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Comparative Statics and Stochastic Dynamics of Age-Structured Populations

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Arguments from the comparative statics of populations with fixed vital rates are of limited use in studying age-structured populations subject to stochastically varying vital rates. In an age-structured population that experiences a sequence of independently and identically distributed Leslie matrices, the expectation of the Malthusian parameters of the Leslie matrices has no exact interpretation either as the ensemble average of the long-run rate of growth of each sample path of the population (Eq. (3)) or as the long-run rate of growth of the ensemble average of total population size (Eq. (4)). On the other hand, the Malthusian parameter of the expectation of a sequence of Leslie matrices is exactly the logarithm of the finite growth rate of the ensemble average of total population size when Leslie matrices are independently and identically distributed (though not in general when Leslie matrices are sequentially dependent). These observations appear to contradict the claims of a recent study using computer simulation of age-structured populations with stochastically varying vital rates.

1. INTRODUCTION

In demography, the intrinsic rate of natural increase or Malthusian parameter r summarizes the long-term or equilibrium growth rate of certain populations. A single-sex closed population with fixed age-specific birth and death rates will have total numbers proportional to e^{rt} for large values of time t. Though r is an implicit function of a population's vital rates and not trivial to calculate numerically in any given instance, it has been extensively studied because of its virtues as a summary measure of growth rate.

It is entirely natural to try to extend the use of r to biological and demographic models other than that from which it was derived. Such efforts have been successful for single-type populations, that is, those without different age classes (Lewontin and Cohen, 1969).

The purpose of this note is to discuss the long-run growth rates of age-structured populations with stochastically varying vital rates, and the relations of these rates to r.

Let us say that an $n \times n$ nonnegative matrix L with elements L_{ij} is in Leslie

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form if every element L_{1i} of the first row and every element $L_{j+1,j}$ of the subdiagonal is positive, $i = 1,..., n$; $j = 1,..., n - 1$, and all remaining elements are 0.

In the theory of age-structured populations without migration, matrices in Leslie form are used to project a vector that describes an age census from one point in discrete time to the next. The elements of the first row of a matrix in Leslie form are interpreted as age-specific effective fertility rates. The elements of the subdiagonal are interpreted as age-specific survival proportions.

If L is in Leslie form, then by the Perron–Frobenius theorem the eigenvalue ρ of L which is largest in modulus is real and positive. Boyce (1977) calls ρ the "finite growth rate." He calls $r = \log_e \rho$ the "Malthusian parameter" of L. (All logarithms in this paper are to the base e.)

On the basis of computer simulations, Boyce (1977) conjectures that the finite growth rate of population size estimated by least squares when populations are projected by independently and identically distributed matrices in Leslie form is the geometric mean of the finite growth rates of the matrices that occur in the projection. He also attempts to justify a conjecture that increasing variation in elements of L lowers a measure of long-run growth under stochastic dynamics, by facts from comparative statics about the behavior of ρ as a function of elements of L. In Section 2, we consider the relation between his and other observations about comparative statics. In Section 3, we examine the main question of the paper: what can facts from the comparative statics of age-structured populations with fixed vital rates tell about the long-run growth rates for age-structured populations with stochastic dynamics? In Section 4 we present a numerical example which supports some of the claims in Section 3.

2. Comparative Statics

The study of the behavior of ρ or r, which are equilibrium values of growth rates, as functions of the age-specific vital rates, which are specified as parameters, is an example of comparative statics in demography.

"It is the task of comparative statics to show the determination of the equilibrium values of given variables (unknowns) under postulated conditions (functional relationships) with various data (parameters) being specified" (Samuelson, 1965, p. 257).

In this section we discuss some recent and new results in comparative statics. In the next section we discuss the possible uses of these results in analyzing stochastic dynamics.

We recall some definitions. If f is a real function of a positive real variable x such that the second derivative $f''(x)$ exists at all $x > 0$, f is convex at x if and only if $f''(x) \geqslant 0$. f is concave at x if and only if $f''(x) \leqslant 0$. If these two inequalities are strict, then f is strictly convex, or strictly concave, at x. We shall say that $f(x)$ is (strictly) convex if f is (strictly) convex at every positive x.

If A is a 2×2 matrix in Leslie form,

$$A = \begin{pmatrix} a & b \\ c & d \end{pmatrix},$$

Boyce (1977, pp. 370–371) shows that r is a strictly concave function of a, elements $d = 0$ and b and c of A being held constant. This result in comparative statics compares the limiting properties of different populations. In each population the vital rates, or elements of A, are held constant in time.

While r is a strictly concave function of a in a 2×2 matrix in Leslie form, ρ is a strictly convex function of a (Cohen, 1978, Theorem 3).

For comparative statics, with fixed vital rates in each population, which function, ρ or r, is the more natural measure of the limiting growth rate as a function of the elements of the Leslie matrix? Given the population, the convexity or concavity (if any) of an acceptable measure of growth rate should be the same regardless of the number of age classes used to describe the population, since the number of age classes is usually chosen for the convenience of the observer.

For any $n \geqslant 2$, the dominant eigenvalue ρ of a matrix L in Leslie form is a strictly convex function of L_{11}, all other elements being held constant (Cohen, 1978, Corollary 5). On the other hand, it is not true that r is a concave function of L_{11} for every $n \geqslant 2$. Specifically, let

$$L = \begin{pmatrix} L_{11} & 1 & 1 \\ 0.1 & 0 & 0 \\ 0 & 0.1 & 0 \end{pmatrix}.$$

By $r(x)$ we mean the value of r when $L_{11} = x$. Then $r(0.1) = -0.69315$, $r(0.2) = -0.60056$, and $r(0.3) = -0.50550$. Since $(r(0.1) + r(0.3))/2 > r(0.2)$, r is not a concave function of L_{11} in general, even for $n = 3$. Thus in general there is no "inherent concavity of r as a function" (Boyce, 1977, p. 368) of an arbitrary positive element of a matrix in Leslie form, though concavity may be observed in special cases.

Boyce (1977) asserts correctly that r is a concave function of each off-diagonal element b and c in a 2×2 matrix in Leslie form when the remaining elements are held constant. This concavity does not generalize to larger matrices in Leslie form. Daley (1979) derives a necessary and sufficient condition for r to be a concave function of each element of a matrix in Leslie form, all other elements held constant.

It is thus not safe to assume that results about 2×2 nonnegative matrices generalize to $n \times n$ nonnegative matrices. Daley (1979) independently makes the same point. The 2×2 case is worth studying mainly as a source of conjectures about $n \times n$ nonnegative matrices or $n \times n$ matrices in Leslie form.

These caveats apply not only to Boyce's results, but also to the results on comparative statics which we now state.

Recall that a 2×2 matrix A in Leslie form, i.e., with $d = 0$, $a, b, c > 0$, must have two real eigenvalues, ρ and (say) τ, where τ is always negative and $\rho + \tau = a > 0$. In a general $n \times n$ nonnegative matrix, no eigenvalue other than the dominant one need be real.

THEOREM 1. *In a* 2×2 *nonnegative matrix* A, *when all other elements are constant, the second eigenvalue* τ *is* (i) *an increasing,* (ii) *concave function of* a; (iii) *a decreasing,* (iv) *convex function of either off-diagonal element. When* A *is in Leslie form,* (i) *to* (iv) *hold strictly.*

Since the eigenvalues of A are identical to those of the real symmetric matrix

$$\begin{pmatrix} a & (bc)^{1/2} \\ (bc)^{1/2} & d \end{pmatrix},$$

Theorem 1(ii) follows from the proof by Lax (1958, p. 182) that the smallest eigenvalue of a real symmetric matrix is a concave matrix function.

The positive ratio $-\tau/\rho$ measures the rate of convergence of the population's age structure to its stable limit. The smaller the ratio $-\tau/\rho$ is, the more rapidly any initial age structure converges to stability under the action of A.

THEOREM 2. *In a* 2×2 *matrix* A *in Leslie form, when all other matrix elements are constant,* $-\tau/\rho$ *is* (i) *a strictly decreasing,* (ii) *strictly convex function of* a; *and* (iii) *a strictly increasing,* (iv) *strictly concave function of either off-diagonal element.*

Theorems 1 and 2 may be proved by explicit elementary calculations, as in Boyce (1977).

3. STOCHASTIC DYNAMICS

Consider a closed, single-sex age-structured population whose vital rates vary in time according to some stochastic process. We exclude from consideration the binomial variability in numbers of actual births and deaths conditional on given vital rates. This source of variability is of primary concern in the theory of multitype branching processes. We also ignore sampling error that may arise from the need to estimate the vital rates observed at each time. We thus assume, for example, that if there are exactly $y_i(t, w)$ individuals in the ith age class at time t, there will be exactly $L_{i+1,i}(t + 1, w)\, y_i(t, w)$ individuals in age class $i + 1$ at time $t + 1$, $i = 1,\dots, n - 1$, whether or not $y_i(t, w)$ and $L_{i+1,i}(t + 1, w)$ are integers. Here w refers to a particular realization or sample path of the stochastic process that produces the vital rates.

By ignoring the variability in births and deaths conditional on given vital rates as well as the sampling error in estimates of the vital rates, we do not assert that these two sources of variability are insignificant in reality. Our purpose rather is to isolate and to study the effects of variations in the vital rates themselves.

Suppose (D. J. Daley, personal communication, 21 June 1978) "a wildlife authority observes a Leslie matrix [$L(t, w_1)$] year by year, [$t = 1, 2, 3,\ldots$] and year by year it computes its current estimate of the population growth rate... . It matters that the procedure used in this estimation should be roughly unbiassed so that the controls are 'correct.'" (My insertions are in brackets.) Here $L(t, w_1)$ refers to the Leslie matrix observed at time t in one particular region w_1; a neighboring park (or another computer simulation with the same instructions but different random numbers) might have a different sequence of observed Leslie matrices $L(t, w_2)$ though the stochastic process governing successive Leslie matrices were the same.

After T years of observation, the wildlife management authority might estimate the long-run growth rate of the population by one of two statistics: the Malthusian parameter of the sample average of the observed Leslie matrices,

$$r(\bar{L}(w_1)) = r\left(\sum_{t=1}^{T} L(t, w_1)/T\right) \tag{1}$$

or the sample average of the Malthusian parameters computed from each observed Leslie matrix,

$$\bar{r}(w_1) = \sum_{t=1}^{T} r(L(t, w_1))/T. \tag{2}$$

Boyce (1977) points out correctly, for 2 × 2 Leslie matrices, that (2) is strictly less than (1) if a single element of $L(t, w_1)$ varies over time. This conclusion follows from Jensen's inequality and the *concavity* of r as a function of individual elements of a 2 × 2 matrix in Leslie form, which Boyce established as a fact of comparative statics.

The main point of this paper is that Boyce's inequality (1) > (2) does not necessarily tell anything about the long-run growth rate of the population until it is established independently that (1) or (2) estimates some meaningful measure of long-run growth rate in a dynamic stochastic model.

To see this point most clearly, define $\rho(\bar{L}(w_1))$ and $\bar{\rho}(w_1)$ by replacing the symbol r with the symbol ρ on both sides of (1) and (2). If the matrices varied only in the L_{11} element (denoted by a in the 2 × 2 case), then, because of Jensen's inequality and the *convexity* of ρ as a function of L_{11}, one has $\bar{\rho}(w_1) > \rho(\bar{L}(w_1))$ (Cohen, 1978). The direction of this inequality is opposite to the direction of Boyce's.

Boyce (1977) assumes that a benighted "population biologist might conclude that a population is increasing" because (1) is greater than 0, "where in reality it may be headed for extinction" (p. 369) because (2), based on the same data, is less than 0.

Unfortunately for the latter conclusion, there is a fundamental difference between single-type populations and age-structured populations. If a single-type population of initial size N_0 at $t = 0$ has finite growth rate ρ_1 at $t = 1$ and ρ_2 at time $t = 2$, then the total population size $N_2 = \rho_2\rho_1 N_0$ at time $t = 2$ is the same as if the population experienced finite growth rate ρ_2 at $t = 1$ and ρ_1 at $t = 2$, because $\rho_1\rho_2 = \rho_2\rho_1$. Thus an estimator like (2), as recommended by Lewontin and Cohen (1969), is appropriate for a single-type population.

In an age-structured population, if L_1 and L_2 are two Leslie matrices, it is not in general true that $L_1L_2 = L_2L_1$ nor that $\rho(L_2L_1) = \rho(L_2)\,\rho(L_1)$. Empirically when Leslie matrices are estimated from the vital rates of various human populations, the product $\rho(L_T)\,\rho(L_{T-1}) \cdots \rho(L_1)$ is a "poor" approximation to $\rho(L_T \cdots L_1)$ (Kim and Sykes, 1976, p. 159; see Fig. 5). In terms of Malthusian parameters, $r(L(T, w) \cdots L(1, w))$ is poorly approximated by $T\bar{r}(w)$, where $\bar{r}(w)$ is given by (2).

To understand an age-structured population with varying vital rates, a more detailed analysis is required. Let $y_i(t, w)$ be the number of individuals in the ith age class, $i = 1, 2,..., n$ at time t of a population subject to stochastically varying matrices in Leslie form. Here w labels a sample path, or sequence, of matrices chosen by some stochastic process. Let $N(t, w)$ be the total population size at time t, $N(t, w) = \sum_{i=1}^{n} y_i(t, w)$. The age-structure vector $y(t, w)$ at time t is given by $y(t, w) = L(t, w)\,L(t-1, w) \cdots L(2, w)\,L(1, w)\,y(0, w)$.

There are at least two plausible measures of the long-run growth rate of total population size in populations with stochastically varying vital rates (Cohen, 1979):

$$\log \lambda = \lim_{t\to\infty}(1/t)\, E_w(\log N(t, w)), \tag{3}$$

$$\log \mu = \lim_{t\to\infty}(1/t) \log E_w N(t, w), \tag{4}$$

where E_w is the expectation over all sample paths w, each weighted according to the probability assigned by the underlying stochastic process. Under reasonable conditions, which are likely to be satisfied in demographic applications, the stochastic process and the matrices in Leslie form are such that the limits in (3) and (4) exist. Equation (3) is due to Furstenberg and Kesten (1960), who denote $\log \lambda$ by E.

It is worthwhile spelling out the difference between λ and μ. To compute λ, one first calculates the long-run growth rate $(1/t) \log N(t, w)$, as t gets large, of each sample path w separately and then averages the growth rates over all available sample paths, wildlife areas, or simulations presumed to be governed by the same process. Thus λ is an average of growth rates, not of population sizes. To compute μ, one first finds the expected population size $E_w N(t, w)$ at time t and then computes the rate of growth of this average as t gets large. Thus μ rests on an average of population sizes, not of growth rates.

In both (3) and (4), the effect of the initial population size vanishes as t gets large. While (1) and (2) are sample statistics, (3) and (4) depend on the underlying stochastic process and its parameters.

If vital rates are variable, then it follows from the concavity of log and Jensen's inequality that $\lambda \leqslant \mu$. When only a single realization (sample path) of the process can be observed, the sample estimates of (3) and (4) obtained by inserting observed values in the right-hand sides will be the same.

If an age-structured population is projected by independently and identically distributed matrices in Leslie form as Boyce (1977) assumed, then μ equals the largest eigenvalue of the expected matrix (Cohen, 1977, p. 467, Corollary 2; the corollary is stated in terms of a finite number of possible matrices, but since a computer can represent matrices only with finite precision, the corollary covers simulations such as Boyce's). When only a single sample path w_1 is observed, as in the biological example which Daley described, a very reasonable sample estimator of μ is

$$\hat{\mu} = \rho\left(\sum_{t=1}^{T} L(t, w_1)/T\right) = e^{r(L(w_1))}. \tag{5}$$

The numerical example in Section 4 shows that this procedure could be seriously misleading if there is dependence between successive Leslie matrices.

If the game warden wished to estimate the average growth rate λ in an ensemble of parks identical to his, even assuming no sequential correlation, he would first have to find the stationary probability distribution of the age structure vector $y(t, w)$ (assuming such a distribution exists) and apply, conditional on each $y(t, w)$, the appropriate distribution of Leslie matrices in order to get an average growth rate.

When successive Leslie matrices are chosen by an aperiodic ergodic finite-state Markov chain, the required limit distributions exist. Numerical procedures for calculating $\log \lambda$ and upper and lower bounds on $\log \lambda$ have been described (Cohen, 1977, 1979). In examples based not on simulation but on numerical solution of exact equations, in general $\log \lambda \neq E_w[r(L(w))]$, even assuming identically and independently distributed Leslie matrices. Thus the measure $\bar{r}$ in (2) espoused by Boyce (1977), which is the natural estimator of $E_w[r(L(w))]$, does not in general estimate either $\log \mu$ or $\log \lambda$ in age-structured populations, with or without sequential dependence in vital rates.

Why, then, does Boyce (1977) recommend $\bar{r}$ as a measure of growth rate?

Boyce argues from simulations in which successive 2×2 Leslie matrices are identically and independently distributed. "Population trajectories from a minimum of 30 simulations (see Fig. 1) were determined by least-squares regression utilizing the *BMDP* package... [pp. 367–368]. The average growth rates realized in the population projections summarized in Fig. 1 were precisely described by $\bar{r}$, the arithmetic mean of r" [p. 369].

However, at least when $Q \geq 0$, the least-squares estimator of the growth parameter Q in an exponential function Pe^{Qt} may be shown analytically to coincide with $\log \mu$ when sufficiently long trajectories are observed (Appendix). Since $\log \mu$ is estimated by (1) $> \bar{r}$ when 2×2 Leslie matrices are independently and identically distributed, and since at least some sets of Boyce's simulations clearly had $Q > 0$ (his Fig. 1), I am unable to understand how $\bar{r}$ could have "precisely described" the results of Boyce's simulations.

4. NUMERICAL EXAMPLE

We describe an example based on artificial, but not biologically implausible, numbers. Consider a closed, single-sex population with two age classes. At each point in discrete time the population is subject to one of three Leslie matrices:

$$x^{(1)} = \begin{pmatrix} 0.5 & 0.4 \\ 0.8 & 0 \end{pmatrix},$$

$$x^{(2)} = \begin{pmatrix} 0.4 & 0.8571429 \\ 0.7 & 0 \end{pmatrix},$$

$$x^{(3)} = \begin{pmatrix} 2.0 & 1.0 \\ 0.2 & 0 \end{pmatrix}.$$

These three matrices have been chosen so that if the population experienced $x^{(1)}$ only, it would eventually decline exponentially. If it experienced $x^{(2)}$ only, it would approach a stationary population. If it experienced $x^{(3)}$ only, it would grow rapidly.

Now let $P = (p_{ij})$ be a 3×3 row-stochastic matrix. If the population experiences Leslie matrix $x^{(i)}$ at time t, then the probability that the Leslie matrix occurring at time $t + 1$ will be $x^{(j)}$ is p_{ij}. Thus $p_{ij} = P_w[L(t + 1, w) = x^{(j)} \mid L(t, w) = x^{(i)}]$. We consider three possible transition matrices P^{I}, P^{II}, and P^{III}, which we label the I.I.D. case, the forward Markov case, and the reverse Markov case. These matrices describe three possible ways a sequence of Leslie matrices might be chosen from the set $\{x^{(1)}, x^{(2)}, x^{(3)}\}$.

Case I (I.I.D.): Let

$$P^{\text{I}} = \begin{pmatrix} 0.1702128 & 0.7234043 & 0.1063830 \\ 0.1702128 & 0.7234043 & 0.1063830 \\ 0.1702128 & 0.7234043 & 0.1063830 \end{pmatrix}.$$

As does Boyce (1977), case I assumes there is no sequential correlation among successive Leslie matrices. Unlike the examples studied by Boyce (1977), more than one element of a Leslie matrix is permitted to vary. This increase in generality is clearly more realistic, yet in no way affects our conclusions concerning the questionable interpretability of $\bar{r}$.

Case II (forward Markov): Let

$$P^{\mathrm{II}} = \begin{pmatrix} 0.5 & 0.3 & 0.2 \\ 0 & 0.9 & 0.1 \\ 0.8 & 0.2 & 0 \end{pmatrix}.$$

P^{II} specifies an ergodic, aperiodic Markov chain with an equilibrium distribution given by any row of P^{I}. Thus $(P^{\mathrm{II}})^t \to P^{\mathrm{I}}$. In the long run the Leslie matrices $x^{(i)}$ occur with the same relative frequencies in case I as in case II. The difference between case I and case II is that case II allows for the possibility of sequential correlation. Partial numerical results for this case have been confirmed by simulation previously (Cohen, 1977).

Case III (reversed Markov): Let

$$P^{\mathrm{III}} = \begin{pmatrix} 0.5 & 0 & 0.5 \\ 0.0705882 & 0.9 & 0.0294118 \\ 0.32 & 0.68 & 0 \end{pmatrix}.$$

To seven decimal places, this is the transition probability matrix that would occur if the Markov chain in case II were run backward in time. Specifically, if π_i is the equilibrium probability of $x^{(i)}$, given by any element in the ith column of P^{I}, then $\pi_i P_{ij}^{\mathrm{III}} = \pi_j p_{ji}^{\mathrm{II}}$, $i, j = 1, 2, 3$. The reversed Markov chain has the same equilibrium probability distribution as do cases I and II (Kemeny and Snell, 1960).

Table I gives the derived parameters which are common to all three cases in this example. Table II gives the derived parameters which differ among the three cases. The numbers in these tables are based, not on simulation, but on numerical evaluation of analytically derived expressions. All derived parameters were computed with at least seven decimal places of precision and rounded to six decimal places for reporting.

To calibrate the computer programs used to obtain these results, examples not presented here were analyzed in which the results were known in advance. These calibrations did not reveal any unexpected behavior.

Tables I and II deserve comment. (Line ($m.n$) refers to line n in Table m.)

(i) The mean Malthusian parameter $\bar{r}$ given in line (1.6) is not a sample estimate based on (2) but is an expectation (the limit of (2) as $T \to \infty$). Observe that $\bar{r}$ equals neither $\log \mu$ (line (2.2)) nor $\log \lambda$ (line (2.4)) in any of the three cases. The absolute size of the numerical differences, small in some instances, merely reflects the happenstance of the choice of parameters. The point is that $\bar{r}$ has no apparent biological interpretation as a measure of long-run growth

TABLE I

An Artificial Example of an Age-Structured Population with Stochastically Varying Vital Rates: Derived Parameters Common to all Three Cases

Line			
(1.1)[a]	$\rho(x^{(1)}) = 0.868466$,	$\rho(x^{(2)}) = 1.000000$,	$\rho(x^{(3)}) = 2.095445$
(1.2)[b]	$r(x^{(1)}) = -0.141027$,	$r(x^{(2)}) = 0.000000$,	$r(x^{(3)}) = 0.739766$
(1.3)[c]	$\pi_1 = 0.170213$,	$\pi_2 = 0.723404$,	$\pi_3 = 0.106383$
(1.4)[d]	$\rho(\sum_{i=1}^{3} \pi_i x^{(i)}) = 1.076971$		
(1.5)[e]	$r(\bar{L}) = \log \rho(\sum_{i=1}^{3} \pi_i x^{(i)}) = 0.074152$		
(1.6)[f]	$\bar{r} = \sum_{i=1}^{3} \pi_i r(x^{(i)}) = 0.054694$		
(1.7)[g]	$\sum_{i=1}^{3} \pi_i \log(\text{least column sum of } x^{(i)}) = -0.267478$		
(1.8)[h]	$\sum_{i=1}^{3} \pi_i \log(\text{greatest column sum of } x^{(i)}) = 0.197484$		

[a] $\rho(x^{(i)})$ = spectral radius of $x^{(i)}$ = "finite growth rate" of $x^{(i)}$.

[b] $r(x^{(i)}) = \log \rho(x^{(i)})$ = "Malthusian parameter" of $x^{(i)}$.

[c] π_i = equilibrium probability of $x^{(i)}$.

[d] Spectral radius of average Leslie matrix.

[e] Malthusian parameter of average Leslie matrix = log of (1.4).

[f] Mean Malthusian parameter.

[g] Lower bound on $\log \lambda$ (Cohen, 1979); also a lower bound for $\bar{r}$.

[h] Upper bound on $\log \lambda$ (Cohen, 1979); also an upper bound for $\bar{r}$.

TABLE II

An Artificial Example of an Age-Structured Population with Stochastically Varying Vital Rates: Derived Parameters Differing among the Three Cases

Line	Case I Independently and identically distributed	Case II Forward Markovian	Case III Reversed Markovian
(2.1)[a]	$\mu^{\mathrm{I}} = 1.076971$,	$\mu^{\mathrm{II}} = 1.077178$,	$\mu^{\mathrm{III}} = 1.060268$
(2.2)[b]	$\log \mu^{\mathrm{I}} = 0.074152$,	$\log \mu^{\mathrm{II}} = 0.074344$,	$\log \mu^{\mathrm{III}} = 0.058521$
(2.3)[c]	$\lambda^{\mathrm{I}} = 1.049788$,	$\lambda^{\mathrm{II}} = 1.057159$,	$\lambda^{\mathrm{III}} = 1.044196$
(2.4)[d]	$\log \lambda^{\mathrm{I}} = 0.048588$,	$\log \lambda^{\mathrm{II}} = 0.055585$,	$\log \lambda^{\mathrm{III}} = 0.043248$
(2.5)[e]	$\mathrm{Var}^{\mathrm{I}} = 0.033771$,	$\mathrm{Var}^{\mathrm{II}} = 0.032650$,	$\mathrm{Var}^{\mathrm{III}} = 0.028433$

[a] Defined by Eq. (4); computed by Corollary 1 of Cohen (1977, p. 466).

[b] log of (2.1).

[c] Defined by Eq. (3); computed by Eq. (5) of Cohen (1979).

[d] log of (2.3).

[e] Var = variance of $\log(\| x^{(i)} y \| / \| y \|)$ computed with respect to the equilibrium joint probability distribution of $(x^{(i)}, y)$ obtained from Corollary 3(iv) of Cohen (1977, p. 27); y = age-structure vector and $\| y \| = \sum_{i=1}^{n} | y_i |$.

when Leslie matrices are chosen I.I.D. or by a regular Markov chain. Moreover, because $\bar{r}$ depends only on the equilibrium distribution and not on the sequential dependence described by P, $\bar{r}$ is intrinsically incapable of revealing variation in λ and μ when P varies while keeping the equilibrium distribution fixed.

(ii) The Malthusian parameter of the average Leslie matrix (line (1.5)) is exactly $\log \mu$ in the I.I.D. case, but not when there is Markovian dependence (line (2.2)). Under Markovian dependence, the long-run rate of growth of average population size may either exceed (case II) or be less than (case III) the rate of growth of average population size in the I.I.D. case.

(iii) Similarly, λ, the average of the rate of growth of each sample path, which in this case is also the almost-sure rate of growth of each sample path (line (2.3)), may be larger (case II) or smaller (case III) under Markovian dependence than in the I.I.D. case.

(iv) Because, in general, Leslie matrices are not commutative, time reversal can significantly affect the long-run growth characteristics of an age-structured population (compare cases II and III in Table II). In this respect, among others, an age-structured population differs fundamentally from a single-type population.

It is hoped that this detailed numerical example will provoke simulations to test and verify the results claimed. We call attention to the recommendations for reporting computation-based results of Hoaglin and Andrews (1975).

5. COMPARATIVE STATICS AND STOCHASTIC DYNAMICS

Comparative statics, developed for analyzing age-structured populations subject to fixed vital rates, as well as tools developed for analyzing single-type populations subject to varying vital rates, are of limited (though not zero) value in understanding age-structured populations subject to stochastically varying vital rates.

Because of the novelty and complexity of the phenomena which arise when vital rates vary stochastically in age-structured populations, it may be easier to perform simulations than it is to interpret them correctly without the help of analytical results.

The mean Malthusian parameter of an age-structured population subject to identically and independently distributed Leslie matrices bears no necessary relation to biologically interpretable measures of long-run population growth. Measures of long-run growth that do have meaning and are computable are available.

APPENDIX: LEAST-SQUARES ESTIMATION OF A LONG-RUN GROWTH RATE

For times $t = 0, \ldots, T$, suppose $y(t)$ is the age-structure vector, $N(t) = \sum_{i=1}^{n} y_i(t)$ is the total population size, and for $t > 0$, $L(t)$ is the matrix in Leslie form, so that $y(t+1) = L(t+1)\,y(t)$. This is the notation of Section 3 without the sample path parameter w. Assume $y(0)$ is a positive constant vector and let $\bar{N}(t) = \sum_{i=1}^{n} [(EL(t))(EL(t-1)) \cdots (EL(1))\,y(0)]_i$. E means expected value. $\bar{N}(t)$ is the total population size which would be obtained if the fixed initial age structure $y(0)$ were projected to time t by the average of the matrices which occur at each time. Assume that, for $t > 0$, $L(t)$ are independently and identically distributed for all t, as in Boyce's (1977) simulations, with a probability density function $g(L(t))$.

We seek estimators of the parameters $P \neq 0$ and Q that will give the least-squares fit of the function Pe^{Qt} to $N(t)$ treated as data. We proceed formally, assuming the existence of all integrals, derivatives, etc. The sum of the squared deviations of the data from Pe^{Qt} is

$$S = \sum_{t=1}^{T} \int \cdots \int g(L(t)) \cdots g(L(1))[N(t) - Pe^{Qt}]^2 \, dL(1) \cdots dL(t) + [N(0) - P]^2. \tag{A1}$$

Then we seek P and Q which satisfy $0 = \partial S/\partial P = \partial S/\partial Q$. Using the independence of successive matrices, we find

$$P = \sum_{t=0}^{T} e^{Qt}\bar{N}(t) \Big/ \sum_{t=0}^{T} e^{2Qt}, \tag{A2}$$

$$\sum_{t=1}^{T} te^{Qt}\bar{N}(t) = P \sum_{t=1}^{T} te^{2Qt}. \tag{A3}$$

Since every possible value of $L(t)$ is a matrix in Leslie form, $EL(t)$ is primitive, so $\rho(EL(t)) > 0$. Moreover, $\mu = \rho(EL(t))$, where μ is defined in (4) (Cohen, 1977, p. 467, Corollary 2). Consequently, for some $K > 0$,

$$\lim_{t \to \infty} \bar{N}(t)/\mu^t = K. \tag{A4}$$

If it were true that, for all t,

$$\bar{N}(t) = K\mu^t, \tag{A5}$$

then substituting into (A2) and (A3) and eliminating P and K would give

$$\left(\sum_{t=0}^{T} e^{2Qt}\right)\left(\sum_{t=1}^{T} te^{Qt}\mu^t\right) = \left(\sum_{t=0}^{T} e^{Qt}\mu^t\right)\left(\sum_{t=1}^{T} te^{2Qt}\right). \tag{A6}$$

Equation (A6) reduces to an identity if $Q = \log \mu$.

Without assuming (A5) for all t, we now use a well-known fact (Pólya and Szegö, 1972, Sect. 70): Let two sequences of real numbers $a_0, a_1, a_2, \ldots$, and $b_0, b_1, b_2, \ldots$, satisfy $b_n > 0$, $n = 0, 1, 2, \ldots$, $\lim_{n\to\infty} \sum_{j=0}^{n} b_j = \infty$, $\lim_{n\to\infty} a_n/b_n = s$. Then $\lim_{n\to\infty} \sum_{j=0}^{n} a_j / \sum_{i=0}^{n} b_i = s$.

Suppose $Q \geqslant 0$. If $b_n = e^{2Qn}$, then $b_n > 0$ and $b_0 + b_1 + b_2 + \cdots$ diverges. Let $a_n = e^{Qn}\bar{N}(n)$. Then, by (A4), $\lim_{t\to\infty} a_t/b_t = K \lim_{t\to\infty} \mu^t/e^{Qt}$. From (A2), $P = \sum_{t=0}^{T} a_t / \sum_{t=0}^{T} b_t = K \lim_{t\to\infty}(\mu/e^Q)^t$, or

$$P/K = \lim_{t\to\infty}(\mu/e^Q)^t. \tag{A7}$$

The only finite values of Q and $P \neq 0$ consistent with (A7) are $P = K$ and $Q = \log \mu$.

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REFERENCES

BOYCE, M. S. 1977. Population growth with stochastic fluctuations in the life table, *Theor. Pop. Biol.* **12**, 366–373; correction: 1978, **14**, 498.

COHEN, J. E. 1977. Ergodicity of age structure in populations with Markovian vital rates, II: General states, III: Finite-state moments and growth rate; an illustration, *Advances in Appl. Probability* **9**, 18–37, 462–475.

COHEN, J. E. 1978. Derivatives of the spectral radius as a function of nonnegative matrix elements, *Math. Proc. Cambridge Philos. Soc.* **83**, 183–190.

COHEN, J. E. 1979. Long run growth rates of discrete multiplicative processes in Markovian environments, *J. Math. Anal. Appl.* **69**, 243–251.

DALEY, D. J. 1979. Bias in estimating the Malthusian parameter for Leslie matrices. *Theor. Pop. Biol.* **15**, 257–263.

FURSTENBERG, H., AND KESTEN, H. 1960. Products of random matrices, *Ann. Math. Statist.* **31**, 457–469.

HOAGLIN, D. C., AND ANDREWS, D. F. 1975. The reporting of computation-based results in statistics, *Amer. Statist.* **29**, 122–126.

KEMENY, J. G., AND SNELL, J. L. 1960. "Finite Markov Chains," Springer–Verlag, New York.

KIM, Y. J., AND SYKES, Z. M. 1976. An experimental study of weak ergodicity in human populations, *Theor. Pop. Biol.* **10**, 150–172.

LAX, P. D. 1958. Differential equations, difference equations and matrix theory, *Comm. Pure Appl. Math.* **11**, 175–194.

LEWONTIN, R. C., AND COHEN, D. 1969. On population growth in a randomly varying environment, *Proc. Nat. Acad. Sci. U.S.A.* **62**, 1056–1060.

PÓLYA, G., AND SZEGÖ, G. 1972. "Problems and Theorems in Analysis I," Springer–Verlag, New York.

SAMUELSON, Paul A. 1965. "Foundations of Economic Analysis," Atheneum, New York.

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