

A STRONG ERGODIC THEOREM FOR SOME NONLINEAR MATRIX MODELS FOR THE DYNAMICS OF STRUCTURED POPULATIONS

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ABSTRACT. A general class of matrix difference equation models for the dynamics of discrete class structured populations in discrete time which possess a certain general type of nonlinearity introduced by Leslie for age-structured populations is considered. Arbitrary structuring is allowed in that transitions between any two classes are permitted. It is shown that normalized class distributions for such nonlinear models globally approach a "stable class distribution" and thus possess a strong ergodic property exactly like that of the classical linear theory of demography. However, unlike in the linear theory according to which the total population size grows or dies exponentially, the dynamics of total population size in these nonlinear models are shown to be governed by a nonlinear, nonautonomous scalar difference equation. This difference equation is asymptotically autonomous, and theorems which relate the dynamics of total population size to those of this limiting equation are proved. Examples in which the results are applied to some nonlinear age-structure models found in the literature are given.

KEY WORDS: Ergodicity, nonlinear matrix models, structured population dynamics, stable class distribution.

1. Introduction. Ever since their introduction in the seminal work of Lewis [1942] and Leslie [1945], matrix difference equation models have been extensively used to describe the dynamics of age-structured populations. The linear theory is a beautiful application of the mathematical theory of nonnegative matrices and the famous Perron-Frobenius theorem. This theory, under certain technical assumptions, predicts the exponential growth of total population size while the normalized age distribution asymptotically tends to a "stable

age distribution" which is determined by the positive unit eigenvector of the projection matrix corresponding to the maximal, positive eigenvalue (e.g., see Impagliazzo [1980]).

Motivated by the usual observation that exponential growth is untenable for large time scales, Leslie considered modifications of the linear matrix models in a later paper (Leslie [1948]). He discussed several nonlinear matrix models for "limited population growth", or what is now referred to as density dependent growth, using the simple logistic model as a prototype. Nonlinear Leslie-type matrix models have been widely used in a variety of contexts since Leslie's 1948 paper. Some examples include Desharnais & Cohen [1986], Fisher & Goh [1984], Guckenheimer et al. [1976], Hassell & Comins [1976], Horwood and Shepherd [1981], Levin and Goodyear [1980], North [1985], Pennycuick [1969], Pennycuick et al. [1968], Travis et al. [1980].

The goal here is to develop and extend the theory of one type of nonlinearity which Leslie introduced in his 1948 paper. Amongst other things a rigorous proof of an observation made by Leslie concerning the asymptotic approach to "stable age distributions" for such nonlinear models will be obtained as a corollary.

Another development in the utilization of matrix models has been their use in modeling the dynamics of populations structured by dynamical variables other than chronological age. There is currently a great deal of interest in the modeling of populations whose dynamics can be understood only by taking into account internal structuring of the population by means of physiological states on which vital birth and death rates depend (Metz and Diekmann [1986]). Such states include size, weight, developmental stages, presence of important metabolical chemicals, various measures of physiological age, etc. There is a growing literature on both continuous and discrete models of these types for both single populations and multispecies interactions among structured populations.

Discrete matrix models for general class structured populations can be constructed in a manner analogous to the Leslie matrix models for age-structured populations, but they result in projection matrices which, unlike "Leslie matrices", may have nonzero entries off the first subdiagonal (see Lefkovich [1965]). Such entries account for the possibility that in one unit of time an individual may move to

a class other than the next class in the ordering. For example, "Usher matrices", which have been extensively used to model forest dynamics using tree diameter classes (Ek [1974], Usher [1966], Usher [1969]), have nonzero entries on both the first subdiagonal and the main diagonal of the projection matrix in order to account for the possibility that an individual remains in the same diameter class, rather than advances to the next diameter class, in one unit of time. Other examples are provided by the matrix models used to study plant dynamics based upon stages of growth and reproduction in which nonzero entries above the main diagonal appear because individuals are allowed to "regress" to earlier stages; see Caswell [1986] and Silvertown [1982]. Other references include Barclay [1986], Buongiorno & Michie [1980], Sarukhán & Harper [1973], Sarukhán & Gadil [1974], van Sickle [1977], Werner & Caswell [1977].

In this paper a general class of matrix models will be considered which possess a special type of nonlinearity introduced by Leslie, but which, unlike the Leslie models for age-structured populations, allow possible transitions between any two classes.

Suppose that the individuals of a population are categorized by means of n classes and that the numbers in each class are contained in an n -vector ρ . (In this paper all lower case Greek letters are vectors, except ϵ, δ and λ which are scalars. Lower case Roman letters are scalars.) In discrete time dynamical models the *density* (or *class distribution*) vector $\rho = \rho(i+1)$ at a given time $i+1$ is related to the density vector $\rho(i)$ at time i for all $i \in J_+ = \{0, 1, 2, 3, \dots\}$.

Let p_k be the probability that an individual in class k survives one unit of time. Let p_{jk} be the probability that an individual in class k at time i will be in class j at time $i+1$ given that it survives one unit of time. Then the expected fraction of individuals in class k that transfer to class j during one unit of time is $t_{jk} = p_k p_{jk} \in [0, 1]$. Let T denote the $n \times n$ transition matrix $T = (t_{jk}) \geq 0$.

To account for births let b_{jk} be the expected number of j -class offspring per k -class individual during one unit of time. If s_j is the probability that a j -class offspring born during any time interval survives to the end of that time interval, then $f_{jk} = s_j b_{jk}$ gives the expected number of j -class newborns per k -class individual at time $i+1$ due to births during the time interval from i to $i+1$. Let F be

the $n \times n$ fertility matrix $F = (f_{jk}) \geq 0$.

Finally, let $A = F + T \geq 0$. If A remains constant in time (and in particular if it is independent of population densities), then the density vector at time $i + 1$ is given by the linear, autonomous matrix equation

$$\rho(i + 1) = A\rho(i).$$

If the n classes are age classes one time unit in length and ordered from youngest to oldest, then A is a Leslie matrix, i.e., the first row consists only of the age specific fertilities f_{1k} , and the remaining $n - 1$ rows contain only the nonzero transition fractions $t_{j,j-1}$. If t_{jj} is also allowed to be nonzero, then A becomes an Usher matrix.

In density dependent growth dynamics the transition probabilities, the death rates and the fertilities at time i , and hence the projection matrix A , depend in some manner on the density vector $\rho(i)$. This of course leads to a nonlinear matrix equation for $\rho(i)$.

The type of nonlinear models considered here is based on two assumptions: that only the survival probabilities depend on ρ and that these probabilities are all affected in the same way by changes in ρ . Thus all survival probabilities p_j and s_j are multiplied by a fraction $h = h(\rho(i)) > 0$ with the result that $\rho(i)$ is now determined by the nonlinear matrix equation

$$(N) \quad \rho(i + 1) = h(\rho(i))A\rho(i).$$

A typical assumption is that the dependence of the factor h on the density vector is through a dependence on a *weighted population size*

$$(1.1) \quad w(i) = \omega \circ \rho(i), \quad \omega \geq 0, \omega \neq 0,$$

i.e., $h = k(w)$. When all weights in the weight vector ω are one, $w(t)$ becomes the *total population size* $p(t)$.

If we assume that A is the projection matrix in the absence of density effects, then $h(0) = 1$.

Let $|p|$ denote the absolute value of a scalar and let $\|\rho\|$ denote the norm of an n -vector obtained by summing the absolute values of its components. Since only nonnegative $\rho(i)$ are of interest here, $p(i) = \|\rho(i)\|$.

The paper is organized as follows. In §2 the main result of the paper is given (Theorem 1), which states that the nonlinear matrix equation (N) has the same strong ergodic property as the related linear matrix equation

$$(L) \quad \phi(i + 1) = A\phi(i)$$

and that the asymptotic dynamics of the total population size are determined by a certain nonlinear, nonautonomous scalar difference equation, namely (2.2). In §3 the fact that this difference equation is asymptotically autonomous is exploited in order to prove some results concerning the asymptotic dynamics of total population size. Applications to model equations appearing in the literature are given in §4. §5 briefly discusses some simple extensions of the results. The results in §3 are obtained by means of some general theorems concerning the relationship between the asymptotic dynamics of a nonautonomous difference equation and the asymptotic dynamics of its limiting autonomous equation which are proved in the appendix.

2. An ergodic theorem. Under the hypothesis

$$(H1) \quad A \text{ is nonnegative, irreducible and primitive}$$

the matrix A has a maximal eigenvalue λ which is positive, simple and has a strictly positive unit eigenvector $\eta > 0$, $\|\eta\| = 1$. The *strong ergodic theorem of demography* (Impagliazzo [1980]) states that if $\phi(0) \geq 0$, $\phi(0) \neq 0$, then the solution of (L) satisfies

$$\phi(i)/\|\phi(i)\| \rightarrow \eta \text{ as } i \rightarrow +\infty.$$

Thus the *normalized density (or class distribution) vector* given by $\phi(i)/\|\phi(i)\|$ asymptotically “stabilizes” to the eigenvector η . The following theorem asserts that the same is true for solutions of the nonlinear equation (N). Let \mathbf{R}^n denote n -dimensional Euclidean space and let $\mathbf{R} = \mathbf{R}^1$.

THEOREM 1. *Assume that assumption (H1) holds and suppose that $h : \mathbf{R}^n \rightarrow (0, 1]$, $h(0) = 1$. Let $\rho(i)$ be a solution of (N) with $\rho(0) \geq 0$, $\|\rho(0)\| > 0$. Then*

$$(2.1) \quad \nu(i) = \rho(i)/\|\rho(i)\| \rightarrow \eta \text{ as } i \rightarrow +\infty$$

and the total population size $p(i) = \|\rho(i)\|$ satisfies the scalar difference equation

$$(2.2) \quad p(i+1) = \|A\nu(i)\|h[\nu(i)p(i)]p(i)$$

$$p(0) = \|\rho(0)\| > 0.$$

PROOF. Since $\rho(0) \geq 0$ and A is nonnegative, it is clear that $\rho(i) \geq 0$ for all i . Moreover, by Gantmacher [1960; Remark 3, p.63], it follows that $\rho(i) \neq 0$ or $\|\rho(i)\| > 0$ for all $i \geq 1$. Thus $\nu(i)$ is well defined by (2.1) and the division of both sides of (N) by $\|\rho(i+1)\|$ shows that $\nu(i)$ satisfies the following equations:

$$\nu(i+1) = A\nu(i)/\|A\nu(i)\|, \quad \|\nu(i)\| = 1, \quad \text{for all } i \geq 0$$

$$\nu(0) = \rho(0)/\|\rho(0)\|.$$

It is not difficult to see that this problem has as its unique solution $\nu(i) = \phi(i)/\|\phi(i)\|$ where ϕ is the unique solution of (L) satisfying $\phi(0) = \rho(0)$. (Divide both sides of (L) by $\|\phi(i+1)\|$.) Thus, by the strong ergodic theorem for (L) under H1, (2.1) follows.

Finally,

$$p(i+1) = \|\rho(i+1)\| = h[\rho(i)] \|A\rho(i)\| = h[\nu(i)p(i)] \|A\nu(i)\|p(i)$$

which verifies (2.2).

An analogous result for continuous time models, but restricted to (continuous) age-structured populations, was discovered by Simmes [1978] (and independently by Busenberg & Iannelli [1985]). These authors seem unaware of the connection between their continuous age-structure models and the discrete models considered by Leslie [1948].

The scalar difference equation (2.2) which determines the dynamics of the total population size $p(i)$ is nonautonomous. The limit (2.1) implies, however, that this nonlinear equation has the autonomous "limiting equation" (LaSalle [1976])

$$(2.3) \quad q(i+1) = \lambda h[\eta q(i)]q(i).$$

One suspects then that the asymptotic dynamics of the total population size $p(t)$ can be determined from the asymptotic dynamics of this scalar

limiting equation. To a certain extent this is true as the results in §3 show.

Scalar difference equations such as (2.3) have been greatly studied in recent years, and it is by now certainly well known that they can possess a wide range of possible asymptotic dynamics, including simple equilibration, limit cycles of various periods and exotic strange attractors and chaos. The simple case of a stable, globally attracting positive equilibrium is the analog of logistic or "limited" growth sought by Leslie. However, even simple equations (2.3), i.e., equations with simple expressions for the density term h , can lead to more exotic and complicated dynamics. Nonetheless, it is interesting to note that by Theorem 1 the normalized class distribution $\nu(i)$ always "stabilizes" in the sense of (2.1) regardless of the dynamics of the total population size $p(i)$.

Some results concerning the asymptotic dynamics of (2.2) will be given in §3 as an application of the results in the Appendix. \square

3. The dynamics of the total population size. We have seen in Theorem 1 that under hypothesis (H1) positive solutions of the nonlinear matrix equation (N) satisfy the ergodic property (2.1) just as do solutions of the linear equation (L). Moreover, Theorem 1 says that the dynamics of the total population size $p(i)$ are governed by the scalar difference equation (2.2). The question is, how does $p(i)$ behave as $i \rightarrow \infty$?

Since (2.2) is asymptotic to the limiting equation (2.3), some answers to this question can be obtained by using Theorems 4-6 in the Appendix. A *solution* of a difference equation like (2.2) or (2.3) is a sequence $p : J_+ \rightarrow \mathbf{R}$ which satisfies the equation for all $i \in J_+$. The range of $p(i)$ is its *trajectory*. A *bounded solution* is one whose range lies in a bounded subset of \mathbf{R} . A solution $p(i)$ *approaches or tends* to a sequence $q(i)$ if $p(i) - q(i) \rightarrow 0$ as $i \rightarrow +\infty$. An *equilibrium* of the autonomous equation is a constant solution $q(i) = q_0$, for all $i \in J = \{0, \pm 1, \pm 2, \pm 3, \dots\}$ for some $q_0 \in \mathbf{R}$. More generally, a *cycle*, or more specifically, a *k-cycle* is a periodic solution, i.e., $q(i+k) = q(i)$, for all $i \in J$ and some (minimal) integer $k \geq 1$.

Theorems 4 and 5, under the assumption that

(H2) $h: R^n \rightarrow (0, 1]$, $h(0) = 1$, is continuously differentiable

yield the following theorem.

THEOREM 2. *Suppose (H1) and (H2) hold. In addition, suppose that the limiting scalar difference equation (2.3) has, in any compact subset of R , at most a finite number of cycles, all of which are hyperbolic. Finally, suppose that every bounded solution of (2.3), which is not itself a cycle, tends asymptotically to a cycle.*

If the total population size $p(i) = \|\rho(i)\|$ obtained from a positive solution $\rho(i)$ of (N) is bounded, then it must tend to a cycle of the limiting equation (2.3). Furthermore, if the equilibrium 0 of (2.3) is unstable, then $p(i)$ will not tend to 0 as $i \rightarrow +\infty$.

If $h \equiv 1$ in (2.3) this result reduces to the classical result for the linear equation (L) that the total population size grows (or dies out) geometrically if the maximal eigenvalue of the projection matrix A satisfies $\lambda > 1$ (or < 1).

An example given in the Appendix shows that the limit cycle in Theorem 2 need not be a stable cycle of the limiting equation (2.3).

Moreover, it is not true in general that if $p(i)$ is initially close to a stable cycle of (2.3), then $p(i)$ tends to this cycle, since initial dependencies on time i in the governing equation (2.2) can cause large deviations. The following theorem gives conditions under which the total population will tend to a stable cycle of (2.3). A proof is given in the Appendix.

THEOREM 3. *Suppose that $q(i)$ is a stable cycle of the limiting equation (2.3). Under the assumptions of Theorem 2 there exists $\delta > 0$ such that $|p(0) - q(0)| < \delta$ and $\|\nu(0) - \eta\| < \delta$ imply $p(i) - q(i) \rightarrow 0$ as $i \rightarrow \infty$.*

Note that in this theorem it is necessary for both the total population size and the normalized class distribution to be sufficiently close initially to the stable cycle and the "stable" class distribution respectively in order to guarantee that the total population size approaches that stable

cycle. It is in general not sufficient to start only the total population size close to a stable cycle in order to guarantee an asymptotic approach to that cycle. Or put another way, even a small disturbance of the total population size from a stable state in a structured population may be *destabilizing* if the disturbance at the same time severely affects the class distribution vector.

A common assumption is that the dependence of h on density ρ is through a dependency on a weighted total population size w as given by (1.1). If $h = k(w)$, $k : R \rightarrow (0, 1]$, $k(0) = 1$, then the limiting equation (2.3) becomes

$$(3.1) \quad q(i+1) = \lambda k[\eta \circ \omega q(i)]q(i),$$

or, if density dependence is determined by total population size (as in Leslie [1948]),

$$(3.2) \quad q(i+1) = \lambda k[q(i)]q(i).$$

Scalar autonomous difference equations of the form (2.3) and its special cases (3.1)-(3.2) have been intensively studied in recent years and a great deal is known about their asymptotic dynamics. It is widely appreciated that the dynamics of simple scalar difference equations, and in particular ones of the form (3.1) or (3.2), can be extremely varied, ranging from simple approach equilibrium to exotic strange attractors and chaos.

Thus one expects, in general, a wide range of dynamical behavior for the total population size of populations governed by (N). We have not established, however, a connection between the dynamics of the limiting equation (2.3) and those of the governing equations (2.2) except under the assumption in Theorem 2 which in effect rules out exotic behavior and allows only equilibrium or limit cycle behavior.

A popular way to study the dynamics of such equations is to use the concepts and tools of bifurcation theory in order to understand how the dynamics depend on parameters in the equations. In the case (2.3), λ is a natural parameter to use. As we have seen in the linear case, the dynamics of total population size depend crucially upon λ and change qualitatively at the critical value $\lambda = 1$. The same can be shown, in a certain sense, for the nonlinear case.

The following facts can be established for the autonomous limiting equation (2.3) using bifurcation theory techniques (see, e.g., Cushing [1988a], Guckenheimer et al. [1976]). For $\lambda < 1$ the trivial solution 0 is stable and for $\lambda > 1$ the trivial solution 0 is unstable. There exists an unbounded continuum for solution "pairs" (λ, q) which bifurcates from $(1, 0)$ and consists (except for $(1, 0)$) of positive equilibria q . Near $(1, 0)$ these positive equilibria are stable if the bifurcation is "to the right or supercritical" (i.e., $\lambda > 1$ for (λ, q) near $(1, 0)$) and unstable if it is "to the left or subcritical". For the equation (2.3) stable supercritical bifurcation occurs if $\eta \circ \Delta_\rho h(0) < 0$, or $k'(0) < 0$ in the special case (3.1), and unstable subcritical bifurcation occurs in the event of the opposite inequality.

The most commonly occurring case is the supercritical stable case in which increases in density result in decreases in the survivability. The scenario in this case usually goes as follows (Guckenheimer *et al.* [1976]). Only 0 is stable for $\lambda < 1$ while a positive equilibrium (usually unique) exists for those $\lambda > 1$ which are stable at least for λ close to 1 but which may lose stability with increased values of λ through a Hopf bifurcation to a stable 2-cycle. The 2-cycles may then lose stability with further increases of λ through a bifurcation to a stable 4-cycle and so forth on through a cascade of period doubling stable bifurcations. Within this regime the hypotheses in Theorem 2 generally hold and the asymptotic dynamics of the total population size $p(i)$ are determined by these limit equation dynamics by means of the results in §3. For larger values of λ the dynamics can become chaotic and the hypotheses in Theorem 2 can fail to hold, although one suspects that the dynamics of (2.2) are nonetheless related to those of the limiting equation (2.3), i.e., are probably also chaotic. See example 5(b) below.

The subcritical bifurcation case is intimately related to the so-called Allee effect in which low level density increases result in enhanced survivability (Cushing [1988b]).

Regardless of the dynamics of total population size as it is determined by (2.2) (whether solutions asymptotically equilibrate or approach limit cycles, whether there are multiple attracting asymptotic states or even whether there are exotic dynamics such as "chaos"), Theorem 1 shows that the normalized class distribution ergodically approaches a "stable class distribution" in a manner identical to that of the linear density independent case (L).

4. Examples. Two examples from the literature will illustrate the results above. The first example is from Leslie's 1948 paper. Amongst other things it rigorously proves (and generalizes) an observation of Leslie concerning the logistic-like growth of the total population size and the ergodic property of the class distribution vector. The second example illustrates the possibility of more exotic asymptotic dynamics for total population size.

(a) Leslie [1948] considers an age-structured population under the assumption that the survival probabilities of all age classes are reduced by the same fraction dependent upon the total population size. In his case A is a "Leslie" matrix. It is assumed here more generally that the population is not necessarily structured by age, but only that the projection matrix A satisfies H1. It is assumed, however, that as in Leslie [1948] the density term h is given by the expression

$$(4.1) \quad h(\rho) = k(\|\rho\|) \text{ where } k(p) = \frac{1}{1 + \alpha p}, \quad \alpha > 0.$$

(In order to meet the technical domain requirements on h above, we redefine k for $p < 0$ in such a way that k is continuously differentiable for all $p \in \mathbf{R}$.)

For this case the equation (2.2) governing the dynamics of the total population size $p(i)$ is

$$(4.2) \quad p(i + 1) = \|A\nu(i)\| \frac{p(i)}{1 + \alpha\|\nu(i)\|p(i)}$$

whose limiting equation (3.2), by the ergodic property (2.1) satisfied by $\nu(i)$, is

$$(4.3) \quad q(i + 1) = \lambda \frac{q(i)}{1 + \alpha q(i)}$$

where $\lambda > 0$ is the maximal eigenvalue of A .

It is easy to see that all solutions of (4.2) are bounded. Furthermore, it is a simple matter to analyze the asymptotic dynamics of (4.3). For $0 < \lambda < 1$ all solutions with $q(0) > 0$ tend to 0 as $i \rightarrow +\infty$. For $\lambda > 1$ all solutions with $q(0) > 0$ tend to the unique equilibrium $(\lambda - 1)/\alpha$.

Noting that no solution of (4.3) with $p(0) > 0$ can vanish in finite time, we conclude from Theorems 1 and 2 that *if A satisfies H1 and if the density term h is given by (4.1), then any solution of the nonlinear matrix equation (N) with $\rho(0) > 0$ satisfies the ergodic property (2.1) and the corresponding total population size $p(i)$ tends to zero if the maximal eigenvalue λ of A is less than one and tends to the equilibrium value $(\lambda - 1)/\alpha$ if the maximal eigenvalue is greater than one.*

Numerical examples can be found in Leslie's 1948 paper.

As a further generalization of Leslie's example, we note that the same result holds if the density term h is assumed to be a function of weighted population size w given by (1.1). The limiting equation (4.3) is modified according to (3.1) and all that changes above is the value of the equilibrium to $(\lambda - 1)/\alpha\eta \circ w$.

(b) If, in the above example, we replace h in (4.1) by

$$(4.4) \quad h = k(p) = \exp(-\alpha p), \quad \alpha > 0,$$

we obtain an example studied by Desharnais & Cohen [1986]. These authors, however, consider only the age-structured case). The resulting nonautonomous difference equation for total population size has a bounded right hand side and hence all solutions are bounded. The limiting equation for this case is

$$(4.5) \quad q(i+1) = \lambda e^{-\alpha q(i)} q(i).$$

For $\lambda < 1$ all solutions of (4.5) with $q(0) > 0$ tend to 0 as $i \rightarrow +\infty$. For $1 < \lambda < e^2$ all solutions with $q(0) > 0$ tend to the unique equilibrium value $q_\infty = \alpha^{-1} \ln \lambda$. At $\lambda = e^2$ there occurs a Hopf bifurcation to a stable 2-cycle. Further increases in λ result in a cascade of period doubling bifurcations until a critical value is reached (approximately $e^{2.6924} \approx 14.767$..) after which chaotic dynamics result. See May and Oster [1976] for a complete description of the dynamics of (4.5).

Applying Theorems 1, 2 and 3 we conclude that *if A satisfies H1 and if the density term h is given by (4.4), then any solution of the nonlinear matrix equation (N) with $\rho(0) > 0$ satisfies the ergodic property (2.1). The corresponding total population size $p(i)$ tends to zero if the maximal eigenvalue λ of A is less than one. If $1 < \lambda < e^2$, then $p(i)$ tends to the equilibrium value $\alpha^{-1} \ln \lambda$. For $\lambda > e^2$ prior to the onset of chaos $p(i)$*

tends to a positive k -cycle for some $k \geq 1$ and any solution $\rho(i)$ initially near a stable k -cycle whose initial class distribution is sufficiently close to the stable distribution η tends to that stable k -cycle.

The dynamics of the total population size when λ lies in a chaotic region of the limiting equation (4.5) remains an open question, although one suspects that it is also chaotic. This is borne out by the numerical examples below.

Tables 1-4 give the results of selected numerically calculated solutions of equation (N) for nonlinearity (4.4) with $\alpha = 1$ with various 3×3 matrices of the form $A = F + T$ with

$$(4.6) \quad F = \begin{bmatrix} 0 & f_{12} & f_{13} \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}, \quad T = \begin{bmatrix} 0 & 0 & 0 \\ p_{21} & 0 & 0 \\ 0 & p_{32} & 0 \end{bmatrix}.$$

This corresponds to a population with three age classes, the first of which consists of nonreproducing juveniles.

The four cases represented in these tables all corroborate the fundamental conclusion above in that, despite the diverse dynamics exhibited by total population size, the normalized age distribution stabilizes to the normalized eigenvalue of A .

The inherent growth rate λ increases from Table 1 to Table 4 in such a way as to produce respectively extinction, equilibration, an asymptotic 2-cycle, and apparent chaos in total population size.

TABLE 1. The *normalized* age distribution vector $\nu(i)$ and the total population size $p(i)$ are given (rounded to three significant digits) for a solution of (N) with matrix $A = F + T$ given by (4.6) with nonzero entries $f_{12} = 2.25$, $f_{13} = 1$, $p_{21} = 0.25$, $p_{32} = 0.75$ and with nonlinearity (4.4) with $\alpha = 1$. The initial distribution is $\rho(0) = (1, 1, 1)$. Rounded to six significant digits, the dominant eigenvalue of this Leslie matrix is $\lambda = 0.880583$ and the corresponding normalized eigenvector is $\text{col}(0.655435, 0.186080, 0.158486)$. (In actuality agreement between these figures and those in the table was obtained to six significant digits.) In this case the total population size tends to 0 as $i \rightarrow +\infty$.

Time i	Components of the			Total population $p(i)$
	Normalized Age Distribution			
0	3.33 E-01	3.33 E-01	3.33 E-01	3.00 E 00
1	7.65 E-01	5.88 E-02	1.76 E-01	2.12 E-01
2	5.68 E-01	3.51 E-01	8.11 E-02	9.32 E-02
3	6.83 E-01	1.11 E-01	2.06 E-01	1.08 E-01
4	6.42 E-01	2.40 E-01	1.17 E-01	6.91 E-02
5	6.59 E-01	1.61 E-01	1.80 E-01	6.44 E-02
:				:
:				:
95	6.55 E-01	1.86 E-01	1.58 E-01	4.33 E-07
96	6.55 E-01	1.86 E-01	1.58 E-01	3.81 E-07
97	6.55 E-01	1.86 E-01	1.58 E-01	3.36 E-07
98	6.55 E-01	1.86 E-01	1.58 E-01	2.96 E-07
99	6.55 E-01	1.86 E-01	1.58 E-01	2.60 E-07
100	6.55 E-01	1.86 E-01	1.58 E-01	2.29 E-07

TABLE 2. The *normalized* age distribution vector $\nu(i)$ and the total population size $p(i)$ are given for a solution of (N) with matrix $A = F + T$ given by (4.6) with nonzero entries $f_{12} = 6$, $f_{13} = 2.67$, $p_{21} = 0.25$, $p_{32} = 0.75$ and with nonlinearity (4.4) with $\alpha = 1$. The initial distribution is $\rho(0) = (1, 1, 1)$. Rounded to six significant digits, the dominant eigenvalue of this Leslie matrix is $\lambda = 1.36603$ and the corresponding normalized eigenvector is $\text{col}(0.779123, 0.142590, 0.782871E - 01)$. (In actuality agreement between these figures and those in the table was obtained to six significant digits.) In this case the total population size tends to an equilibrium value as $i \rightarrow +\infty$.

Time i	Components of the			Total population $p(i)$
	Normalized Age Distribution			
0	3.33 E-01	3.33 E-01	3.33 E-01	3.00 E 00
1	8.97 E-01	2.57 E-02	7.76 E-01	4.81 E-01
2	5.98 E-01	3.70 E-01	3.20 E-02	1.80 E-01
3	8.44 E-01	5.47 E-02	1.02 E-01	4.11 E-01
4	7.04 E-01	2.48 E-01	4.82 E-02	2.31 E-01
5	8.17 E-01	8.90 E-02	9.40 E-02	3.64 E-01
:				:
:				:
95	7.79 E-01	1.43 E-01	7.83 E-02	3.11 E-01
96	7.79 E-01	1.43 E-01	7.83 E-02	3.11 E-01
97	7.79 E-01	1.43 E-01	7.83 E-02	3.11 E-01
98	7.79 E-01	1.43 E-01	7.83 E-02	3.11 E-01
99	7.79 E-01	1.43 E-01	7.83 E-02	3.11 E-01
100	7.79 E-01	1.43 E-01	7.83 E-02	3.11 E-01

TABLE 3. The *normalized* age distribution vector $\nu(i)$ and the total population size $p(i)$ are given for a solution of (N) with matrix $A = F + T$ given by (4.6) with nonzero entries $f_{12} = 300$, $f_{13} = 133^{1/3}$, $p_{21} = 0.25$, $p_{32} = 0.75$ and with nonlinearity (4.4) with $\alpha = 1$. The initial distribution is $\rho(0) = (1.0, 0.2, 0.0)$. Rounded to six significant digits, the dominant eigenvalue of this Leslie matrix is $\lambda = 8.82234$ and the eigenvector is $\text{col}(0.970171, 0.274919\text{E-}02, 0.233712\text{E-}03)$. (In actuality agreement between these figures and those in the table was obtained to six significant digits.) In this case the total population size tends to a 2-cycle as $i \rightarrow +\infty$.

Time i	Components of the			Total population $p(i)$
	Normalized Age Distribution			
0	8.33 E-01	1.67 E-01	0.00 E 00	1.20 E 00
1	0.93 E-01	4.14 E-03	2.48 E-03	1.82 E-01
2	8.62 E-01	1.36 E-01	1.70 E-03	4.17 E-07
3	9.92 E-01	5.20 E-03	2.47 E-03	1.73 E-05
4	8.82 E-01	1.16 E-01	1.82 E-03	3.70 E-05
5	9.91 E-01	6.25 E-03	2.46 E-03	1.30 E-03
:				:
:				:
195	9.70 E-01	2.75 E-02	2.34 E-03	3.22 E 00
196	9.70 E-01	2.75 E-02	2.34 E-03	1.13 E 00
197	9.70 E-01	2.75 E-02	2.34 E-03	3.22 E 00
198	9.70 E-01	2.75 E-02	2.34 E-03	1.13 E 00
199	9.70 E-01	2.75 E-02	2.34 E-03	3.22 E 00
200	9.70 E-01	2.75 E-02	2.34 E-03	1.13 E 00

TABLE 4. The *normalized* age distribution vector $\nu(i)$ and the total population size $p(i)$ are given for a solution of (N) with matrix $A = F + T$ given by (4.6) with nonzero entries $f_{12} = 1200$, $f_{13} = 533^{1/3}$, $p_{21} = 0.25$, $p_{32} = 0.75$ and with nonlinearity (4.4) with $\alpha = 1$. The initial distribution is $\rho(0) = (1.01, 0.01, 0.01)$. Rounded to six significant digits, the dominant eigenvalue of this Leslie matrix is $\lambda = 17.4848$ and the eigenvector is $\text{col}(0.985308, 0.140880\text{E-}02, 0.604297\text{E-}04)$. (In actuality agreement between these figures and those in the table was obtained to six significant digits.). In this case the total population size has no apparent asymptotic regularity as $i \rightarrow +\infty$.

Time i	Components of the			Total population $p(i)$
	Normalized Age Distribution			
0	9.81 E-01	9.71 E-03	9.71 E-03	1.03 E 00
1	9.85 E-01	1.44 E-02	4.26 E-04	2.08 E-01
2	9.85 E-01	1.39 E-02	6.08 E-04	2.29 E 00
3	9.85 E-01	1.43 E-02	6.04 E-04	2.91 E 00
4	9.85 E-01	1.39 E-02	6.05 E-04	2.79 E 00
5	9.85 E-01	1.43 E-02	6.04 E-04	2.97 E 00
6	9.85 E-01	1.39 E-02	6.05 E-04	2.70 E 00
7	9.85 E-01	1.43 E-02	6.04 E-04	3.14 E 00
8	9.85 E-01	1.39 E-02	6.05 E-04	2.41 E 00
9	9.85 E-01	1.42 E-02	6.04 E-04	3.75 E 00
10	9.85 E-01	1.39 E-02	6.05 E-04	1.55 E 00
:				:
:				:
190	9.85 E-01	1.41 E-02	6.04 E-04	3.24 E 00
191	9.85 E-01	1.41 E-02	6.04 E-04	2.22 E 00
192	9.85 E-01	1.41 E-02	6.04 E-04	4.22 E 00
193	9.85 E-01	1.41 E-02	6.04 E-04	1.08 E 00
194	9.85 E-01	1.41 E-02	6.04 E-04	6.43 E 00
195	9.85 E-01	1.41 E-02	6.04 E-04	1.81 E 00
196	9.85 E-01	1.41 E-02	6.04 E-04	2.65 E 00
197	9.85 E-01	1.41 E-02	6.04 E-04	3.26 E 00
198	9.85 E-01	1.41 E-02	6.04 E-04	2.19 E 00
199	9.85 E-01	1.41 E-02	6.04 E-04	4.28 E 00
200	9.85 E-01	1.41 E-02	6.04 E-04	1.04 E 00

5. Some generalizations. For simplicity only the autonomous matrix equation (N) for a single structured population was considered above. Several extensions and generalizations of the results above are rather obviously obtainable in a straightforward manner.

For example, the density term h was assumed dependent on time i only through a dependency on the density $\rho(i)$. However, Theorem 1 is still valid and the theorems of the Appendix still apply to the limiting equation if h depends explicitly on i , say $h = h(i, \rho(i))$, in such a way that $\lim_{i \rightarrow \infty} h(i, x) = g(x)$.

The asymptotic equivalence results of §3 can be based upon abstract results of LaSalle [1976] which can also handle nonautonomous limiting equations, i.e., $g = g(i, x)$, although the details are more complicated due to such things as the nature of convergence. This is not pursued here, except to say that if h is asymptotically periodic, i.e., $g = g(i, x)$ is k -periodic in its first variable, then results similar to those above can be obtained by application of the methods in the Appendix to the k -fold composition of the equation (N). This case would be of interest, for example, in treating cases with seasonal periodicities in mortality.

Finally, we point out that systems of interacting species each of whose dynamics are modelled by matrix equations of the form (N), but whose density terms h (which may be different for each species) depend on the densities of other species, can be shown to satisfy an ergodic theorem like Theorem 1. Each species has a "stable distribution", and the dynamics of all total population sizes will be governed now by a system of difference equations which are asymptotically autonomous.

6. Summary. It has been seen that, for a certain type of nonlinearity introduced by Leslie for discrete time, discrete class structured population growth models, the classical linear ergodic theory remains valid. That is to say, the normalized class distribution asymptotically approaches the so-called "stable class distribution". This stable class distribution is the same as that for the density independent, linear case (i.e., it is the positive unit eigenvector of the projection matrix).

Unlike in the classical linear theory, however, the total population size does not in general grow or decrease geometrically but instead has asymptotic dynamics determined by a nonlinear, nonautonomous scalar difference equation which has an autonomous limiting equation.

Thus, while the normalized class distribution “stabilizes”, the total population may behave in a number of different ways; for example, it may equilibrate or it may approach a limiting k -cycle for some k . Although the case is not studied here, the total population size may even have exotic dynamics in that there may be strange attractors or chaos. Regardless of the dynamics of the total population size, however, the normalized class distribution is ergodic for this special class of nonlinear models.

APPENDIX

In this Appendix some theorems concerning the relationship between a scalar difference equation and its asymptotic limiting equation are given. Many of these results can be proved by reference to general results of LaSalle [1976]. However, for completeness and in order to relieve an interested reader from having to delve into and cope with the abstract setting in LaSalle’s book, elementary, self-contained proofs are given.

Consider the nonautonomous difference equation

$$(DE) \quad x(i + 1) = f(i, x(i))$$

where $f : J_+ \times R \rightarrow R$ is continuously differentiable in $x \in R$ for each i . A *solution* of (DE) is a sequence $x : J_+ \rightarrow R$ which satisfies (DE) for all $i \in J_+$. The range of $x(i)$ is its *trajectory*. A *bounded solution* of (DE) is one whose trajectory lies in a bounded subset of R . A solution $x(i)$ *approaches or tends* to a sequence $y(i)$ if $x(i) - y(i) \rightarrow 0$ as $i \rightarrow +\infty$. The set of limit points Ω of a solution $x(i)$ of (DE) is called the *limit set* of the solution. If $x(i)$ is bounded then Ω is compact. It is not difficult to show that x approaches its limit set in the sense that the distance between Ω and $x(i)$ tends to zero as $i \rightarrow +\infty$.

Under the assumption

$$(H3) \quad \begin{array}{l} f(i, x) \rightarrow g(x) \text{ uniformly on compact subsets of } R \\ \text{as } i \rightarrow +\infty \text{ where the function} \\ g : R \rightarrow R \text{ is once continuously differentiable} \end{array}$$

the equation (DE) is associated with the *limiting equation*

$$(LE) \quad y(i + 1) = g(y(i)).$$

An *equilibrium solution* of this autonomous equation (LE) is a solution $y(i) = y_0$, for all $i \in J = \{0, \pm 1, \pm 2, \pm 3, \dots\}$, where $y_0 \in \mathbf{R}$ is a fixed point of g , i.e., $y_0 = g(y_0)$. More generally, a *cycle*, or more specifically, a *k-cycle* of (LE) is a periodic solution, i.e., $y(i+k) = y(i)$ for all $i \in J$ and some (minimal) integer $k \geq 1$. A solution $y(i)$ is a *k-cycle* if and only if $y(0) = y_0$ is a fixed point of the k -fold composition g^k of g with itself (and no smaller order composition of g), i.e., $y_0 = g^k(y_0)$. A *k-cycle* is *hyperbolic* if the derivative of g^k at its fixed point is not $+1$ or -1 . A *k-cycle* is *stable* if the derivative of g^k at its fixed point is less than one in absolute value. Otherwise a hyperbolic *k-cycle* is *unstable*. A set is said to contain a cycle if it contains the trajectory of the cycle. Assume that

(H4) in any compact subset of R the limiting equation (LE) has at most a finite number of cycles, all of which are hyperbolic, and every bounded solution of (LE) which is not a cycle tends asymptotically to a cycle.

This assumption means that the asymptotic dynamics of the limiting equation (LE) are "well behaved" in the sense that there are no homoclinic orbits, strange attractors, etc.

We begin with some preliminary lemmas. The first lemma is a special case of an "invariance" theorem of LaSalle [1976, Theorem 5.5, 48].

LEMMA 1. *Suppose that $x(i)$ is a bounded solution of (DE) and Ω is its limit set. If $y_0 \in \Omega$, then the solution $y(i)$ of the limiting equation (LE), for which $y(0) = y_0$, satisfies $y(i) \in \Omega$ for all $i \in J_+$.*

PROOF. If $y_0 \in \Omega$, then there exists a subsequence $x(i_j) \rightarrow y_0$. By writing $f(i_j, x(i_j)) - g(y_0) = f(i_j, x(i_j)) - g(x(i_j)) + g(x(i_j)) - g(y_0)$ and using H3, one easily sees that $x(i_j+1) = f(i_j, x(i_j)) \rightarrow g(y_0) = y(1)$ and hence that $y(1) \in \Omega$. An induction shows that $y(i) \in \Omega$ for all $i \in J_+$.
□

LEMMA 2. *Suppose that $x(i)$ is a bounded solution of (DE) and that Ω is its limit set. If Ω contains a stable cycle of (LE) then Ω consists solely of this cycle.*

PROOF. For simplicity, assume that Ω contains a stable equilibrium e of (LE). For k -cycles with $k \geq 2$ the following proof can be applied to the k -fold self composition g^k of g instead of g itself for the case $k \geq 2$.

Since $x(i)$ is bounded, its trajectory, as well as its compact limit set Ω , can be enclosed in the interior of a compact interval $C \subset R$. Let $N(e, \delta)$ denote the interval

$$N(e, \delta) = \{y \in R : |y - e| \leq \delta\}.$$

Since $|dg(e)/dx| < 1$ there exists a $\delta > 0$ and a real $\beta \in (0, 1)$ such that $N(e, \delta) \subset C$ and $y \in N(e, \delta)$ implies $|dg(y)/dx| \leq \beta < 1$.

Let $\epsilon > 0$ be arbitrary but $\epsilon < \delta$. Define $\epsilon' = \epsilon(1-\beta)^2 > 0$. By H3 and the fact that $e \in \Omega$, there exists an integer m such that $x(m) \in N(e, \delta)$ and

$$|f(i, x) - g(x)| \leq \epsilon' \quad \text{for all } i \geq m \text{ and for all } x \in C.$$

Suppose that $x(i) \in N(e, \delta)$ for some $i \geq m$. An application of the mean value theorem to g and the fact that $\epsilon' < \epsilon'(1-\beta)^{-1} = \epsilon(1-\beta) < \delta(1-\beta)$ shows that

$$\begin{aligned} |x(i+1) - e| &\leq |f(i, x(i)) - g(x(i))| + |g(x(i)) - g(e)| \\ &\leq \epsilon' + \beta\delta < \delta(1-\beta) + \beta\delta < \delta. \end{aligned}$$

and hence that $x(i+1) \in N(e, \delta)$. It follows by induction that $x(i) \in N(e, \delta)$ for all $i \geq m$. From this fact and a straightforward induction

$$\begin{aligned} |x(m+j) - e| &\leq \epsilon'(1 + \dots + \beta^{j-1}) + \beta^j\delta \leq \epsilon'(1-\beta)^{-1} + \beta^j\delta \\ &\leq \epsilon(1-\beta) + \beta^j\delta \leq \epsilon + \beta^j\delta \end{aligned}$$

for all $j \geq 1$. This inequality and $\beta < 1$ imply, in the limit as $j \rightarrow +\infty$, that $0 \leq \limsup_{i \rightarrow +\infty} |x(i) - e| \leq \epsilon$. But $\epsilon > 0$ was arbitrary and hence it follows that $0 = \limsup_{i \rightarrow +\infty} |x(i) - e| = \lim_{i \rightarrow +\infty} |x(i) - e|$. \square

The following theorem establishes a connection between the limit sets of bounded solutions of (DE) and those of the limiting equation (LE).

THEOREM 4. *Assume (H3) and (H4). Then every bounded solution of (DE) approaches a k -cycle of the limiting equation (LE).*

PROOF. Let $x(i)$ be a bounded solution of (DE) and let Ω be its limit set. Both Ω and its trajectory can be enclosed in a compact interval $C \subset R$. By Lemma 1 the trajectory of the solution $y(i)$ of (LE) passing through any given point in Ω remains in Ω for all $i \in J$. Thus $y(i)$ is bounded and by H4 it is either a hyperbolic k -cycle or it asymptotically approaches a hyperbolic k -cycle of (LE).

Consider the latter case. Suppose $k = 1$ and $y(i)$ is not a hyperbolic equilibrium, but does approach a hyperbolic equilibrium e of (LE). (Apply the following argument to g^k if $k \geq 2$.) Then e must be stable. For suppose that e is unstable so that there exist constants $\epsilon > 0$ and $\beta > 1$ for which $|dg(y)/dx| \geq \beta$ for all $y \in N(e, \epsilon)$. Let $m \in J_+$ be such that $y(m) \neq e$ and $i \geq m$ implies $y(i) \in N(e, \epsilon)$. The mean value theorem yields for $j \geq 1$ that

$$|y(m+j) - e| = |g(y(m+j-1)) - g(e)| \geq \beta |y(m+j-1) - e|$$

and by induction that $|y(m+j) - e| \geq \beta^j |y(m) - e|$. This clearly contradicts $y(i) \in N(e, \epsilon)$ for all $i \geq m$.

Thus if Ω contains a non-cyclic trajectory of (LE), then it contains a stable hyperbolic cycle of (LE). Since $x(i)$ approaches its limit set Ω , Lemma 2 implies the desired result.

To finish the proof we are left with the possibility that Ω contains only unstable cycles of (LE). The proof will be complete when it is argued that, in this case, Ω contains exactly one unstable cycle. By H4, Ω must be finite.

Once again assume that $k = 1$ and that Ω contains an unstable equilibrium e (otherwise replace g by g^k). Suppose for the purposes of contradiction that Ω does contain points other than e . Let $y \in \Omega$ be the closest point to e and let $d = |y - e| > 0$. By H2 there exists a $\delta \in (0, d/4)$ and an integer $m \in J_+$ such that $|f(i, x) - g(x)| < d/4$, $|g(x) - g(e)| < d/4$ for all $i \geq m$ and $x \in N(e, \delta)$. There exist infinitely many $x(i)$ in $N(e, \delta)$ and infinitely many $x(i)$ in $N(y, \delta)$. It follows that a subsequence can be chosen so that $x(i_j) \in N(e, \delta)$ and $x(i_j + 1) \notin N(e, \delta)$. Now

$$\begin{aligned} |x(i_j + 1) - e| &\leq |f(i_j, x(i_j)) - g(x(i_j))| \\ &\quad + |g(x(i_j)) - g(e)| < d/2 \end{aligned}$$

so that $x(i_j + 1) \in N(e, d/2)$, which in turn implies that $x(i_j + 1) \notin N(y, d/4)$. The bounded sequence $x(i_j + 1)$ must have a limit point y^* which must satisfy $y^* \in N(e, d/2)$, but $y^* \notin N(e, \delta)$ and $y^* \notin N(y, d/4)$. Since $y^* \in \Omega$ we have a contradiction to the assumption that y was the closest point in Ω to e . \square

One might suspect that a limit cycle of (LE) approached by a bounded solution of (DE) must be stable. That this need not be the case is demonstrated by the following example.

EXAMPLE. Choose any function g for which H4 is satisfied and for which $g(0) = 0$, $dg(0)/dx > 1$, so that 0 is an unstable equilibrium (1-cycle). Then

$$f(i, x) = \begin{cases} 0, & i = 0 \\ g(x), & i \geq 1 \end{cases}$$

satisfies H3. All solutions of (DE) approach the unstable equilibrium $y = 0$ of (LE); in fact $x(i) = 0$ for all $i \geq 1$.

There is one case of direct importance to the total population size equation (2.2) for which more can be said about the convergence to an unstable equilibrium of (LE). Assume

(H5) $f(i, x)$ is continuously differentiable in x and $\partial f(i, x)/\partial x \rightarrow dg/dx$ uniformly on compact subsets of R as $i \rightarrow +\infty$ and $f(i, 0) = 0$ for all $i \in J_+$.

THEOREM 5. Assume (H3), (H4) and (H5) hold. Suppose that 0 is an unstable equilibrium of (LE). If Ω is the limit set of a bounded solution $x(i)$ of (DE) and $0 \in \Omega$, then there exists an integer $m \in J_+$ such that $x(i) = 0$ for all $i \geq m$.

PROOF. By assumption $|g'(0)| > 1$, and therefore by H5 there exists a positive integer m and real numbers $\delta > 0$, $\beta > 1$ such that $|f_x(i, x)| \geq \beta > 1$ for all $i \geq m$ and $x \in N(0, \delta)$. By Theorem 4, Ω consists solely of the equilibrium 0, and thus $x(i) \rightarrow 0$ as $i \rightarrow +\infty$. Choose m larger if necessary so that also $|x(i)| \leq \delta$ for all $i \geq m$.

For purposes of contradiction suppose that there exists an inte-

ger $i \geq m$ for which $x(i) \neq 0$. By the mean value theorem $|x(i+1)| = |f(i, x(i))| \geq \beta|x(i)|$ and an easy induction yields $|x(i+j)| \geq \beta^j|x(i)|$ for all $j \in J_+$ which, because $\beta > 1$ and $x(i) \neq 0$, yields the contradiction that $x(i) \rightarrow +\infty$. Thus it must be the case that $x(i) = 0$ for all $i \geq m$. \square

In the example above any stable cycle that (LE) happens to possess attracts no solution of (DE). This illustrates how, over any finite time interval, the dynamics of (DE) can be dominated by the nonautonomous dependence on i and have asymptotic dynamics quite different from the limiting equation (LE). Thus, clearly any solution of (DE) which starts initially near a stable cycle of (LE) in general need not asymptotically approach that cycle. The next theorem gives some conditions under which a stable equilibrium of (LE) will attract nearby solutions of (DE). A similar theorem is valid for k -cycles of (LE), $k \geq 2$. In the definitions of $c(\epsilon)$ and m and in the proof below f and g just need to be replaced by their k -fold self composites.

Suppose that $y_0 \in \mathbf{R}$ is a fixed point of g . Define

$$m = \max_{i \in J_+} |f(i, y_0) - g(y_0)|$$

$$c(\epsilon) = \max_{\substack{i \in J_+ \\ x \in N(y_0, \epsilon)}} |f_x(i, x)|.$$

By (H3), m is finite. The next theorem demands more, namely that $f(i, x)$ be close to g for all $i \in J$ in the sense that m is sufficiently small.

THEOREM 6. *Assume (H3) and (H4) hold. Suppose that $y_0 \in \mathbf{R}$ is an equilibrium of (LE) for which there exists an $\epsilon > 0$ such that*

$$(A.1) \quad c(\epsilon) < 1 \text{ and } m < (1 - c(\epsilon))\epsilon.$$

Then y_0 must be a stable equilibrium of (LE). Moreover, if $x(i)$ is any solution of (DE) for which $x(0) \in N(y_0, \epsilon)$, then $x(i) \rightarrow y_0$ as $i \rightarrow +\infty$.

PROOF. If $x(i) \in N(y_0, \epsilon)$ then, by the mean value theorem and the assumptions on m and $c(\epsilon)$,

$$\begin{aligned} |x(i+1) - y_0| &= |f(i, x(i)) - g(y_0)| \\ &\leq |f(i, x(i)) - f(i, y_0)| + |f(i, y_0) - g(y_0)| \\ &\leq c(\epsilon)|x(i) - y_0| + m \leq c(\epsilon)\epsilon + m \leq \epsilon \end{aligned}$$

so that $x(i + 1) \in N(y_0, \epsilon)$. By induction $x(i) \in N(y_0, \epsilon)$ for all $i \in J_+$ and hence $\Omega \subset N(y_0, \epsilon)$. By Theorem 4, Ω is a k -cycle of (LE). Suppose that $k = 1$ (the case $k \geq 2$ being handled by a similar argument applied to composites of f and g), i.e., suppose Ω is an equilibrium e . Then $x(i) \rightarrow e$. From the mean value theorem

$$\begin{aligned} |x(i + 1) - y_0| &\leq |f(i, x(i)) - f(i, y_0)| + |f(i, y_0) - g(y_0)| \\ &\leq c|x(i) - y_0| + |f(i, y_0) - g(y_0)| \end{aligned}$$

which, by (H3), implies as $i \rightarrow +\infty$ that $|e - y_0| \leq c(\epsilon)|e - y_0|$. Since $c(\epsilon) < 1$ it follows that $e = y_0$. \square

PROOF OF THEOREM 3. Equations (2.2) and (2.3) have the form (DE) and (LE) with f and g defined by

$$f(i, x) = \|A\nu(i)\|h(\nu(i)x)x, \quad g(x) = \lambda h(\eta x)x.$$

By Theorem 1, $\nu(i) \rightarrow \eta$ and hence $\|A\nu(i)\| \rightarrow \lambda$. These facts together with the assumptions in Theorem 2 imply that the hypotheses (H3), (H4), and (H5) hold. Theorem 3 will follow from an application of Theorem 6 as soon as (A.1) is verified.

Suppose first that $q(i) = q_0$ is a stable equilibrium of the limiting equation (2.3). Then $|dg(q_0)/dx| < 1$ and it follows from (H5) that, for all sufficiently small $\epsilon > 0$, $c(\epsilon) < 1$. It only remains to be shown that, for any such ϵ , the inequality on m in (A.1) can be satisfied by choosing $\|\nu(0) - \eta\|$ sufficiently small. But this follows from the definition of f and g above and the Lemma 3 below. \square

As pointed out just prior to the statement of Theorem 6, an analogous theorem is valid for k -cycles, $k \geq 2$, with f and g replaced by their k -fold self composites in the definitions of $c(\epsilon)$ and m . A similar proof for higher order k -cycles can then be given and the proof of Theorem 3 is complete.

LEMMA 3. *Given $\delta_1 > 0$ there exists a $\delta_2 > 0$ such that $\|\nu(0) - \eta\| \leq \delta_2$ implies $\|\nu(i) - \eta\| \leq \delta_1$ for all i .*

PROOF. It was shown in the proof of Theorem 1 that $\nu(i) = \phi(i)/\|\phi(i)\|$, $\phi(0) = \rho(0)$. Let \mathbf{R}_1^n be the space of vectors in R^n which are

perpendicular to the positive, unit eigenvector η . The initial vector $\rho(0)$ can be written $\rho(0) = a\eta + \xi$ where $0 < a \in R$ and $\xi \in R_{\perp}^n$. Define the continuous function $u : R_{\perp}^n \rightarrow R$ by

$$u(\chi) = \left| \frac{a\eta + \chi}{\|a\eta + \chi\|} - \eta \right| \geq 0.$$

Since $u(0) = 0$, there exists a $\delta' > 0$ such that $\|\chi\| \leq \delta'$ implies $u(\chi) \leq \delta_1$. Now $\|\nu(0) - \eta\| = u(\xi)$ and $\|\nu(i) - \eta\| = u(A\xi^i/\lambda^i)$ (since $\phi(i) = A^i\phi(0)$). By H1 there exists a $\delta'' > 0$ such that $\|\xi\| \leq \delta''$ implies $\|A^i\xi/\lambda^i\| \leq \delta'$ for all $i \in J_+$ (see (5.109) in Impagliazzo [1980]). Furthermore, it is easy to see that $\|\xi\|$ is small if and only if $\|\nu(0) - \eta\|$ is small, i.e., there exists a $\delta_2 > 0$ such that $\|\nu(0) - \eta\| \leq \delta_2$ implies $\|\xi\| \leq \delta''$. \square

REFERENCES

- H. Barclay [1986], *Models of host-parasitoid interactions to determine the optimal instar of parasitization for pest control*, Nat. Res. Mod. **1**, 81-104.
- J. Buongiorno and B. R. Michie [1908], *A matrix model of uneven-aged forest management*, Forest Sci. **26**, 609-625.
- S. Busenberg and M. Iannelli [1985], *Separable models in age dependent population dynamics*, J. Math. Biol. **22**, 145-173.
- H. Caswell [1986], *Matrix models and the analysis of complex plant life*, Proceedings of the 1985 Symposium on Some Mathematical Questions in Biology, Lec. on Math. in the Life Sciences **18**, AMS, Providence.
- J.M. Cushing [1988a], *Equilibria and stability in nonlinear matrix models for structured populations*, Nat. Res. Mod. **2**, 539-580.
- [1988b], *The Allee effect in age-structured population dynamics*, in Mathematical Ecology (S.A. Levin & T. Hallam, eds.), World Scientific Publ., New Jersey.
- R.A. Desharnais and J.E. Cohen [1986], *Life not lived due to disequilibrium in heterogeneous age-structured populations*, Theo. Pop. Biol. **29**, 385-406.
- A.R. Ek [1974], *Nonlinear models for stand table projection in northern hardwood stands*, Can. J. For. Res. **4**, 23-27.
- M.E. Fisher and B.S. Goh, *Stability results for delayed recruitment models in population dynamics*, J. Math. Biol. **19**, 147-156.
- F.R. Gantmacher [1960], *The Theory of Matrices*, Vol. 2, Chelsea, New York.
- J. Guckenheimer, G.F. Oster and A. Ipaktchi [1976], *The dynamics of density dependent population models*, J. Math. Biol. **4**, 101-147.
- M.P. Hassell and H.N. Comins [1976], *Discrete time models for two species competition*, Theo. Pop. Biol. **9**, 202-221.
- J.W. Horwood and J.G. Shepherd [1981], *The sensitivity of age structured populations to environmental variability*, Math. Biosci. **57**, 59-82.

J. Impagliazzo [1980], *Deterministic Aspects of Mathematical Demography*, Biomathematics **13**, Springer, Berlin.

J.P. LaSalle [1976], *The Stability of Dynamical Systems*, Reg. Conf. Series in Appl. Math., SIAM, Philadelphia.

L.P. Lefkovich [1965], *The study of population growth in organisms grouped by stages*, Biometrics **25**, 309-315.

P.H. Leslie [1945], *On the use of matrices in certain population mathematics*, Biometrika **33**, 183-212.

——— [1948], *Some further notes on the use of matrices in population mathematics*, Biometrika **35**, 213-245.

S.A. Levin and C.P. Goodyear [1980], *Analysis of an age structured fishery model*, J. Math. Biol. **9**, 245-274.

E.G. Lewis [1942], *On the generation and growth of a population*, Sankhya **6**, 93-96.

R.M. May and G.F. Oster [1976], *Bifurcations and dynamic complexity in simple ecological models*, Amer. Natur. **110**, 573-599.

J.A.J. Metz and O. Diekmann [1986], *The Dynamics of Physiologically Structured Populations*, Lec. Notes in Biomath. **68**, Springer, Berlin.

P.M. North [1985], *A computer modelling study of the population dynamics of the screech owl (*Otus asio*)*, Ecol. Modelling **30**, 105-114.

L. Pennycuik [1969], *A computer model of the Oxford great tit population*, J. Theor. Biol. **22**, 381-400.

C.J. Pennycuik, R.M. Compton and L. Beckingham [1986], *A computer model for simulating the growth of a population or of two interacting populations*, J. Theor. Biol. **18**, 316-329.

J. Sarukhán and J.L. Harper [1973], *Studies on plant demography: *Ranunculus repens* L., *R. bulbosus* L. and *R. acris* L. I. population flux and survivorship*, J. Ecol. **61**, 675-716.

——— and M. Gadil [1974], *Studies on plant demography: *Ranunculus repens* L., *R. bulbosus* L. and *R. acris* L. III. a mathematical model incorporating multiple modes of reproduction*, J. Ecol. **62**, 921-936.

J. van Sickle [1977], *Analysis of a distributed parameter population model based on physiological age*, J. Theor. Biol. **64**, 571-586.

J.W. Silvertown [1982], *Introduction to Plant Population Ecology*, Longman, New York.

S.D. Simmes [1978], *Age dependent population dynamics with nonlinear interactions*, Ph.D. dissertation, Carnegie-Mellon University, Pittsburgh, Pa.

C.C. Travis, W.M. Post, D.L. DeAngelis and J. Perkowski [1980], *Analysis of compensatory Leslie matrix models for competing species*, Theo. Pop. Biol. **18**, 16-30.

M.B. Usher [1966], *A matrix approach to the management of renewable resources, with special reference to selection forests*, J. Appl. Ecol. **3**, 355-367.

——— [1969], *A matrix approach to the management of renewable resources, with special reference to selection forests - two extensions*, J. Appl. Ecol. **6**, 247-248.

P.A. Werner and H. Caswell [1977], *Population growth rates and age versus stage distribution models for teasel (*Dipsacus sylvestris* Huds.)*, Ecology **58**, 1103-1111.