\ 0 & Q(X^0, 0) \end{bmatrix} \begin{bmatrix} Z \\ Y \end{bmatrix} + \Omega(r, Z, Y)$$

where  $\Omega = O(|Z|^2 + |Y|^2)$  near  $(Z, Y) = (0, 0)$  (uniformly on finite  $r$  intervals). To this form of the equilibrium equation the global bifurcation theorems of Rabinowitz (1971) can again be applied to obtain the following general equilibrium existence result.

**THEOREM 4 (Equilibrium existence).** Under assumptions H1 and H2, there exists a "global" continuum (i.e. closed connected set) of nontrivial equilibria "pairs"  $(r; X, Y)$  for Eq.(11) that bifurcates from (i.e. contains) the trivial pair  $(1; X^0, 0)$  and that consists of positive equilibria  $(X, Y) > 0$  at least locally near  $(1; X^0, 0)$ .

The remarks following Theorem 1 concerning what is meant by "global" remain valid (with the obvious modification to the appropriate cross product space).

Liapunov-Schmidt expansion techniques can be used to establish a connection between the direction of bifurcation and the local stability of the bifurcating branch of positive equilibria. It turns out that the direction of bifurcation is determined by the sign of the quantity

$$\rho = -W^0 \cdot MV^0 \tag{13}$$

where  $M$  is the matrix

$$M = \left[ \nabla_X q_{ij}(X^0, 0) \cdot (I - J_X G(X^0, 0))^{-1} J_Y G(X^0, 0) V + \nabla_Y q_{ij}(X^0, 0) \cdot V^0 \right].$$

Namely, the bifurcation in Theorem 4 is to the right if  $\rho > 0$  and to the left if  $\rho < 0$ .

In order to establish the connection between the direction of bifurcation and the stability of the bifurcating branch two additional hypotheses are needed. The first assumes that the resident species equilibrium is stable:

H3: the eigenvalues of  $J_X G(X^0, 0)$  satisfy  $|\lambda| < 1$ .

Note that H3 implies H1. By H2,  $Q(X^0, 0)$  and consequently  $N(X^0, 0) + T(X^0, 0)$  have eigenvalue 1. This fact is strengthened by assuming

H4: 1 is a strictly dominant eigenvalue of  $N(X^0, 0) + T(X^0, 0)$ .

The following analog of Theorem 3 for the multi-species model equations (11) can now be shown.

**THEOREM 5** (Stability and direction of bifurcation). Assume H2, H3, and H4. Near the bifurcation point  $(r; X, Y) = (1; X^0, 0)$  the trivial equilibrium  $(X^0, 0)$  loses stability as  $r$  increases through 1, i.e.  $(X^0, 0)$  is (locally asymptotically) stable for  $r < 1$  and unstable for  $r > 1$ . Furthermore, the positive equilibria near the bifurcation point  $(1; X^0, 0)$  guaranteed by Theorem 4 are (locally asymptotically) stable if  $\rho > 0$  and unstable if  $\rho < 0$ .

## 7. Applications

Two multi-species applications will be considered. The first is an age-structured host-parasite model of Barclay (1986) to which Theorems 4 and 5 both apply. This application is a typical stable bifurcation example. The second application is a size-structured competition model studied by Cushing (1992a) and Crowe (1991) to which Theorem 4 applies but, because  $\rho = 0$ , Theorem 5 does not apply. Indeed in this application there is a "vertical" bifurcation (of neutrally stable) equilibria.

### 7.1. An Age-Structured Host Parasite Model

Barclay (1986) has investigated several discrete, age-structured, and density dependent models of a host-parasitoid interaction. In this work he is interested in relating host equilibrium numbers to the instar that is parasitized and in the implications of this relationship with regard to the use of parasitoids for pest control. Here one of his models will be considered from the point-of-view taken in Sec. 6.

Let  $X = \text{col}(x_1, \dots, x_m, x_{m+1})$  denote the vector of host densities and  $Y = \text{col}(y_1, \dots, y_w)$  the vector of adult parasitoid densities. Here  $x_i$  is the number of non-parasitized larva of age  $i \leq m$  and  $x_{m+1}$  is the number of adult hosts. The model takes the form of Eqs.(11) with

$$G(X(t), Y(t)) = A(X(t), Y(t))X(t), \quad B(X, Y) = F(X, Y) + T(X, Y)$$

$$F(X, Y) = \frac{1 - e^{-q\Pi(Y)}}{\Pi(Y)} u^{n-k} p^k x_a \begin{bmatrix} 1 & 1 & \dots & 1 \\ 0 & 0 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & 0 \end{bmatrix}, \quad T(X, Y) = \begin{bmatrix} 0 & 0 & \dots & 0 & 0 \\ s & 0 & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & s & 0 \end{bmatrix}.$$

$$A(X, Y) = \begin{bmatrix} 0 & 0 & \dots & 0 & \dots & 0 & fe^{-gx_m} \\ p & 0 & \dots & 0 & \dots & 0 & 0 \\ 0 & p & \dots & 0 & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & pe^{-q\Pi(Y)} & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & 0 & \dots & p & 0 \end{bmatrix} \leftarrow a+1$$

$\uparrow$   
 $a$

In this model the parameters have the following interpretations:

- $a$  = the age of only parasitized larva
- $p$  = mortality of non-parasitized hosts ( $< 1$ )
- $g$  = density coefficient for adult hosts
- $q$  = constant related to search efficiency
- $s$  = survivability of adult parasites ( $< 1$ )
- $n$  = development time for parasites
- $k$  = time after which parasites affect host mortality (assumed  $\leq n$ )
- $u$  = survivability of parasitized hosts after  $k$  time units ( $u < 1$ )

$$\Pi(Y) = \sum_{i=1}^W y_i = \text{total adult parasite numbers.}$$

For more details about this model and its derivation see Barclay (1988). In keeping with the approach above the dynamics of the host population will first be investigated in the absence of the parasitoids. Eq.(10) has a unique positive equilibrium given by

$$X^0 = \text{col}(x_1^0, \dots, x_{m+1}^0) = g^{-1} p^{-m} \ln(fp^m) \text{col}(1, p, \dots, p^m) > 0$$

provided the host inherent net reproductive number (in absence of parasites) exceeds one, i.e.  $fp^m > 1$ . An easy calculation shows that  $J_X G(X_0, 0)$  has

eigenvalues  $(1 - \ln(fp^m))^{1/(m+1)}$  which are less than one in magnitude if and only if  $1 < fp^m < e^2$ . Thus hypothesis H3 and hence H1 hold if

$$1 < fp^m < e^2 \quad (14)$$

which is assumed true.

For the host-parasite equations (11)

$$R(X,Y) = (I - T(X,Y))^{-1}F(X,Y) = \frac{1 - e^{-q\Pi(Y)}}{\Pi(Y)} u^{n-k} p^k x_a \begin{bmatrix} 1 & 1 & \dots & 1 \\ s & s & \dots & s \\ \vdots & \vdots & \dots & \vdots \\ s^{w-1} & s^{w-1} & \dots & s^{w-1} \end{bmatrix}.$$

There are two distinct eigenvalues of the matrix in this expression, namely 0 (with multiplicity  $w - 1$ ) and  $S = 1 + s + \dots + s^{w-1}$ . This means that  $R(X^0,0)$  has eigenvalues 0 and  $r = qSu^{n-k} p^k x_a^0 > 0$ . Writing  $F(X,Y) = rN(X,Y)$  where

$$N(X,Y) = \frac{1 - e^{-q\Pi(Y)}}{Sq\Pi(Y)} \frac{x_a}{x_a^0} \begin{bmatrix} 1 & 1 & \dots & 1 \\ 0 & 0 & \dots & 0 \\ \vdots & \vdots & \dots & \vdots \\ 0 & 0 & \dots & 0 \end{bmatrix}.$$

From  $Q(X,Y) = (I - T(X,Y))^{-1}N(X,Y)$  it follows that

$$Q(X^0,0) = \frac{1}{S} \begin{bmatrix} 1 & 1 & \dots & 1 \\ s & s & \dots & s \\ \vdots & \vdots & \dots & \vdots \\ s^{w-1} & s^{w-1} & \dots & s^{w-1} \end{bmatrix}$$

has eigenvalue 0 (with multiplicity  $w - 1$ ) and 1 (with multiplicity 1) and that the eigenvectors associated with 1 are  $V^0 = S^{-1} \text{col}(1, s, \dots, s^{w-1}) > 0$  and  $W^0 = \text{col}(1, \dots, 1) > 0$ . Thus H2 holds.

From Theorem 4 the existence of a global branch of nontrivial and locally positive equilibria that bifurcates from  $(X^0,0)$  at  $r = 1$  is guaranteed.

In order to apply Theorem 5 and determine the local stability of these positive equilibria near  $r = 1$  hypothesis H4 needs to be investigated. The eigenvalues of the matrix

$$N(X^0,0) + T(X^0,0) = \begin{bmatrix} 1/S & 1/S & \dots & 1/S & 1/S \\ s & 0 & \dots & 0 & 0 \\ 0 & s & \dots & 0 & 0 \\ \vdots & \vdots & \dots & \vdots & \vdots \\ 0 & 0 & \dots & s & 0 \end{bmatrix} \quad (15)$$

are the roots of the real characteristic polynomial  $p(\lambda) = q(\lambda)/S$ ,  $q(\lambda) = S\lambda^w - \lambda^{w-1} - s\lambda^{w-2} - \dots - s^{w-1}$ . Clearly  $\lambda = 1$  is a root of  $p(\lambda)$ . It will now be shown that  $\lambda = 1$  is strictly larger than the magnitude of all other roots. The polynomial  $q$  satisfies  $g(1) = 0$ ,  $g'(1) = 1 + 2s + \dots + ws^{w-1} > 0$  and hence  $g(u) > 0$  for real  $u$  greater than, but close to 1. Thus, for



any such number  $u$  and for any complex number  $\lambda$  satisfying  $|\lambda| = u$ , the inequalities

$$1 > \frac{u^{w-1} + su^{w-2} + \dots + s^{w-1}}{Su^w} \geq \left| \frac{\lambda^{w-1} + s\lambda^{w-2} + \dots + s^{w-1}}{S\lambda^w} \right| = \left| 1 - \frac{q(\lambda)}{S\lambda^w} \right|$$

hold. By Rouché's theorem  $\lambda^w$  and  $q(\lambda)$  (hence  $p(\lambda)$ ) have the same number of roots, counting multiplicities, inside the circle  $|\lambda| = u$  of the complex plane, namely  $w$ . Since  $u$  can be arbitrarily close to 1 it follows that all complex roots of  $p(\lambda)$  lie inside or on the circle  $|\lambda| = 1$ . But the matrix (15) is a Leslie matrix whose largest eigenvalue is known to be dominant (because, for example, there are two adjacent fertile age classes; Impagliazzo (1980)). Consequently, 1 is a strictly dominant eigenvalue of (15) and H4 holds.

Theorem 5 implies that the local, positive equilibria are stable if the bifurcation is to the right. The direction of bifurcation is determined by the sign of the quantity  $\rho$  in (13) which turns out to be positive by assumption (14):

$$\rho = \frac{1}{2} q^2 S^2 u^{n-k} p^{k+a-m-1} (2 - \ln(fp^m)) > 0$$

Theorem 5 now implies that a stable bifurcation of positive equilibria occurs at  $r = 1$  in this model. Stable positive equilibria represent stable host-parasitoid coexistence states.

Barclay (1986) determined the existence of positive equilibria by geometric arguments, while bifurcation theory has been used here. One advantage of the bifurcation theory approach is that it could easily be applied to more general model equations such as might be obtained, for example, from using more general nonlinearities, by allowing parasitism on more than one instar, etc. Such possibilities will not be pursued here. Another reward of our approach is the establishment of the stability of the positive bifurcating branch; Barclay investigated stability only by selected numerical simulations.

Also of importance in this application is the dependency of equilibrium levels on model parameter values. In the absence of explicit formulas for equilibria this kind of problem can be analytically difficult. The classical expansion (Liapunov-Schmidt) methods provide one way to obtain some results. If the bifurcating branch of positive equilibria is parameterized by an auxiliary parameter  $\varepsilon > 0$ , the expansion

$$(r; X, Y) = (1; X^0, 0) + (r^1; X^1, V^0)\varepsilon + O(\varepsilon^2)$$

substituted into the equilibrium equations (12), and coefficients of like powers of  $\epsilon$  equated, expressions for the first order coefficients  $r^1$  and  $X^1$  in terms of the model parameters can be obtained. Consider for example the parameter  $a$  (the age of the parasitized larva), which for the moment is allowed to be a continuous variable. Using this procedure the derivative

$$\frac{dx_{m+1}}{da} = \left( -Sqg^{-1} \ln(p) \right) \epsilon + O(\epsilon^2) > 0$$

can be calculated for  $\epsilon > 0$  small. Thus it is concluded, as in Barclay, that the host (pest) adult population equilibrium level is smallest when  $a = 1$ , i.e. the youngest larval stage is parasitized.

## 7.2. Interference Competition for Size-Structured Species

In conclusion, a two species example is given for which Theorem 4 applies but, because  $\rho = 0$ , Theorem 5 does not apply. The failure to obtain stability from Theorem 5 in this example is an expression of the competitive exclusion principle. How in this application the bifurcation point-of-view taken in this paper can be extended to non-equilibrium states will be briefly examined. Biologically the results illustrate that the classical competitive exclusion principle is very much an equilibrium theory and can be violated if non-equilibrium attractors are considered.

The following model equations for competing size-structured populations were derived and studied by Cushing (1991c, 1992a). A more general model with a dynamical resource population were studied by Crowe (1991). Let  $X$  and  $Y$  be size class distributions in which the  $i^{\text{th}}$  component is the number of individuals of length  $s_i$ . In Eq.(11) let  $G(X,Y) = A(X,Y)X$  with  $A = F_1 + T_1$ ,  $B = F_2 + T_2$  and

$$F_i = F_i(\Sigma) = r_i N_i(\Sigma) = \begin{bmatrix} \pi_{i1} \alpha_{i1} e^{-\Sigma} & \pi_{i2} \alpha_{i2} e^{-\Sigma} & \dots & \pi_{im} \alpha_{im} e^{-\Sigma} \\ 0 & 0 & \dots & 0 \\ \vdots & \vdots & \dots & \vdots \\ 0 & 0 & \dots & 0 \end{bmatrix}$$

$$T_i = T_i(\Sigma) = \begin{bmatrix} \pi_{i1}(1-\beta_{i1}e^{-\Sigma}) & \dots & 0 & 0 \\ \pi_{i1}\beta_{i1}e^{-\Sigma} & \dots & 0 & 0 \\ \vdots & & \vdots & \vdots \\ 0 & \dots & \pi_{i,m-1}(1-\beta_{i,m-1}e^{-\Sigma}) & 0 \\ 0 & \dots & \pi_{i,m-1}\beta_{i,m-1}e^{-\Sigma} & \pi_{im} \end{bmatrix}$$

where  $p_i(t) = \sum_{j=1}^m s_j x_j^{(i)}(t)$  is a weighted to population size, or more precisely the total population surface area, at time  $t$  and where  $\Sigma = \Sigma(p_1, p_2) = \sum_{j=1}^2 d_j p_j(t)$ , the  $d_j > 0$  being (interference) competition coefficients. The fraction  $\pi_{ij}$  is the probability that an individual of size  $j$  from the  $i^{\text{th}}$  species survives one unit of time. The coefficients  $\alpha_{ij}$  and  $\beta_{ij}$  are the "reproductive" and "growth" coefficients of the  $j^{\text{th}}$  size class of the  $i^{\text{th}}$  species respectively. These coefficients are related to basic physiological parameters such as per unit surface area resource uptake rates, fractions of consumed resource allocated to growth and reproduction, conversion factors of resource to offspring, etc.; see Cushing (1992a) for further details.

Consider first species  $X$  in the absence of  $Y$ :

$$X(t+1) = A(X(t), 0)X(t) \quad (16)$$

$$A(X, 0) = r_1 N_1(\Sigma(p_1, 0)) + T_1(\Sigma(p_1, 0))$$

It turns out that the dominant eigenvalue of  $Q_1(\Sigma) = (I - T_1(\Sigma))^{-1} N_1(\Sigma)$  is

$$n_1(\Sigma) = c(\Sigma)/c(0)$$

$$c_i(\Sigma) = \sum_{j=1}^m \alpha_{ij} \pi_{ij} \prod_{k=1}^j \frac{\pi_{i,k-1} \beta_{i,k-1}}{(\pi_{ik} \beta_{ik} + (1-\pi_{ik}) \exp(\Sigma))}$$

For notational convenience  $\pi_{10} = \beta_{10} = 1$ ,  $\beta_{1m} = 0$  have been defined. As in Sec. 3 the invariance of  $r_1 n_1$  along the equilibrium branch (see Eq.(7)) implies that the equation

$$r_1 n_1(\Sigma(p_1, 0)) = 1$$

holds for all pairs  $(r_1, X) \in \mathbb{R} \times \mathbb{R}^m$  on the branch, which in this case can be characterized as a branch  $(r_1, p_1)$  in  $\mathbb{R} \times \mathbb{R}$ . Inasmuch as  $0 < c(\Sigma)$  and hence  $n(\Sigma)$  is a decreasing function of  $\Sigma$  and  $c(+\infty) = 0$  it is seen that there exists a positive (single species) equilibrium for each  $r_1 > 1$  and

that this bifurcation is consequently to the right and stable.

Consider now the competition between the two species  $X$  and  $Y$ . As with the case of  $X$  alone just considered, it is not necessary to analyze the hypotheses H1-H4. The equilibrium situation can be discerned from the invariance of  $r_1 n_1$  for both species

$$r_1 n_1(\Sigma(p_1, p_2)) = 1, \quad r_2 n_2(\Sigma(p_1, p_2)) = 1. \quad (16)$$

Thus, if we fix an equilibrium  $(r_1, X^0)$  or  $(r_1, p_1^0)$ ,  $r_1 > 1$ , for species  $X$  in the absence of  $Y$  and look for the branch of coexistence equilibria  $(r_2; p_1, p_2)$  bifurcating from  $(1; p_1^0, 0)$ , from Eq.(16) it follows that  $r_2$  can only be one possible value, namely  $r_2 = 1/n_2(n_1^{-1}(1/r_1))$ , which by the normalization in Sec. 6 equals 1. That is to say, while Theorem 4 holds, the bifurcation is "vertical". Consequently, the bifurcation is neither to the right nor the left. Theorem 5 is inapplicable because  $\rho = 0$ .

Biologically this means that "generically" these two species cannot coexist in equilibrium. This is, of course, consistent with the competitive exclusion principle. If  $X^0$  is a stable equilibrium of Eq.(16) (which is true by Theorem 3 for  $r_1 > 1$  sufficiently close to 1), a straightforward linearization argument shows that  $(X, Y) = (X^0, 0)$  loses stability as  $r_2$  increases through 1 as asserted by Theorem 5. Although it has not been proved globally, this suggests that species  $X$  wins if  $r_2 < 1$  and species  $Y$  wins if  $r_2 > 1$ .

If, however,  $X^0$  is an unstable equilibrium of Eq.(16), then  $(X^0, 0)$  is unstable for all  $r_2$ . This does not mean that  $X$  and  $Y$  cannot coexist, however. For example, it can happen that Eq.(16) has a stable cycle instead of a stable equilibrium. The bifurcation point-of-view taken in this paper towards equilibria can be applied to cycles as well (i.e. to equilibria of an appropriate composition of Eq.(16)). This can lead to a bifurcating branch of coexisting cycles, which may not be vertical, and hence to a competition model in which although equilibrium coexistence is not possible, oscillatory coexistence is possible because stable cycles exist for an interval of  $r_2$  values, in contradiction to the classical notion of competitive exclusion for two species and one resource. For the mathematical details of this idea for these kinds of size-structured models see Crowe (1991) in which a nonlinear version of the classical strong ergodic theorem is used.

## 8. Concluding remarks

One possible approach to the existence and stability of equilibria of nonlinear matrix equations of the form (2) has been described above. The approach, utilizing bifurcation theory methods, is very general in its scope and provides one way of obtaining an overview of the basic equilibrium dynamics of these types of models. The results in Theorems 1-5 are similar to those obtained for continuous age-structured models by Cushing (1985, 1987), but are more general in that they allow for arbitrary structuring and for births into all classes (except for Theorem 3). The generality of the mathematical methods used here suggests that a similar approach could be applied to other types of discrete models. This includes, for example, models with periodically or seasonally varying parameters (as was done for continuous age-structured models by Cushing (1986)), models with delays (see Cushing (1985, 1987)), or models with spatial structure (Usher & Williamson (1970)).

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## CAPTIONS FOR FIGURES

Fig. 1

(consisting of Fig. 1a and Fig. 1b)

If  $\rho > 0$  in Theorem 3, then there exist positive equilibria  $X > 0$  for  $r$  greater than and near the critical bifurcation value  $r = 1$ . This fact is schematically represented in Fig. 1a by a bifurcation diagram in which the magnitude of the equilibrium vector  $X$  is plotted against the inherent net reproductive number  $r$ . If  $\rho < 0$  in Theorem 3, then the positive equilibria  $X$  that bifurcate from 0 are unstable for  $r$  less than and near the bifurcation point  $r = 1$  as is shown in Fig. 1b. Also shown is the loss of stability of the trivial (extinction) equilibrium  $X = 0$  as  $r$  increases through 1.

Fig. 2

The nonlinear effects of population density on adult fertility are determined by the factor  $f(w)$  as a function of the weighted population size  $w$ . That  $f(w)$  increases for "small" values of  $w$  between 0 and  $w_0$ , before monotonically decreasing for  $w > w_0$ , expresses an Allee effect on fertility.

Fig. 3

The branch of positive equilibria bifurcates to the left and are unstable near  $(r, X) = (1, 0)$ , as predicted by Theorem 3. In fact the branch is unstable until it "turns around" at the critical value  $r_{cr}$ , where a saddle-node bifurcation occurs with the upper branch of positive equilibria being stable at least for  $r$  near  $r_{cr}$ . The branch bifurcates to the left because of the Allee condition in  $f(w)$ , but turns around because  $f(w)$  ultimately decreases with increasing  $w$ .

Fig.1 a

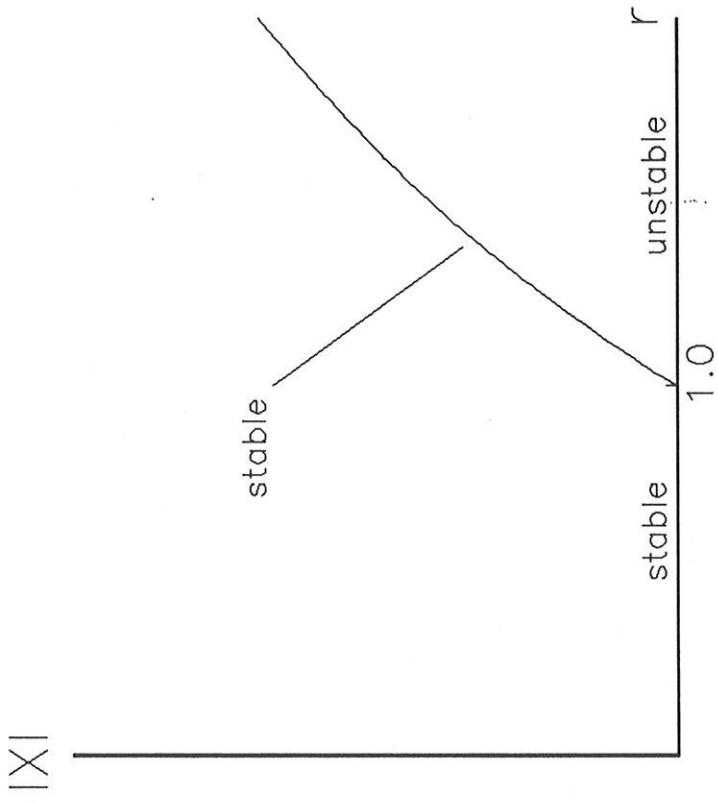


Fig.1 b

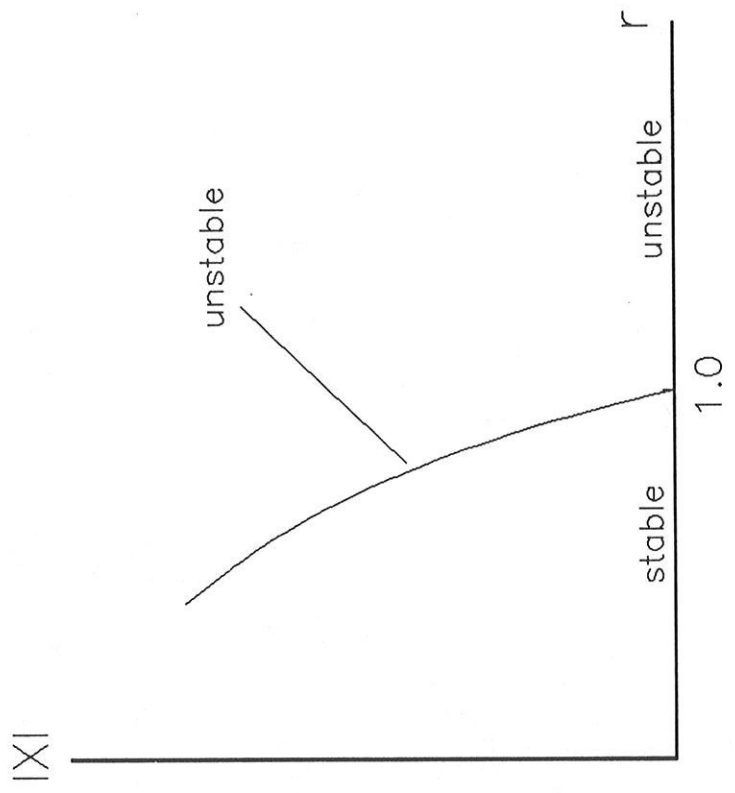


Fig. 2

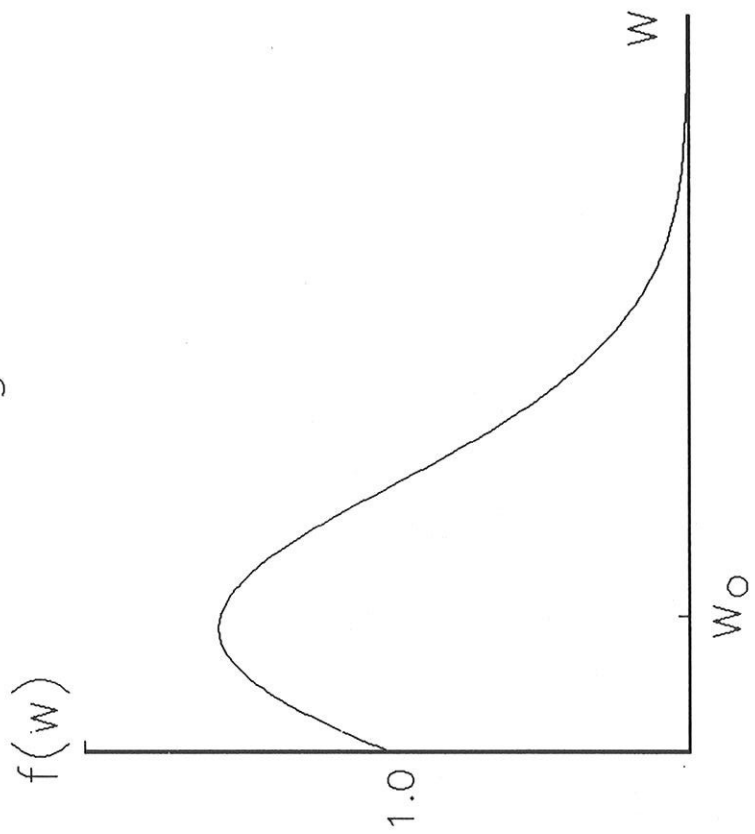
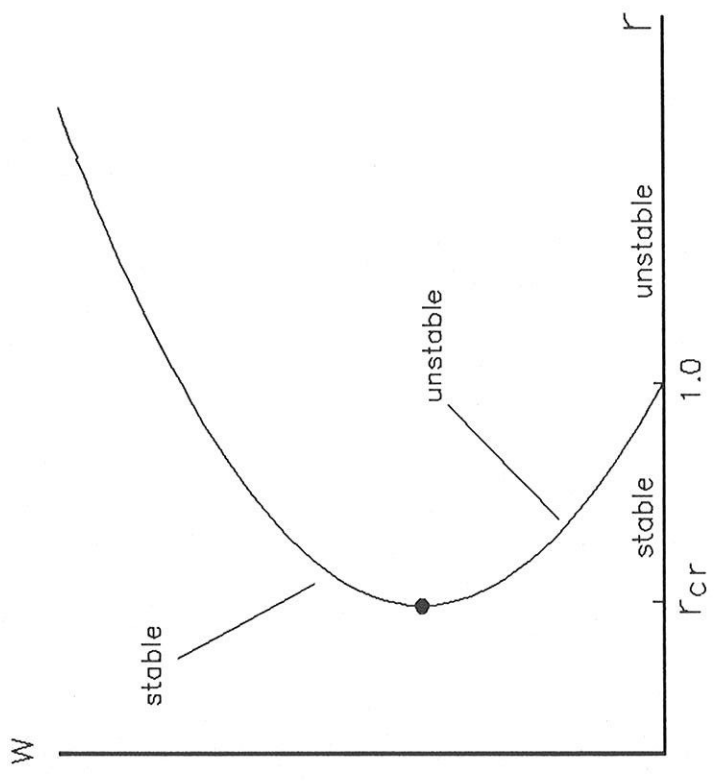


Fig. 3



## CAPTIONS FOR FIGURES

Fig. 1

(consisting of Fig. 1a and Fig. 1b)

If  $\rho > 0$  in Theorem 3, then there exist positive equilibria  $X > 0$  for  $r$  greater than and near the critical bifurcation value  $r = 1$ . This fact is schematically represented in Fig. 1a by a bifurcation diagram in which the magnitude of the equilibrium vector  $X$  is plotted against the inherent net reproductive number  $r$ . If  $\rho < 0$  in Theorem 3, then the positive equilibria  $X$  that bifurcate from 0 are unstable for  $r$  less than and near the bifurcation point  $r = 1$  as is shown in Fig. 1b. Also shown is the loss of stability of the trivial (extinction) equilibrium  $X = 0$  as  $r$  increases through 1.

Fig. 2

The nonlinear effects of population density on adult fertility are determined by the factor  $f(w)$  as a function of the weighted population size  $w$ . That  $f(w)$  increases for "small" values of  $w$  between 0 and  $w_0$ , before monotonically decreasing for  $w > w_0$ , expresses an Allee effect on fertility.

Fig. 3

The branch of positive equilibria bifurcates to the left and are unstable near  $(r, X) = (1, 0)$ , as predicted by Theorem 3. In fact the branch is unstable until it "turns around" at the critical value  $r_{cr}$ , where a saddle-node bifurcation occurs with the upper branch of positive equilibria being stable at least for  $r$  near  $r_{cr}$ . The branch bifurcates to the left because of the Allee condition in  $f(w)$ , but turns around because  $f(w)$  ultimately decreases with increasing  $w$ .