

Discrete Demographic Models with Density-Dependent Vital Rates*

Peter E. Smouse and Kenneth M. Weiss**

Department of Human Genetics, University of Michigan, Ann Arbor, Michigan 48104

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Summary. The standard Leslie model of population growth in an age structured population is modified so as to incorporate density-dependent feedback control on each parameter of the standard projection matrix. Under fairly general conditions, the population converges to a stable age-distribution and a constant population size. This steady-state solution is uniquely determined by the parameters of the model. In general, fertility damping results in a flatter age-distribution than yielded by the undamped Leslie model. General survival damping results in the Leslie age-distribution. Post-infant survival damping results in a very steep age-distribution. For populations with high intrinsic growth rates, these differences in stable age-distributions are pronounced. For populations of low intrinsic growth rate, the patterns are the same, but the differences in stable age-distribution are more subtle. The age-distribution usually converges rapidly to the steady-state array, although population size generally takes longer to approach a stable value. Convergence properties are described for a series of cases which show periodicity. Such cases arise from "periodic" behavior of certain fertility-damping strategies, and ultimately approach a stable steady-state, although convergence may be very slow. Although the model is very general, it can be considerably simplified in practice. Special cases, which can be constructed, are the Malthusian (Leslie) model and the Logistic model. As a generality, the model is approximately Logistic, once the age-distribution approaches the steady-state array. One may use this fact for purposes of population projection.

Introduction

Theoretical approaches to population dynamics generally take one of two basic forms: ecological or demographic. Both treatments have been used extensively and with great success in furthering our knowledge of the structure and ecology of populations, but there has been to date little effort at combining the strengths of each in order to derive a single model as informative as both and yet free of the deficiencies of each.

The traditional ecological approach to biological populations has been to treat the trajectories of their total sizes over time. Such treatments deal with net birth and death rates, which are allowed to change as the population size approaches some limit, called the carrying capacity. The model is therefore *density dependent*. The logistic model of Verhulst (1938) and Pearl and Reed (1920) is often used to describe the growth trajectory. The approach is extended to the competition equations of Lotka (1925) and Volterra (1926), which has been used extensively to examine the density-dependent relations among species or groups within a single ecosystem (mixed populations). Each population is treated as an

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** Present address: Center for Demographic and Population Genetics, University of Texas, Houston, Texas 77025.

homogeneous assemblage of individuals in all of these approaches, and details of the age structure or age-specific vital rates are omitted.

The other traditional approach has been that of classical demographic theory. Here, age-specific birth and death rates are considered in a derivation of the age composition to be found in a given population at various times. Separate cohorts of individuals within the population are traced through their life histories in this treatment, whose formal mathematics are due to Leslie (1945) and Lotka (1925). This approach also forms the cornerstone of population genetics theory (Fisher, 1930; Norton, 1926). The vital rates are presumed to be inherent in the organism and a function of its age only. There is no consideration of density effects and such models are therefore *density independent*; populations are allowed to grow without bound, solely as determined by the vital rates. This is the Malthusian approach to population, and since real populations are density regulated, it is insufficient for ecological studies. Where equilibrium states are to be treated by this method, a careful selection of vital rates providing an intrinsic growth rate of exactly zero is necessary, and it must further be assumed that the population has reached its equilibrium size. These are artifices at best, and lead to serious theoretical limitations at worst.

As increasing attention is paid to construction of more complete models for population behavior, it becomes necessary to unite the two approaches and to consider the internal structure of a population as well as its density-dependent relations with its environment. Although Lotka dealt with, and in fact derived, the basic formulations of both models, he never united them in this way, and the first notable effort to do this was made by Leslie (1948, 1959), who considered the impact of very simple forms of density dependence on steady-state age distributions. More recently, Anderson and King (1970), King and Anderson (1971), Charlesworth and Giesel (1972), and Charlesworth (1972, 1973) have approached genetic variability from this point of view, considering the genetic results of age-structured populations which were density-damped.

These previous efforts have used only very restricted forms of density-dependent feedback. Here we attempt to construct a model which generalizes population-size-dependent feedback on vital rates, and which combines the traditional models. We restrict ourselves to consideration of single-sex cases of one genotype. Our primary interest is to examine the impact of various density-dependent damping strategies on steady-state age-distribution and on the rate of convergence to this distribution.

Review of the Leslie Model

We shall first review some basic properties of the discrete-time model of a single-sex, age-structured population, as formulated by Leslie (1945); we shall modify this treatment to include density-dependent feedback in the next section.

Consider a population of (K) age classes, indexed $i=1, \dots, K$, and all of equal length. Individuals in a particular age class either die in a unit time interval (chosen to be the same length as an age class interval) or survive to the next age class. All members of the K -th age class die during the interval. The probability of surviving from age class (i) to age class ($i+1$) is denoted by P_i , and $P_K=0$. Mortality is visualized as occurring at the end of the time interval.

Each individual in age class (i) reproduces with probability F_i . The length of the age-class interval is chosen to be small enough so that no more than one birth may occur in a single interval. This is not an essential feature of the model, and can be relaxed if necessary. We define all $F_i < 1$, for convenience, so it is necessary that at least two $F_i > 0$ (Lopez, 1961). All F_i need not be greater than zero, and in fact, very young and very old individuals usually do not reproduce.

Reproduction is assumed to occur continuously during the time interval, and we require also the net probability of survival of infants into the first age class P_0 . Assume that P_0 is not a function of parental age, so that the net contribution of an individual of age class (i) to the first age class one time unit later is $F_i P_0$. The above probabilities are assumed to be parametric features of the organism, and are not responsive to current population density or age structure.

The dynamics of the population are described by the recurrence relation

$$\mathbf{N}(t+1) = \mathbf{M}\mathbf{N}(t), \quad (1)$$

where $\mathbf{N}(t) = \{N_i(t)\}$, and similarly for $\mathbf{N}(t+1)$. The i -th element of the first row of the projection matrix \mathbf{M} is $P_0 F_i$, while the elements of the principal subdiagonal are the P_i : $i = 1, \dots, K-1$. All other elements of \mathbf{M} are zero. The age distribution of the population may be described by $\mathbf{f}(t) = \{N_i(t)/N(t)\}$, where $N(t) = \sum_{i=1}^K N_i(t)$.

Keyfitz (1968) shows that as $t \rightarrow \infty$, $\mathbf{f}(t) \rightarrow \mathbf{f}$, where \mathbf{f} is the principal eigenvector of \mathbf{M} . After the stable age-distribution \mathbf{f} is established, the total population grows according to $N(t) = \lambda N(t-1) = \dots = \lambda^t N(0)$, where the finite rate of increase λ satisfies the characteristic equation

$$\lambda^K - P_0 F_1 \lambda^{K-1} - P_0 P_1 F_2 \lambda^{K-2} - \dots - P_0 P_1 \dots P_{K-1} F_K = 0. \quad (2)$$

A standard demographic measure related to λ is the net reproductive rate, $R_0 = L_1 F_1 + \dots + L_K F_K$, where $L_i = P_0 P_1 \dots P_{i-1}$. R_0 is the average number of same-sex offspring born to an individual in its lifetime. Clearly, $R_0 \geq 1$ as $\lambda \geq 1$. Population size increase if $R_0 > 1$, decreases if $R_0 < 1$, and becomes stationary if $R_0 = 1$.

The Density Dependent Model

We now add density-dependent feedback explicitly to the model. Assume that all probabilities of the \mathbf{M} matrix are now continuous functions of population density and age distribution. We define

$$\begin{aligned} P_i(t) &= P_i \Psi_i[N(t)] & i &= 0, \dots, K-1 \\ F_i(t) &= F_i \theta_i[N(t)] & i &= 1, \dots, K. \end{aligned} \quad (3)$$

A variety of possible forms may be chosen, and two such possibilities are presented by Leslie (1948) and Charlesworth (1972). We prefer a specific choice of functions, motivated as follows. Imagine a single individual of age class (i), placed alone into a large habitat. The individual survives to the next age class with probability P_i (in the absence of density stress). Now repeat the experiment, but add a single individual of age class (j). The effect upon survival of the first individual may be described by $P_i B_{ij}$, where B_{ij} is a constant of proportionality slightly less than unity. Adding a second individual of age class (j) reduces the residual probability of survival proportionately, and the total effect of two competitors of the j -th

age class may be described by $(P_i \times B_{ij}) \times B_{ij} = P_i B_{ij}^2$. This may be generalized to include any number of competitors of any age class, yielding

$$\begin{aligned} P_i(t) &= P_i \left\{ \prod_{j=1}^K [B_{ij}]^{N_j(t)} \right\} \\ &= P_i \exp \left[- \sum_{j=1}^K b_{ij} N_j(t) \right]. \end{aligned} \quad (4)$$

Similar reasoning with respect to fertility leads to

$$F_i(t) = F_i \exp \left[- \sum_{j=1}^K a_{ij} N_j(t) \right]. \quad (5)$$

From (4) to (5), it is seen that

$$\begin{aligned} 0 < \Psi_i[N(t)] &= \exp \left[- \sum_{j=1}^K b_{ij} N_j(t) \right] = \exp [-\mathbf{B}'_i \mathbf{N}(t)] < 1 \\ 0 < \theta_i[N(t)] &= \exp \left[- \sum_{j=1}^K a_{ij} N_j(t) \right] = \exp [-\mathbf{A}'_i \mathbf{N}(t)] < 1, \end{aligned} \quad (6)$$

and that

$$0 \leq P_i(t) \leq P_i \quad \text{and} \quad 0 \leq F_i(t) \leq F_i.$$

The recurrence relation is the same as that in (1), except that the constant matrix \mathbf{M} is replaced by a density-dependent matrix $\mathbf{M}(t)$, where the F_i are replaced by $F_i(t)$ and the P_i are replaced by $P_i(t)$. The exponential form of density-dependence is particularly convenient wherever terms must be multiplied, and all elements of $\mathbf{M}(t)$ remain strictly non-negative for any choice of positive $\mathbf{N}(t)$.

The Steady-State Population

We enquire into the conditions necessary for the existence of a non-trivial steady-state solution (constant population size and stable age distribution). Suppose initially that such an equilibrium exists, i.e., that there is at least one array \mathbf{N}^* such that $\mathbf{N}^* = \mathbf{M}^* \mathbf{N}^*$. Any such steady-state solution also satisfies

$$N_1^* = P_0 \exp[-\mathbf{B}'_0 \mathbf{N}^*] \left\{ \sum_{i=1}^K F_i N_i^* \exp[-\mathbf{A}'_i \mathbf{N}^*] \right\} \quad (7)$$

and

$$N_{i+1}^* = P_i N_i^* \exp[-\mathbf{B}'_i \mathbf{N}^*] \quad i = 1, \dots, K-1 \quad (8)$$

Repeated substitutions of (8) into (7), reduce (7) to

$$N_1^* = N_1^* \left\{ \sum_{i=1}^K L_i F_i \exp[-\mathbf{C}'_i \mathbf{N}^*] \right\} = N_1^* R_0^*, \quad (9)$$

where $\mathbf{C}_i = [\mathbf{A}_i + \mathbf{B}_0 + \dots + \mathbf{B}_{i-1}]$. If $N_1^* > 0$, then $1 = R_0^* < R_0$ and $1 = \lambda^* < \lambda$. Clearly, if R_0 and $\lambda < 1$, Eq. (9) cannot be satisfied, and the only solution is $N_1^* = \dots = N_K^* = 0$. For a non-trivial solution, R_0 and λ must be greater than unity. That is, the population must be capable of growth at some positive rate when not crowded. We shall restrict all future discussion to such cases.

This is not a sufficient condition for the existence of a non-trivial steady-state.

Suppose for example that $\mathbf{C}_i = 0$ for $i = 1, \dots, H < K$ and that $1 < \sum_{i=1}^H L_i F_i < R_0$.

This would be analogous to damping only the fertility of post-menopausal adults. Regardless of the degree of density-dependent damping exerted on the last $(K-H)$ age classes, the population can never satisfy (7), (8), or (9). It is necessary to damp sufficient age classes that (7), (8), and (9) can be satisfied. A *sufficient*, but *not necessary* condition for existence of a non-trivial steady-state is that all elements of C_i be positive for $i=1, \dots, K$. If this is assumed, then $R_0(*)=1$ for some sufficiently large $N(*)$ for any $f(*)$. The restrictions of (8), in addition to that of (9), will establish the particular $f(*)$ and $N(*)$ in question. It has been our experience that the steady state solution $\langle N(*), M(*) \rangle$ is unique, irrespective of the initial state of the system $\langle N(0), M(0) \rangle$, although a completely rigorous proof of this last contention has eluded us to date.

The Impact of Intrinsic Growth Rate and Damping Strategy on the Steady-State Age Distribution

The steady-state solution is determined by the growth rate λ , intrinsic in the density-independent vital rates of the Leslie model, and the damping vectors $(A_i: i=1, \dots, K)$ and $(B_i: i=0, \dots, K-1)$. Although this solution is not explicitly derivable in the general case, it is easily obtained by iterating the basic projection relation, $N(t+1)=M(t)N(t)$. Here we examine nine specific cases to demonstrate the joint impact of λ and different density-dependent damping strategies upon the steady-state age distribution. We shall employ three different density-dependent damping strategies for each of three different growth rates λ . To do this, we employ three different (5×5) Leslie matrices, with a constant value in all positions of the first row and principal subdiagonal. The constant values for the three matrices are 0.99, 0.75, and 0.51, yielding principal eigenvalues of 1.946, 1.514, and 1.002, respectively. The first of these λ -values is a near maximum, the third a near minimum for population growth, and the second is a moderate growth rate. Since each of these matrices may be converted into each of the others by a change in overall mortality rate, the undamped Leslie age-distribution is the same for all three models (Keyfitz, 1968, p. 187-188).

Case 1: Generalized Damping on Reproduction

Leslie (1948) considered the case where fertility alone is subjected to density-dependent damping on total population size. The result is a flattening of the stable age distribution, relative to that of the undamped model. The treatment of reproductive damping may be extended considerably. At equilibrium the values of $E_i(*)$ affect the age distribution only through $\lambda(*)$. But $\lambda(*)=1$ at this point, and the stable age distribution, under reproductive damping, is given by $f'(*)=\alpha \cdot [1, P_1, P_1 P_2, \dots, P_1 P_2 \dots P_{K-1}]$, where α is a normalizing scalar. This distribution also results from other choices for the set of vectors $\{A_i + B_0: i=1, \dots, K\}$, since no distinction is made in the model relative to the source of infants, once produced. The damping coefficients chosen are

$$\begin{aligned} A'_1 = \dots = A'_5 &= (1, \dots, 1) \times 10^{-3} \\ B'_0 = \dots = B'_4 &= (0, \dots, 0). \end{aligned} \tag{10}$$

For each of the three Leslie matrices, the principal subdiagonal remains constant, since these terms are not density-dependent. The elements of the first row are all equal, for each particular matrix, but change as a function of population size. All cases converge to stable population size and stable-age distribution. The equilibrium values for first row positions $P_0 F_i(*)$ are 0.2040, 0.3278, and 0.5075, respectively, for the 0.99, 0.75, and 0.51 matrices. In each case, the matrix $M(*)$ has principal eigen-value $\lambda(*)=1$. The steady-state age-distributions are listed in the appropriate lines of Table 1.

Case 2: Generalized Damping on Survival

Leslie (1948, 1959) dealt with this case by invoking density dependence of survival probability on total population size. He showed that the resulting age distribution is identical with that predicted by the undamped model. We can extend this case by setting $B_0=B_1=\dots=B_{K-1}=B$. The elements of B may take any non-negative values, provided at least one element is positive. The stable age distribution of the undamped Leslie model is recovered under this sort of damping. We assume the same three Leslie matrices as above, and set

$$\begin{aligned} A_1 &= \dots = A_5 = (0, \dots, 0) \\ B_0 &= \dots = B_4 = (1, \dots, 1) \times 10^{-3}. \end{aligned} \quad (11)$$

For each matrix, all non-zero elements remain equal, but change with population density. At equilibrium, all non-zero elements $= 0.5087$ for all three matrices. The principal eigen-value $\lambda(*)=1$. The stable age-distribution is listed in the appropriate lines of Table 1, and is given by $f(*)=\alpha \cdot [1, P_1/\lambda, P_1 P_2/\lambda^2, \dots, P_1 P_2 \dots P_{K-1}/\lambda^{K-1}]$, where α is a normalizing scalar.

Case 3: Generalized Damping on Post-Infant Survival

This situation involves the assumption that density-dependence applies only to the survival of individuals who have reached the first age class. Formally, we set

$$\begin{aligned} A_1 &= \dots = A_5 = B_0 = (0, \dots, 0) \\ B_1 &= \dots = B_4 = (1, \dots, 1) \times 10^{-3}, \end{aligned} \quad (12)$$

and utilize the same three Leslie matrices as before. For this situation, the first row of $M(t)$ remains constant, and the elements of the principal subdiagonal (though equal) change with population size. The three populations eventually come to equilibrium, with the subdiagonal elements of the matrices equal to 0.0100, 0.2508, and 0.5071, respectively. The steady-state age distributions are listed in Table 1.

Since $N_1(*) > N_2(*) > \dots > N_K(*)$, the limiting case is a horizontal age-distribution. With high λ , the reproductive damping case approaches this condition. The other extreme is provided by high λ and post-infant survival damping, which has a very steep age-distribution. The generalized survival damping case has intermediate steepness, regardless of λ . It is clear from Table 1 that as $\lambda \rightarrow 1+$, the three cases tend to yield the same steady-state age-distribution. Populations with low density-independent growth rate have little flexibility in their potential

Table 1. Stable population arrays under three different damping regimes for populations of three different growth rates (λ)

Intrinsic growth rate (λ)	Density damping strategy	Stable age-distributions					Equilibrium population size
		f_1	f_2	f_3	f_4	f_5	
1.946	Fertility	0.2040	0.2020	0.2000	0.1980	0.1960	1580
	Survival	0.5087	0.2587	0.1316	0.0669	0.0341	666
	Post-infant survival	0.9900	0.0099	0.99×10^{-4}	0.99×10^{-6}	0.99×10^{-8}	4595
1.514	Fertility	0.3278	0.2458	0.1844	0.1383	0.1037	838
	Survival	0.5087	0.2587	0.1316	0.0669	0.0341	388
	Post-infant survival	0.7500	0.1880	0.0472	0.0118	0.0030	1096
1.002	Fertility	0.5072	0.2589	0.1321	0.0674	0.0344	5.9
	Survival	0.5087	0.2587	0.1316	0.0669	0.0341	3.2
	Post-infant survival	0.5103	0.2586	0.1310	0.0664	0.0336	6.9

range of stable age distributions, and the undamped Leslie stable-age distribution provides a very useful approximation, under any sort of damping.

Table 1 also exhibits the equilibrium (zero-growth) population sizes for the nine specific cases. Given any particular damping strategy (*relative* sizes of damping parameters), population size is determined by intrinsic growth rate and the general *level* of damping. Changing the general level of the damping parameters results in a change in population size, but no change in stable age-distribution \mathbf{f}^* . The reason for this is easily seen. The stable age-distribution is determined by the P_i^* values, since $\lambda^*=1$, and these equilibrium values may be described by $P_i^*=P_i \exp[-N^* \cdot \mathbf{B}_i^* \mathbf{f}^*]$ for $i=0, \dots, K-1$. The P_i^* are not altered if the vectors \mathbf{B}_i are multiplied by a scalar constant, provided N^* is divided by that same constant. In practice, this allows one to independently determine N^* and \mathbf{f}^* .

Convergence Properties and Periodicity

We have yet to discuss the rate of convergence of the system $\langle \mathbf{N}(t), \mathbf{M}(t) \rangle$ to the steady state condition. To do this, it is first necessary to define two measures of convergence. The first is the *index of numerical convergence*, which measures the convergence of population size to a stable value, *i.e.*, an index of the instantaneous disparity of the system from zero population growth. The second is the *index of angular convergence*, which measures the disparity between two successive age distributions.

The trajectory of total population size may be described by $N(t+1)=\mathbf{J}'\mathbf{N}(t+1)=\mathbf{J}'\mathbf{M}(t)\mathbf{N}(t)=V(t)N(t)$, where $\mathbf{J}'=(1, \dots, 1)$ and $V(t)$ is given by

$$V(t)=\sum_{i=1}^K [P_0(t)F_i(t)+P_i(t)]f_i(t), \quad (13)$$

with $P_k(t)=0$ for all t . Stable population size is approached as $V(t) \rightarrow 1$. This approach to the "zero growth" condition is more conveniently gauged by the measure $\varrho(t)=V(t)-1$, which can also be written as $\varrho(t)=[N(t+1)-N(t)]/N(t)$,

the proportional rate of change in $N(t)$. We denote $\varrho(t)$ as the *index of numerical convergence*.

We find it convenient to describe the disparity of two successive age-distributions in terms of the angular displacement between them. One can calculate

$$\cos \phi(t) = \frac{\sum_{i=1}^K f_i(t-1) \times f_i(t)}{\left[\sum_{i=1}^K f_i^2(t-1) \right]^{1/2} \left[\sum_{i=1}^K f_i^2(t) \right]^{1/2}} \quad (14)$$

and we define $\phi(t)$ as the *index of angular convergence*. Since $f_i(t)$ is restricted to the first "hyperquadrant", $0 \leq \phi(t) \leq \pi/2$, and $\phi(t)$ converges to zero as the age-distribution converges to a stable form.

As a rule of thumb, one can expect reasonable convergence of $\phi(t)$ within K -steps, and close convergence within $2K$ -steps, irrespective of initial age distribution. Convergence of $\varrho(t)$ generally takes a longer time, but this depends both on λ and the initial population size. The greater the disparity between $N(0)$ and $N(*)$, and the closer λ is to unity, the slower the convergence. One may define measures of the time required for $\varrho(t)$ or $\phi(t)$ to reach some arbitrarily small value, and we thus formally define the *span of numerical convergence* at the e -level to be $S_{e,e} = \{t: |\varrho(t)| < e\}$, and the *span of angular convergence* at the g -level to be $S_{\phi,g} = \{t: |\phi(t)| < g\}$. These spans of convergence, of course, depend not only upon the parametric features of any particular model, but upon the disparity between the initial $\langle N(0), \mathbf{M}(0) \rangle$ and final $\langle N(*), \mathbf{M}(*) \rangle$ states of the system. These measures will thus vary from case to case.

We should point out at this juncture that all of the convergence measures defined above are defined relative to the current state of the system $\langle N(t), \mathbf{M}(t) \rangle$, rather than relative to the final state $\langle N(*), \mathbf{M}(*) \rangle$. This is a necessity, since one cannot explicitly solve for the final equilibrium state in most cases. Inasmuch as one is normally interested in medium range changes in the system $\langle N(t), \mathbf{M}(t) \rangle$, rather than in the asymptotic steady state, this should create no difficulty in practice. Our own empiric observations on the system, for cases where we know the solution, indicate that as $\varrho(t)$ and $\phi(t)$ become small, the system $\langle N(t), \mathbf{M}(t) \rangle$ approaches $\langle N(*), \mathbf{M}(*) \rangle$. We infer from this that our convergence measures are good reflections of convergence to steady-state.

To gain any real appreciation of the behavior of these convergence measures, it is necessary to examine cases which are ill behaved and which converge only very slowly. We have found them to be most useful in the study of various cyclical or periodic cases. It should be mentioned at the outset that periodicity *does not* arise from unusual strategies of density-dependent survival damping. The model is susceptible to periodicity, however, under two different types of unusual density-dependent fertility damping. We find it particularly illuminating to describe each of these situations below, in the context of specific examples.

Periodic Fertility

Bernardelli (1941) first described demographic periodicity in certain insects, which spend most of their lives in various stages of metamorphosis and which

end their lives in a brief adult stage and a burst of reproduction. Periodicity can be shown to result from any such situation where all but the last F_i -value are zero.

This simple example has formed the basis for extensive discussion in the demographic literature (Leslie, 1945; Lopez, 1961; Sykes, 1969; Parlett, 1970). The Leslie matrix is non-negative and irreducible (we follow the usual demographic convention of considering only that portion of the matrix describing behavior up to the age of menopause). It therefore has a single, real-positive eigenvalue (assumed greater than unity here). If the matrix is also *primitive*, i.e., if there is no other eigenvalue of modulus equal to that of this principal eigenvalue, then $\mathbf{f}(t)$ will converge to the stable age-distribution \mathbf{f}^* . If one or more eigenvalues have modulus equal to the principal eigenvalue, cycles result in $\mathbf{f}(t)$. The number of eigenvalues of equal modulus to that of the dominant root can be determined by examining Eq. (3). Sykes (1969) has shown that the matrix is primitive (non-periodic) if the greatest common divisor of the difference between successive exponents of λ in Eq. (3) is unity. If various F_i are zero, this condition may be violated, and the matrix becomes imprimitive (periodic). The theory presented above is all for undamped population growth, and we need to consider the implication of density-dependent fertility for periodicity.

In order to avoid periodicity for the damped model, we have arbitrarily set all $F_i > 0$. One may still obtain demographic cycles, however, since certain types of fertility-damping produce fertility patterns which mimic imprimitive (periodic) cases. To illustrate the point, we employ a (6×6) Leslie matrix, with 0.99 in all positions of the first row and principal subdiagonal. We define damping parameters

$$\begin{aligned} A'_2 = A'_4 = A'_6 &= (0, \dots, 0) \\ A'_1 = A'_3 = A'_5 &= (A, \dots, A) \neq (0, \dots, 0) \\ B'_0 = \dots = B'_5 &= (1, \dots, 1) \times 10^{-3}. \end{aligned} \quad (15)$$

All elements of C_i are positive for $i = 1, \dots, K$, and the system must have a non-trivial steady-state solution. The value of (A) was varied over a broad range, and convergence of the model was tracked for each case. The behavior of $\phi(t)$ is

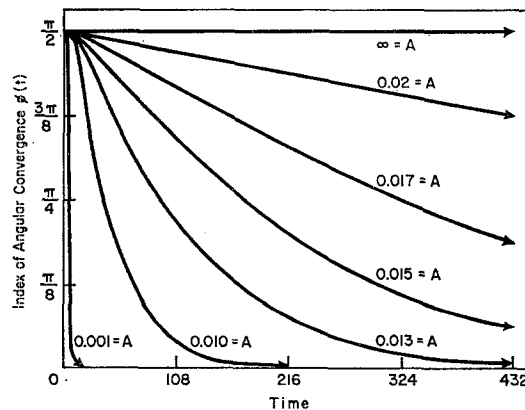


Fig. 1. Trajectories of the index of angular convergence $\phi(t)$, for models with periodic fertility caused by fertility damping levels (A)

shown in Fig. 1 for a series of increasing values of (A), and the rate of convergence is inversely proportional to (A). In the limit ($A = \infty$), the system becomes perfectly periodic.

The value of $\varrho(t)$ oscillates around zero, with period $h=2$. Both the amplitude of the oscillation and the *span of convergence* to any desired level increase with (A). The pattern of age-specific fertilities changes with time, and is shown for ($A = 0.013$) in Table 2. The matrix $M(t)$ is, for all practical purposes, imprimitive initially, but becomes less so as time proceeds. The span of convergence depends on (A), and the imprimitivity (periodicity) persists for very long periods if (A) is large. This can be seen in Table 3, where age-specific fertilities are listed at $t=432$. For large values of (A), oscillations in population size and $\varrho(t)$ will persist indefinitely.

Table 2. Age-specific fertilities and the index of numerical convergence $\varrho(t)$ at various times (t), under periodic fertility Damping ($A = 0.013$)

Time (t)	Index $\varrho(t)$	Age-specific fertility					
		F_1	F_2	F_3	F_4	F_5	F_6
1	-0.2716	0.83×10^{-6}	0.3642	0.83×10^{-6}	0.3642	0.83×10^{-6}	0.3642
2	-0.3062	0.0060	0.6878	0.0060	0.6878	0.0060	0.6878
3	+0.1988	0.0009	0.5999	0.0009	0.5999	0.0009	0.5999
4	-0.2521	0.0146	0.7327	0.0146	0.7327	0.0146	0.7327
5	+0.1127	0.0020	0.6373	0.0020	0.6373	0.0020	0.6373
6	-0.2321	0.0191	0.7468	0.0191	0.7468	0.0191	0.7468
11	+0.2528	0.0068	0.6938	0.0068	0.6938	0.0068	0.6938
12	-0.1890	0.0291	0.7695	0.0291	0.7695	0.0291	0.7695
23	+0.2327	0.0079	0.7010	0.0079	0.7010	0.0079	0.7010
24	-0.1696	0.0279	0.7672	0.0279	0.7672	0.0279	0.7672
47	+0.1787	0.0088	0.7066	0.0088	0.7066	0.0088	0.7066
48	-0.1389	0.0242	0.7595	0.0242	0.7595	0.0242	0.7595
95	+0.1046	0.0105	0.7156	0.0105	0.7156	0.0105	0.7156
96	-0.0894	0.0197	0.7483	0.0197	0.7483	0.0197	0.7483
191	+0.0364	0.0127	0.7254	0.0127	0.7254	0.0127	0.7254
192	-0.0341	0.0160	0.7374	0.0160	0.7364	0.0160	0.7364
383	+0.0046	0.0141	0.7306	0.0141	0.7306	0.0141	0.7306
384	-0.0046	0.0145	0.7321	0.0145	0.7321	0.0145	0.7321
∞	0.0000	0.0143	0.7313	0.0143	0.7313	0.0143	0.7313

Table 3. Age-specific fertilities at $t=432$, for each of six age-classes, as a function of fertility damping level (A)

Fertility damping (A)	Age specific fertility					
	F_1	F_2	F_3	F_4	F_5	F_6
0.001	0.3447	0.5842	0.3447	0.5842	0.3447	0.5842
0.007	0.0681	0.7085	0.0681	0.7085	0.0681	0.7085
0.010	0.0317	0.7240	0.0317	0.7240	0.0317	0.7240
0.013	0.0144	0.7318	0.0144	0.7318	0.0144	0.7318
0.015	0.0090	0.7378	0.0090	0.7378	0.0090	0.7378
0.017	0.0064	0.7479	0.0064	0.7479	0.0064	0.7479
0.020	0.0042	0.7634	0.0042	0.7634	0.0042	0.7634
0.050	4×10^{-6}	0.7767	4×10^{-6}	0.7767	4×10^{-6}	0.7767
∞	0	0.7767	0	0.7767	0	0.7767

Seasonal Periodicity

A rather different sort of periodicity results when all fertilities are heavily damped on a "periodic sequence" of age-classes. We assume the same (6×6) Leslie matrix as above, and we define

$$\begin{aligned} A'_1 = \dots = A'_6 &= (A, 0, A, 0, A, 0) \\ B'_0 = \dots = B'_5 &= (1, \dots, 1) \times 10^{-3}, \end{aligned} \quad (16)$$

where (A) can be varied at will. Again, all elements of C_i are positive for $i = 1, \dots, K$, and a non-trivial steady state must exist, regardless of (A) . Before describing the outcome, it would be useful to explain how this pattern of fertility-damping leads to periodicity. We have schematized the situation in Fig. 2. Suppose the population is initiated with large $N_1(0)$, but with all other age classes empty. The population progresses through time, as shown in Fig. 2. Whenever age-classes 1, 3, and 5 are essentially empty, fertility is high. Whenever age-classes 1 or 3 or 5 are filled, fertility is nil. Total reproduction is thus periodic, with period $h = 2$, and the system becomes caught in a cycle, from which it will only gradually recover. Other starting vectors can lead to the same phenomenon.

Setting $N_1(0) = 1000$ and $N_2 = \dots = N_6 = 0$, one obtains the trajectories of $\phi(t)$ shown in Fig. 3 for various values of (A) . The *span of convergence* increases rapidly with increasing (A) , and in the limit $(A \rightarrow \infty)$, the system becomes perfectly periodic, i.e., $\langle N(t), M(t) \rangle \rightarrow \langle N(t+h), M(t+h) \rangle$. The period here is $h = 2$, but differs for other models, depending upon the sequence of damping age-classes. We have not been able to decipher the exact relationship between this sequence and the period (h) , but it is easily shown that the system $\langle N(t), M(t) \rangle$ cycles through h different states. For lack of a better term, we call this "*seasonal periodicity*". As a consequence of the fact that $M(t) \rightarrow M(t+h)$, one also has $\varrho(t) \rightarrow \varrho(t+h)$ as $t \rightarrow \infty$. This is clearly demonstrated in Table 4 for a particularly slow case of convergence ($A = 0.009$). From the patterns shown in Table 4, it should also be clear that $\varrho(t) \rightarrow \varrho(t+h) \rightarrow 0$ as $t \rightarrow \infty$, but that convergence

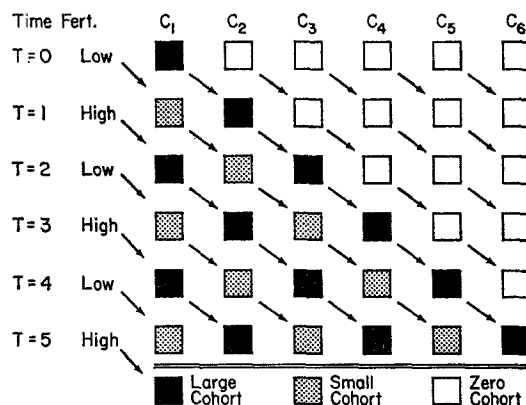


Fig. 2. Age-distribution changes for models with seasonal periodicity, caused by fertility damping on alternate age classes. Fertility is low when classes 1, 3, or 5 are filled, high otherwise

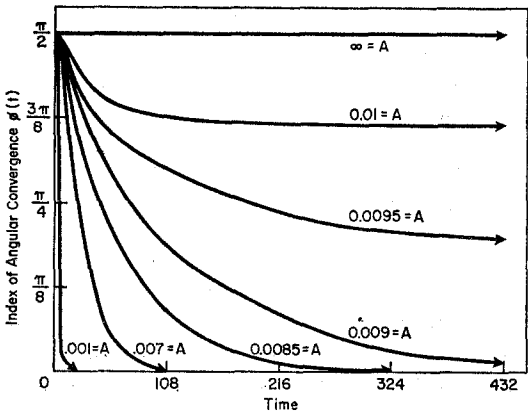


Fig. 3. Trajectories of the index of angular convergence $\phi(t)$, for models with seasonal periodicity caused by fertility damping levels (A)

Table 4. Instantaneous values of the index of numerical convergence $\rho(t)$, under seasonal fertility damping ($A = 0.009$)

$r =$	Time (t) =					
	$r + 1$	$r + 2$	$r + 3$	$r + 4$	$r + 5$	$r + 6$
0	-0.6358	0.3753	-0.3350	0.4396	-0.5053	0.4424
6	-0.3766	0.4374	-0.3689	0.4134	-0.3621	0.3934
12	-0.3340	0.3795	-0.3280	0.3644	-0.3169	0.3508
24	-0.2795	0.3075	-0.2719	0.2985	-0.2648	0.2900
48	-0.2103	0.2259	-0.2060	0.2209	-0.2018	0.2161
96	-0.1352	0.1411	-0.1329	0.1386	-0.1307	0.1362
192	-0.0632	0.0642	-0.0622	0.0632	-0.0612	0.0622
384	-0.0148	0.0148	-0.0146	0.0146	-0.0144	0.0144
∞	0.0000-	0.0000+	0.0000-	0.0000+	0.0000-	0.0000+

may be incredibly slow. It should be noted that the value of (A) is not the critical determinant of the strength and persistence of demographic cyclicity. Rather, it is the disparity between A and B that is the crucial feature; one may either decrease A or increase B to reduce the degree of periodicity. Numerous other examples can be contrived, and the strength and persistence of periodicity is determined by the difference between the intensity of the “periodic fertility damping” and that of the “background damping,” represented by A and B , respectively, in the example above.

It is difficult to gauge, on purely theoretical grounds, the prevalence of pronounced demographic periodicity. While natural examples are known (Bernardelli, 1941), the generality of the phenomenon is difficult to gauge. Some degree of cyclicity is probably fairly common, but the amplitude of oscillations is likely to be small and damping rapid. Even in the models presented above, only the most contrived cases supported persistent periodicity.

Discussion

We have described a system $\langle N(t), M(t) \rangle$ with $2K$ density-independent vital rates and $2K^2$ density-dependent damping parameters. Clearly, a system with $2K(K+1)$ parameters is likely to be unwieldy in practice, and is even a bit too general for theoretical comfort. We have given the model such generality for completeness, but we shall now attempt to simplify matters.

Except for the sorts of contrived periodicity just described, we have generally found that $\phi(t)$ converges rapidly to zero, and it appears that most populations will spend most of their time not very far from f^* . This allows us to write

$$\begin{aligned}\Psi_0(t) \theta_i(t) &\approx \exp[-N(t) \cdot (A'_i + B'_0) f^*] = \exp[-(q_i + s_0) N(t)] \\ \psi_i(t) &\approx \exp[-N(t) \cdot B'_i f^*] = \exp[-s_i N(t)] \\ i &= 1, \dots, K\end{aligned}\quad (17)$$

as an adequate first approximation to the more detailed model. We are not claiming that the details of the A_i and B_i are unimportant; we have shown that (along with λ) they determine f^* . Rather we are claiming that we can construct an adequate first approximation with a smaller set ($2K$) of damping parameters. If in addition, λ is known to be small, one may simply use a generalized survival damper. This is so, as mentioned above, because populations of low intrinsic growth have very little flexibility in their stable-age distributions. For such cases, the Leslie distribution is an adequate approximation to f^* .

Demographers commonly recognize that the matrix M is subject to change. Quite apart from temporal changes in the underlying parameters, one is almost inevitably observing $M(t)$, rather than either M or M^* . The ability to simplify $M(t)$ by means of (17) should permit the projection of damped population growth trends, without the types of *ad hoc* adjustments currently in use.

It should be clear from our development of this model that the classical density-independent or Malthusian counterpart is simply a degenerate case, *i.e.*, all $A_i = B_i = 0$. It is a matter of some interest to determine the relationship between the density-dependent model and the density-dependent Logistic growth model. As indicated earlier, one may write $N(t+1) = V(t) N(t)$. If we may invoke (17), then it is possible to write

$$V(t) \approx \sum_{i=1}^K [m_i \exp\{-(q_i + s_0) N(t)\} + l_i \exp\{-s_i N(t)\}], \quad (18)$$

where $m_i = P_0 F_i f_i^*$, $l_i = P_i f_i^*$, and $l_K = 0$. In the case of general survival damping, $q_i = 0$ and $s_i = \beta$ for all i . Eq. (18) reduces to

$$V(t) \approx \left\{ \sum_{i=1}^K [m_i + l_i] \right\} \exp\{-\beta N(t)\}, \quad (19)$$

and $N(t+1) \approx r N(t) \exp[-\beta N(t)]$, the discrete version of the Logistic equation. Similar treatment of generalized fertility damping or generalized post-infant survival damping leads to $N(t+1) \approx N(t) \{\gamma + r \exp[-\beta N(t)]\}$, which is only approximately logistic. In the more general case, $V(t)$ is given by (18), and the approximation is less adequate.

The generality of the density-dependent damping scheme described above permits extension of the model to the situation where the population consists

of two or more components. We are currently investigating two such extensions. The first is the two-sex model. The problem with most two-sex models is that differential vital rates in the two sexes can result in different maximum growth rates, leading to mathematical difficulty. Our model will ultimately yield zero population growth for both sexes, irrespective of undamped vital rates or the mating scheme in force. The second is the multiple genotype model. Anderson and King (1970) and Charlesworth and Giesel (1972) have investigated diploid sexual models under generalized density-dependence. We are investigating both asexual and sexual models, particularly with respect to the consequences of differential damping strategies for the various genotypes.

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Dr. P. E. Smouse
Department of Human Genetics
University of Michigan
Ann Arbor, Michigan 48104, USA