SMR.478 - 19

THIRD AUTUMN COURSE ON MATHEMATICAL ECOLOGY

(29 October - 16 November 1990)

**"Demography in Stochastic Environments:
Growth and Convergence Rates"**

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These are preliminary lecture notes, intended only for distribution to participants.

Demography in stochastic environments

II. Growth and convergence rates

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1. Introduction

An appealing generalization of classical demography replaces the constant vital rates of Leslie's projection matrix by randomly time-varying vital rates (Sykes (1969), Pollard (1973)). More recently the theory of such stochastic models has been extensively developed (Cohen (1977a, b), Tuljapurkar and Orzack (1980), Heyde and Cohen (1985)) along with some applications (Cohen et al. (1983), Slade and Levenson (1982), (1984), Tuljapurkar (1982b)). A quantity of central interest in such models is population growth rate which is, of course, a random variable. It is known that the steady state average growth rate is the almost sure long run growth rate of every population trajectory, and it would be useful to know how this average growth rate depends on the underlying vital rates. Although some exact and approximate results are available (Cohen (1979), (1980), Tuljapurkar op. cit.) these fall short of a demographically complete characterization. A related issue of demographic importance, about which little is known, is the rate at which a population with random vital rates approaches the statistical steady state. The results presented here provide ways of analyzing this rate of convergence together with new insights into the determinants of convergence and growth rates.

The models studied here describe an age-structured population at time t by the vector N_t of numbers in each of k age classes, and describe the dynamics of N_t by the equation

$$N_{t+1} = X_{t+1} N_t, \tag{1}$$

where X is a matrix of vital rates. The sequence of X matrices experienced by a population is determined by a random process. In the next two sections I analyze convergence to the stochastic steady state in (1), defining and comparing several rates of convergence; this analysis also applies to more general versions of (1) such as models for size-structured populations. I show in particular that a partial analog to a classical convergence rate is found in the second largest characteristic exponent of (1) (definition in Sect. 3). However there is considerable

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information about the process which is not given by this quantity and other measures are discussed here. Subsequent sections consider the matrices X in (1) to be Leslie matrices, and present classes of matrices for which the average growth rate and in some cases a convergence rate can be explicitly computed. These are nontrivial examples and are presented both for their intrinsic interest and for the insight they yield into the dynamics of (1). The final section summarizes the key results.

2. Dynamics with random rates

In most applications involving time dependent vital rates the population is assumed to be weakly ergodic in the demographic sense (Hajnal (1976)), although I will later analyze one important example where this is not true. Demographic ergodicity coupled with random rates can result in a population approaching a statistical steady state. This is analogous to the classical process of convergence to a stable age distribution which occurs when vital rates are fixed, and is very similar to the convergence to a time-dependent age-structure under a particular time series of rates (Kim and Sykes (1976), Kim (1985)). In this section, I first specify assumptions under which a steady state will occur, and then briefly summarize the dynamics of (1) under the assumptions. With this background I then consider definitions and measures of convergence in Sect. 3. In both Sects. 2 and 3 the matrices X in (1) need not be of the Leslie type, but can be general nonnegative matrices which satisfy the assumptions; such matrices arise in Markov chains, size-structured models, and models of spatially dispersed populations.

2.1. Assumptions

For a population obeying (1) to approach some steady state, we need conditions on demographic weak ergodicity (Hajnal (1976)) and on the memory and eventual stationarity of the random process generating the time-dependent vital rates.

Throughout this section I will assume (cf. Heyde and Cohen (1985) for variants and discussion) that:

(A1) $X_1, X_2, \ldots$, is a stationary ergodic random sequence of $k \times k$ matrices with nonnegative elements;

(A2) There is an integer n_0 such that any product of any n_0 matrices from the sequence of X's has all its elements positive with probability one.

(A3) With $M_i =$ (maximum positive element of X_i), $m_i =$ (minimum positive element of X_i), there is a constant C, $1 < C < \infty$, such that for every matrix X_i

$$1 \leqslant M_i / m_i \leqslant C$$

with probability 1.

(A4) Letting E indicate an expectation with respect to the random process generating the matrices,

$$E|\log M_1|^2 < \infty.$$

(A5) The random process generating the sequence $X_1, X_2, \ldots$ is rapidly mixing (e.g., as in condition (7), Theorem 1 of Heyde and Cohen (1985)) so that

$$(\sigma \sqrt{t})^{-1}(\log\|X_t \cdots X_1\| - at) \tag{2}$$

converges in distribution to the normal $N(0, 1)$ as $t \to \infty$, for some $\sigma > 0$ and some a, where $\| \cdot \|$ is any matrix norm.

I will also consider the special case where in addition to (A5) it is assumed that:

(A6) The random process generating the sequence $X_1, X_2, \ldots$ is a finite state Markov chain.

I will refer to (A1)-(A5) as describing *stationary* rates and (A1)-(A6) as describing *Markov* rates.

2.2. Dynamics

Consider Eq. (1) with some (nonrandom) initial population N_0 and stationary rates (assumptions (A1)-(A5)). Define the norm of a vector as $|A| =$ (sum of the absolute value of components of A) so that the population age-structure is $Y_t = N_t/|N_t|$. As time t increases there is population convergence to a statistical steady state characterized as follows:

(i) The long run average growth rate of population size converges almost surely regardless of N_0 and X_1 to the number

$$a = \lim_{t \to \infty} \frac{1}{t} \ln|N_t| = \lim_{t \to \infty} \frac{1}{t} E \ln|N_t|, \tag{3}$$

with E as in (A4).

(ii) This average growth rate is also the asymptotic one period average growth rate

$$a = \lim_{t \to \infty} E \ln|N_{t+1}|/|N_t| = \lim_{t \to \infty} E \ln|X_{t+1} Y_t|. \tag{4}$$

(iii) From any initial age-structure vector y_0 the age-structure converges to a (time-dependent) stationary random sequence Y_t as $t \to \infty$. The limiting age structures are independent of y_0.

(iv) The probability distribution of sequences of vital rate matrices and age-structures $\{X_1, Y_1, X_2, Y_2, \ldots\}$ can be described by a measure on the space of sequences (cf. Furstenberg and Kesten (1960)). This measure evolves under the action of (1) to a stationary measure.

(v) There is the central limit convergence to lognormality of total population implied by (2).

When random vital rates are Markov (Assumptions A1-A6) one knows more:

(vi) With Markov rates (Cohen (1977a, b)) there is a unique steady state probability distribution P for the pair of random variables X_i, Y_i. This distribution reproduces itself under the action of (1) and can therefore be computed. Any reasonable initial distribution converges to P as $t \to \infty$.

(vii) With Markov rates one can compute explicitly moments of all orders of N_t (Cohen (1977b), Tuljapurkar (1982a)) and these grow asymptotically at geometric rates.

3. Convergence with random rates

To put the question of convergence in perspective, recall what happens if vital rates are fixed in (1) with $X = A$. Assumption A2 of Sect. 2 now guarantees that population growth rate converges to $r = \ln \lambda$ where λ is the dominant eigenvalue of A, and age-structure Y_t becomes proportional to the corresponding eigenvector u. The convergence questions (Keyfitz (1968), Coale (1973)) are: how rapidly does growth rate approach r and Y_t approach u? What oscillations in N_t are observed as $Y_t \to u$?

When vital rates are random the analogous questions concern random variables, and one has to ask how fast average growth rate approaches a, or how fast statistical distributions reach a steady state. As Sect. 2.2 indicates there are many aspects to convergence with random rates and it is not obvious how one ought to analyze convergence. I will describe below several natural measures of convergence along with their properties. Some of the results below are only applicable with Markov vital rates and are so labelled.

3.1. Characteristic exponents

Perhaps the most obvious approach to convergence is to seek a generalization of the subdominant eigenvalues of a fixed Leslie matrix. A partial generalization is found in the work of Oseledec (1968) on matrix products (see also Ruelle (1979) for a relevant discussion). Assuming stationary rates in (1), as described in Sect. 2.1, Oseledec's theorem says that there are k numbers called Liapunov characteristic exponents,

$$\rho_k \leqslant \rho_{k-1} \leqslant \cdots \leqslant \rho_1 = a, \tag{5}$$

of which say only $m \leqslant k$ are distinct, and associated random subspaces

$$V_1 \subset V_2 \subset \cdots \subset V_m = R^k, \tag{6}$$

such that if we pick a random initial vector $M_0 \in V_i / V_{i-1}$ and then compute M_t using (1) (with $V_0 = \{0\}$),

$$\rho_i = \lim_{t \to \infty} \frac{1}{t} \ln |M_t|, \tag{7}$$

where ρ_i is the appropriate exponent from (5). As (7) suggests the quantities $\exp(\rho_i t)$ are asymptotically the singular values of the random product matrix $X_t X_{t-1} \cdots X_1$.

To compute the ρ's requires a different definition, based on Raghunathan (1979): choose j linearly independent vectors $w_1(0), \ldots, w_j(0)$ and apply (1) to each of these, then $a + \rho_2 + \cdots + \rho_j$ is the maximum over all choices of the w's of

$$\lim_{t \to \infty} \frac{1}{t} \ln \| w_1(t) \wedge \cdots \wedge w_j(t) \| \tag{8}$$

where $\| w_1 \wedge \cdots \wedge w_j \|$ is the volume of the parallelepiped spanned by $w_1, \ldots, w_j$.

For numerical use of this algorithm see Benettin et al. (1980). In the special case of (8) with $j = k$ one gets

$$a + \rho_2 + \cdots + \rho_k = \lim_{t \to \infty} \frac{1}{t} \sum_{j=1}^{t} \ln \left\{ \frac{\| X_j w_1(j-1) \wedge \cdots \wedge X_j w_k(j-1) \|}{\| w_1(j-1) \wedge \cdots \wedge w_k(j-1) \|} \right\}$$

$$= \lim_{t \to \infty} \frac{1}{t} \sum_{j=1}^{t} \ln \text{Det} (X_j) = E \ln \text{Det}(X_1), \tag{9}$$

where Det means determinant. This result makes intuitive sense if one recalls that the ρ's are related to singular values.

I will now show that ρ_2 is an analog to the quantity $s = \{\ln|\text{first subdominant eigenvalue}|\}$ which describes convergence for a fixed Leslie matrix. Observe from (8) that if one picks any two vectors $w_1(0), w_2(0)$, then $(a + \rho_2)$ gives the maximum possible asymptotic growth rate of the area spanned by

$$W_1(t) = X_t X_{t-1} \cdots X_1 w_1(0) \tag{10}$$

and $W_2(t)$ defined likewise. Now recall from Sect. 2.2 that as $t \to \infty$,

$$[W_1(t)/| W_1(t)| - W_2(t)/| W_2(t)|] \to 0.$$

Therefore the area spanned by these normalized vectors

$$\|(W_1(t)/| W_1(t)| \wedge (W_2(t))/| W_2(t)|)\| \to 0 \quad \text{as } t \to \infty.$$

Recalling the definitions of a and (8) it follows that

$$\lim_{t \to \infty} \frac{1}{t} \ln\{\|(W_1(t)/| W_1(t)|) \wedge (W_2(t)/| W_2(t)|)\|$$

$$= \lim_{t \to \infty} \left\{ \frac{1}{t} \ln\| W_1(t) \wedge W_2(t)\| - \frac{1}{t} \ln| W_1(t)| - \frac{1}{t} \ln| W_t(t)| \right\} \tag{11}$$

$$\leqslant (\rho_2 + a) - 2a = (\rho_2 - a).$$

The result (11) says that the initial difference between the *directions* of $W_1(t)$, $W_2(t)$ (i.e. the corresponding age-structures) goes to zero at the maximum rate $\exp[-(a - \rho_2)t]$ as $t \to \infty$. Clearly $(\rho_2 - a)$ is a convergence rate in the demographic sense. In general for nonproportional initial vectors $w_1(0), w_2(0)$ chosen arbitrarily one expects that $W_1(t) \wedge W_2(t)$ will in fact change at the maximum rate. If one takes the matrices X to be fixed at A one can show that the rate in (11) reduces to the classical convergence rate.

Note however two important differences between the ρ's and the higher eigenvalues of a fixed matrix. First the real ρ's yield no information about the oscillatory transients in (1). Second, the subspaces corresponding to the different ρ's in (6) are random: they depend on the sequence of vital rates which will appear in (1), and it is not possible to specify them at a given initial time without knowledge of future rates. Thus the classical decay in components of age-structure orthogonal to a fixed stable structure does not generalize in any easy way. (It is

useful to compare the analysis of deterministically varying vital rates by Kim and Sykes (1976) where similar questions arise.)

The result (9) is particularly useful for Leslie matrices which have (1) the form

$$X_t = \begin{pmatrix} F_1(t) & \cdots & F_R(t) \\ P_1(t) & \cdots & 0 \\ \vdots & & \\ & P_{k-1}(t) & 0 \end{pmatrix} \quad (12)$$

where F's are fecundities and P's are survival rates. With (12) the result (9) simplifies to

$$a + p_2 + \cdots + p_k = E \ln(P_1 \cdots P_{k-1} F_k). \quad (13)$$

In the $k = 2$ case (to be discussed shortly) this yields p_2 directly.

3.2. Other approaches to measuring convergence rate

One is the construction of a measure on the sequence space $\{X_1, Y_1, X_2, Y_2, \ldots\}$. The random process of vital rates can be described by a measure on the projected sequences $\{X_1, X_2, \ldots\}$ and one can view the bivariate sequence space as a skew-product dynamical system (Abramov and Rohlin (1967)). Ruelle (1978, Corollary 6.23) and Furstenberg and Kesten (1960) consider the construction of a suitable measure on the bivariate sequence space. One can now generalize the results in Tuljapurkar (1982c) to show that the entropy of this skew-product system provides a lower bound on the rate at which the equilibrium measure is approached in sequence space.

Another approach is to examine the distributional convergence of total numbers scaled to $\ln|N_t|/\sqrt{t}$ as in (2). A numerically based analysis for Markov vital rates is given in Tuljapurkar and Orzack (1980).

The situation is much clearer with Markov rates (Cohen (1977a, b)). Here the state of the pair $\{X_t, Y_t\}$ can be represented as a point in a (product) space of $k^2 + (k-1)$ dimensions (matrix plus normalized vector). Suppose that μ is a measure on this space which is reproduced under the action of (1). Then it obeys an equation of the form

$$\mu(dz) = \int K(dz, v)\mu(dv) \quad (14)$$

where K is a nonnegative transition kernel. In general one expects a family of eigensolutions of (13)

$$\lambda\phi_\lambda(dz) = \int K(dz, v)\phi_\lambda(dv). \quad (15)$$

From the theory of positive operators (Schaefer (1974)) one has $|\lambda| \leq 1$ and $\lambda = 1$ corresponds to the solution (14). Thus a natural convergence rate is given by the eigenvalue λ for which $|\lambda|$ closest to 1.

A final approach is to ask how rapidly moments of N_t approach their asymptotic growth trends. With Markov rates it is known (Tuljapurkar (1982a))

that

$$E(N_t \otimes N_t \otimes \cdots \otimes N_t) \sim \beta_i^t(\text{Constants}) + \gamma_i^t(\text{Constants}), \\ l \text{ times} \quad (16)$$

with β_i and γ_i, $|\gamma_i| < \beta_i$, explicitly computable as eigenvalues of a particular matrix. Therefore one has a family of convergence rates given by $|\gamma_i|/\beta_i$. In the above paper the β_i, γ_i are studied for the case when $\|X_t - E(X_t)\|$ is small and it is shown that the ratios $|\gamma_i|/\beta_i$ decline rapidly with increasing l. This suggests that $|\gamma_i|/\beta_i$ may be an adequate index of convergence for the moments. Note that when the matrices X_t are independently and identically distributed this ratio reduces to the clasical quantity $\exp(r - \ln|\text{subdominant eigenvalue}|)$ for the matrix $A = E(X_t)$.

4. Leslie matrices with restricted reproduction

Ecologists and demographers (Cole (1954), Bernardelli (1941)) have been interested in populations where only one or a few age classes reproduce. I consider two cases, assuming (A1), (A3), (A4) of Sect. 2.1 (Assumption (A2) will not hold here).

4.1. Semelparity: one age-class fertility

The Leslie matrices for such a population have the form

$$X_t = \begin{pmatrix} 0 & \cdots & F(t) \\ P_1(t) & \cdots & 0 \\ \cdots & P_{k-1}(t) & 0 \end{pmatrix}, \quad (17)$$

where I ignore post-reproductive age classes. To solve (1) let $B_t = N_t(1) = (\text{Births at time } t)$.

Then

$$B_t = P_{k-1}(t)P_{k-2}(t-1) \cdots P_1(t-k+1)F(t)B_{t-k}. \quad (18)$$

Iterating this and using stationarity (the rightside below is independent of t)

$$a = (1/k)\{E \ln F(t) + E \ln P_1(t) + \cdots + E \ln P_{k-1}(t)\}. \quad (19)$$

(Cohen et al. (1983) solved the special case of a 2×2, fixed $F(t) = f$, version of (17)). For the special matrices (17) all the Liapunov exponents can be calculated as follows. Observe that the X_t in (17) can be rewritten as the product

$$X_t = HD_t = H \begin{pmatrix} P_1(t) & & & \\ & P_2(t) & & \\ & & \ddots & \\ & & & F(t) \end{pmatrix},$$

$$H = \begin{pmatrix} 0 & 0 & \cdots & \cdot & 1 \\ 1 & \cdot & \cdots & \cdot & \cdot \\ \cdot & \cdot & \cdots & \cdot & \cdot \\ 0 & \cdot & \cdots & 1 & 0 \end{pmatrix}.$$

The product of k of the X's in (17) can also be written in this form with different entries in the diagonal matrix; thus

$$X_k X_{k-1} \cdots X_1 = HD_{1k}, \quad \text{say}.$$

Iterating this,

$$X_{nk} X_{nk-1} \cdots X_1 = HD_{nk} = H \begin{pmatrix} d_{nk}(1) & & \\ & \ddots & \\ & & d_{nk}(k) \end{pmatrix}$$

and since H is unitary one has (Raghunathan op. cit.)

$$\rho_i = \lim_{n \to \infty} \frac{1}{nk} \ln d_{nk}(i).$$

From the form of D_t one concludes that

$$\rho_2 = \cdots = \rho_k = \mathbf{a}, \tag{20}$$

which is precisely analogous to the eigenvalue degeneracy encountered for a fixed matrix of the form (17). There is no convergence to a steady state.

Observe the remarkable fact that **a** is here independent of serial autocorrelation of the random process generating the vital rates. The simplicity of (19), (20) is lost as soon as the matrix acquires another fertility.

4.2. Imprimitivity: two age-classes fertile

Letting n, m be any two integers with $1 < n < nm = k$, consider Leslie matrices whose first row has the form

$$(0 \cdots 0 \quad F_1(t) \quad 0 \cdots F_2(t)), \tag{21}$$
$$\qquad\qquad \uparrow \qquad\qquad\quad \uparrow$$
$$\qquad\quad n\text{th} \qquad (nm) = k\text{th}$$
$$\qquad\quad \text{column} \qquad \text{column}$$

the rest of the matrix being as in (12) or (17). The resulting Leslie matrices are irreducible but not primitive, so here too there is no convergence to a steady state for the full process. Letting $B_t = (\text{Births at time } t)$ we have

$$B_t = F_1(t) L_n(t) B_{t-n} + F_k(t) L_k(t) B_{t-k}, \tag{22a}$$

with survivorships defined by

$$L_j(t) = \begin{cases} 1, & j = 1, \\ P_{j-1}(t-1) P_{j-2}(t-2) \cdots P_1(t-j+1), & 1 < j \le k. \end{cases} \tag{22b}$$

Now consider births at the times $t = n, 2n, 3n, \ldots$; in general at $t = Tn$, T an integer. Then define a new process $Z_k = B_{kn}$ and from (22) get

$$Z_T = F_1(nT) L_n(nT) Z_{T-1} + F_2(nT) L_{nm}(nT) Z_{T-m}. \tag{23}$$

Notice that the new Z_T has a stable limiting behavior as $T \to \infty$ since (23) can be thought of as a version of (1) involving primitive Leslie matrices. Hence the degeneracy of (20) disappears under a suitable time scaling; for (23) assumption (A2) of Sect. 2.1 will apply even though it does not for (22). Hence in (23) one has the strict inequality $\mathbf{a} > \rho_2$ since weak ergodicity now holds (cf. Sect. 3.1).

5. Two age-classes

In Tuljapurkar (1984) a number of 2 age-class versions of (1) are studied and the actual steady state distribution solving (14) is found. It is obvious from (9) and (13) that in all these cases (one of which uses Markov rates) one can find both **a** and the convergence rate ρ_2. Here I consider only one example in which the matrix X_t of (1) has the form

$$\begin{pmatrix} m_1 F_t & m_2 F_2 \\ p & 0 \end{pmatrix}$$

with $(1/F_t)$ being an i.i.d. sequence with a gamma distribution; the probability density of this gamma is

$$G(w) = [n^n/(n-1)!] w^{n-1} \exp(-nw).$$

Define the variable (proportional to a ratio of old to young)

$$R_t = (m_2 N_t(2)/m_1 N_t(1))$$

and put $z = (m_1^2/m_2 p)$. The paper cited above shows that the steady state probability density of R_t is

$$C(x) = (\text{constant}) x^{n-1} (1+x)^{-n} \exp(-nzx).$$

From these results one has the following exact results:

$$\mathbf{a} = \int_0^\infty dw\, G(w) \int_0^\infty dx\, C(x) \{\ln[m_1(1+x) + pw] - \ln(w/m_2) - \ln(m_2 + m_1 x)\},$$

$$\rho_2 = \int_0^\infty dw\, G(w) \ln(pm_2/w) - \mathbf{a}.$$

For large n the distribution $G(w)$ concentrates around $w = 1$ while $C(x)$ concentrates around the (deterministic) value $x = (1/4 + 1/z)^{1/2} - 1/2$, and it is possible to approximate **a** and ρ_2 accurately by asymptotic series. For small n a numerical calculation seems necessary.

6. Leslie matrices with constraints

Kim and Sykes (1978) studied an interesting class of Leslie matrices with time-dependent vital rates. They argue that density or other autoregulation will constrain vital rates so that the NRR of the population is always unity. Both the form of their constraint and their argument can be greatly generalized as follows. Consider a collection of vital rate matrices $A_1, A_2, \ldots$; the collection *shares reproductive value* if there is a positive vector v and positive numbers $\lambda_1, \lambda_2, \ldots$ such that

$$v^T A_i = \lambda_i v^T, \quad i = 1, 2, \ldots, \quad |v| < \infty, \tag{24}$$

where subscript T means transpose. The collection *shares stable structure* if there is a positive vector u and positive numbers $\lambda_1, \lambda_2, \ldots$ such that

$$A_i u = \lambda_i u, \quad i = 1, 2, \ldots, \quad |u| < \infty. \tag{25}$$

Suppose now that there is a stationary stochastic process which chooses the X's in (1) from a collection of matrices of type (24) or (25), and that the stationary rate assumptions of Sect. 2.1 hold. Take specifically the type (24) and observe that an initial vector N_0 becomes

$$N_t = A_{i_t}A_{i_{t-1}} \cdots A_{i_1}N_0, \qquad (26)$$

where $i_0, i_1, \ldots$ are integers which depend on the underlying stochastic process. Now using (24)

$$v^T N_t = \lambda_{i_t}\lambda_{i_{t-1}} \cdots \lambda_{i_1}v^T N_0,$$

and so

$$\mathbf{a} = \operatorname*{Lim}_{t \to \infty} \frac{1}{t} \ln|N_t|$$

$$= \operatorname*{Lim}_{t \to \infty} \frac{1}{t} \ln(v^T N_t) \quad \text{(because } |v| \text{ is bounded)}$$

$$= \operatorname*{Lim}_{t \to \infty} \frac{1}{t} \sum_{m=1}^{t} \ln \lambda_{i_m}$$

$$= E \ln \lambda, \qquad (27)$$

where the expectation is over the underlying stochastic process.

An identical result is obtained for matrices of type (25).

There are some remarkable aspects of (27). Under the stationary rate assumptions the average $E(\ln \lambda)$ is *independent* of serial autocorrelation in the vital rate sequence. With respect to growth rate the product (26) behaves as if the matrices commuted which they do not except in very special cases. Therefore the conditions (24) or (25) result in an effectively one-dimensional growth rate sequence (the relationship between one-period and long-run growth rates in (27) is generally true only for scalar processes) for an otherwise complex age-structured process. For example the age-structure in (26) under condition (24) does *not* converge to a degenerate (single vector) limit. It is easy to see this from Kim and Sykes's work on 2 age-classes with time-dependent rates. Similarly in the case of (25), although age-structure does converge to the degenerate limit u, the reproductive values does not.

These effects are brought about by the internal correlation structure of the vital rates imposed by (24) or (25). It is instructive to construct some examples. First take case (24) for 3 age-classes and let

$$v^T = (1, 1+t, 1-s), \qquad t > 0, \qquad s > 0, \qquad (28)$$

so that reproductive value is peaked at age class 2. Set

$$A_i = \begin{pmatrix} m_{1i} & m_{2i} & m_{3i} \\ p_{1i} & 0 & 0 \\ 0 & p_{2i} & 0 \end{pmatrix}, \qquad (29)$$

choose positive numbers λ_i, and observe that (24) implies

$$m_{1i} = \lambda_i - (1+t)p_{1i},$$

$$m_{2i} = (1+t)\lambda_i - (1-s)p_{2i}, \qquad (30)$$

$$m_{3i} = \lambda_i(1-s).$$

For example pick $t = s = 0.2$ in (28), $\lambda_1 = 1.1$, $\lambda_2 = 1.2$, $\lambda_3 = 1.3$, and $p_{i1} = 0.8$, $p_{i2} = 0.6$ for $i = 1, 2, 3$ to get

$$A_1 = \begin{pmatrix} 0.14 & 0.84 & 0.88 \\ 0.8 & 0 & 0 \\ 0 & 0.6 & 0 \end{pmatrix},$$

$$A_2 = \begin{pmatrix} 0.24 & 0.96 & 0.96 \\ 0.8 & 0 & 0 \\ 0 & 0.6 & 0 \end{pmatrix},$$

$$A_3 = \begin{pmatrix} 0.34 & 1.08 & 1.04 \\ 0.8 & 0 & 0 \\ 0 & 0.6 & 0 \end{pmatrix}.$$

It is easily verified that $A_1 A_2 \neq A_2 A_1$ and in general that the above matrices do not commute. A little more algebra would produce a set which did not share survival rates. Yet the growth rate of a population whose vital rates were chosen from the set $\{A_1, A_2, A_3\}$ according to a stationary process (as in Sect. 2.1) would have $\mathbf{a}$ given by (27). In the present case if $\pi_i = $ (long-run frequency of choosing A_i),

$$\mathbf{a} = \sum_{i=1}^{3} \pi_i \ln \lambda_i.$$

A similar construction is easily made starting from (25).

The general pattern of (24) is that at every age fertility and survival rate are inversely correlated in each time interval. On the other hand, (25) fixes survival rates uniquely and results in negative correlations between fertility at all ages in each time interval. In terms of possible regulatory mechanisms these differences are substantial.

7. Summary and discussion

The results obtained in this paper concern the average growth rate and convergence properties of age-structured populations with randomly varying vital rates. The specific results obtained are as follows.

Result 1. Given random rates and demographic weak ergodicity it is known that different initial age-structures will converge to the same time-dependent limit. I show that the rate of this convergence is measured by the second (Liapunov) characteristic exponent for the population's vital rate sequence (Sect. 3).

Result 2. The sum of the characteristic exponents is shown to be determined by a relationship between the average growth rate a and the average value of the determinant of the vital matrix (Sect. 3).

Result 3. The average growth rate a and all the characteristic exponents are computed explicitly for semelparous populations (Sect. 4).

Result 4. The average growth rate a and the second characteristic exponent are found explicitly for some 2 age-class models (Sect. 5).

Result 5. Alternative measures of convergence to the statistical steady state are defined with respect to the statistical probability distribution of population and vital rates, and some of their properties discussed (Sect. 3).

Result 6. Two classes of Leslie matrices are defined for which the long-run average growth rate a is explicitly computable. These allow the construction of nontrivial systems of random vital rates which display the effects of correlation between vital rates on growth (Sect. 6).

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0268