THIRD AUTUMN COURSE ON MATHEMATICAL ECOLOGY

(29 October - 16 November 1990)

"Stochastic Population Models"

Shripad TULJAPURKAR
Stanford University
Department of Biological Sciences
Stanford, CA 94305
U.S.A.

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

3

DETERMINISTIC TEMPORAL VARIATION

I now consider what happens when the fixed matrix b of (2.1.2) is replaced by a deterministically varying sequence of matrices. This is a long-standing problem with Norton (1928), Coale (1957), and Lopez (1961) being the classical contributions. Golubitsky *et al.* (1977), Hajnal (1976), Kim and Sykes (1976), Seneta (1981), Cohen (1979b), Tuljapurkar (1984) and Kim (1987) are more recent explorations. This work is a prerequisite to the study of random rates. I first consider general variation, and then cyclical variation.

1 General Temporal Changes

The time-varying version of the population model is

$$n_{t+1} = b_{t+1} n_t. \tag{3.1.1}$$

Here I use $(t+1)$ as an index for b because b_{t+1} contains vital rates which act on n_t in the interval $[t, t+1)$ to produce n_{t+1}. Starting with some initial n_0, suppose that we have a particular sequence of matrices $b_1, b_2, \ldots, b_t$. Successive age structures obey the equation

$$y_{t+1} = b_{t+1} y_t / (e, b_{t+1} y_t), \tag{3.1.2}$$

and growth rates are

$$\eta_{t+1} = m_{t+1}/m_t = (e, b_{t+1} y_t), \tag{3.1.3}$$

where m_t, as before, is total population at time t.

The key to making sense out of this time-varying situation is to ask *when* the demographic process *forgets* its initial state. The answer is, when the sequence of matrices in (3.1.1) obeys demographic **weak ergodicity**. This happens if the product matrix $b_t b_{t-1} \ldots b_1$ (which determines n_t) ends up having all entries positive for large t. In that case, there is a stable but time-varying age structure sequence $\hat{y}_t$ such that $y_t \to \hat{y}_t$ in (3.1.2), independent of y_0, for large t.

There are various sufficient conditions for demographic weak ergodicity, reviewed by Seneta (1981). In this book, I use Hajnal's (1976) notion of an **ergodic set**: this is a collection of matrices accompanied by an integer

g, such that every product of g matrices from the collection is a matrix with every element positive. Thus, demographic weak ergodicity in (3.1.1) is assured if all the matrices which can appear belong to an ergodic set. The simplest example (and a useful one) of an ergodic set is a collection of nonnegative matrices which all have positive elements and zeroes in the same locations, with any one matrix being primitive. If we construct a matrix with 1s where this collection has positive entries and 0's whenever this collection has zeroes, we obtain what is called the incidence matrix for the collection. A nonnegative matrix is primitive if and only if its incidence matrix is primitive, so the ergodicity of our collection is established.

Given demographic weak ergodicity, it is possible and useful to extend the concept of reproductive value to the time-varying case. Recall that the vital rates have the interpretation

$$(b_t)_{ij} = \text{Number of class } i \text{ individuals at time } t \text{ per class } j$$
$$\text{individual at time } t - 1. \tag{3.1.4}$$

Consider now a quantity $w_t(i)$, to be called the undiscounted reproductive value of an individual in class i at time t, and defined as the total number of descendants (*i.e.* children, grandchildren, and so on) produced by an individual who is in class i at time t. From this definition and the interpretation of the vital rates above, it follows that

$$w_t(i) = \sum_j (b_{t+1})_{ji} w_{t+1}(j). \tag{3.1.5}$$

The vector form of this recursion is

$$w_t = b_{t+1}^T w_{t+1} = b_{t+1}^T b_{t+2}^T \ldots b_{t+m}^T w_{t+m}. \tag{3.1.6}$$

To deal with the obvious possibility that the w's are likely to be unbounded, define instead the normalized (or discounted) reproductive value vector

$$v_t = w_t/(e, w_t) \tag{3.1.7}$$

which follows the recursion

$$v_t = b_{t+1}^T v_{t+1}/(e, b_{t+1}^T v_{t+1}). \tag{3.1.8}$$

Take two times, k and $\ell = (k + m) > k$, and consider

$$z(k, \ell) = b_\ell b_{\ell-1} \ldots b_{k+1} \tag{3.1.9}$$

which is a product of m matrices. Demographic weak ergodicity implies (Hajnal 1976) that this product will have its rows all proportional as m increases. Thus there is a number $\rho(k, \ell)$ and vectors $v(k, m)$ and $u(\ell, m)$ such that

$$z(k, \ell) \sim \rho(k, \ell) u(\ell, m) v^T(k, m) \quad \text{as} \quad m \uparrow. \tag{3.1.10}$$

Further we know there is stability of age structure, meaning that $u(\ell, m)$ approaches some $u(\ell)$ asymptotically independent of m; similarly $v(k, m)$ approaches some $v(k)$. Thus asymptotically for large m

$$z(k, \ell) \sim \rho(k, \ell) u(\ell) v^T(k). \qquad (3.1.11)$$

Numerical insights into (3.1.11) are to be found in Kim and Sykes (1976). Suppose now that we start with a population vector n^* at time $t = k$. Then at time ℓ we have asymptotically a population vector

$$n_\ell \sim \rho(k, \ell) \left(v(k), n^* \right) u(\ell),$$

with population structure $y_\ell \sim u(\ell)$. The growth rate here is contained in $\rho(k, \ell)$, so that $\log \rho(k, \ell) / (\ell - k)$ is the long run growth rate for $(\ell - k) \to \infty$. The normalized reproductive value at time k is $v(k)$. To find $v(k)$ simply start with an arbitrary nonnegative vector $\hat{v} \neq 0$ at time $t = \ell \gg k$ in (3.1.8) and iterate backwards.

Notice that the vital rate matrices in (3.1.2) act to propagate population vectors forward in time, and that the stable age structure at each time is an accumulation of the past. In contrast, the transposed vital rate matrices in (3.1.8) act to propagate reproductive value backward in time, and the reproductive value at each time is a summation of the future.

2 Cyclically Changing Vital Rates

Seasonal variation will often drive marked periodic variation in a population's vital rates. Human populations can be influenced by longer economic cycles; both human and natural populations can be affected by long period climate cycles. Formal analysis of such cycles was (probably) initiated by MacArthur (1968) who studied a model with 2 age classes. Coale (1972) allowed fertility to vary cyclically and used Fourier methods to explore the dynamics. Here I summarize a discrete time extension of Coale's results due to Tuljapurkar (1985). The analysis uses a perturbation technique to develop a systematic understanding of dynamics with cyclical rates.

The model for cyclical rates is

$$n_{t+1} = \left[b + d \cos(\omega t) \right] n_t. \qquad (3.2.1)$$

Here $\omega = (2\pi/T)$ is the angular frequency corresponding to the cycles of period T. The vital rates have average values contained in matrix b, and their cyclical amplitudes are contained in d. Since the total matrix on the right of (3.2.1) is nonnegative, one has $|d_{ij}| \leq b_{ij}$ whenever $b_{ij} \neq 0$, and $d_{ij} = 0$ otherwise. I assume that

$$\max_{i,j} \left(|d_{ij}| / b_{ij} \right) = g < 1, \qquad (3.2.2)$$

RANDOM RATES: GENERAL THEORY

Demographic theory with random vital rates is built on powerful general properties of random matrix products. This chapter sets out the kinds of random models I want to analyze, and summarizes general random matrix properties. Later chapters consider applications and questions which require a more concrete study of particular models.

1 Models and Questions

The classical projection model is easily generalized to include vital rates which change over time in potentially unpredictable ways. At time t, let the population vector be N_t, the population structure vector be Y_t (we use capitals to show that these are random variables). Over the interval t to $t + 1$ demographic processes operate on these vectors, and their overall effect is contained in a time-dependent matrix of vital rates X_{t+1}. The dynamics of population are given by the equation

$$N_{t+1} = X_{t+1}N_t. \qquad (4.1.1)$$

The matrix subscript is $(t + 1)$ rather than t to emphasize that these rates apply to the vector N_t. Thus in some cases (e.g., the I.I.D. model below) N_t and X_{t+1} are independent. In order to proceed, we must specify the kind of uncertainty that occurs in the vital rates. The models I consider have the following implicit structure: there is an exogenously determined time-dependent random variable called the "environment." Vital rates at each time depend on the state of the environment. Examples of subsequent interest are:

The I.I.D. Model: The entries of X are chosen randomly for each t from the same fixed (in general multivariate) distribution. There may be correlations between vital rates within each period, but there is no serial correlation between rates at different times. Here the environment is completely unpredictable. The number of possible environments can be finite (e.g., a "good" and a "bad" state), or infinite (e.g., if there is a continuously distributed variable like temperature).

The Markov Model: From one time interval to the next, vital rates change according to time invariant transition probabilities. There are three sub-

cases, according as the set of possible values of vital rates is finite. countable but infinite (*e.g.*, discrete environmental states but infinitely many of them), or uncountable (usually continuously distributed) set. Here the environment is predictable to the extent that there is serial autocorrelation over time.

The ARMA Model: The elements of the vital rates follow a linear time series model of the ARMA type (Box and Jenkins 1976). This model is most useful in situations where a time series of vital rate values is used to identify and fit a statistical model (*cf.* Lee 1974). Ecologists often prefer ARMA models in situations where serial autocorrelation over several time intervals is expected to be important.

The Semi-Markov Model: The possible values (states) of vital rates are as in the Markov case, but the time taken to make a transition from any one state to another in governed by a probability distribution which depends in general on both initial and final states. Here the history of the environment plays a stronger role.

The Catastrophe Model: This is a case of the I.I.D. model dealing with rare large environmental changes. One formulation is to suppose that in each time interval there is a very small probability of an event which will cause vital rates to reach extremely low levels; another formulation allows a probability distribution of times between successive catastrophic events, along with a distribution for the intensity of the catastrophic effect of vital rates. The biological view behind this model is of a population buffered against most small changes but vulnerable to large changes in environment.

Irrespective of the particular model used, we shall always assume that the random (environmental) process generating the vital rates converges towards an ergodic stationary state. *In general, we assume that the random process is in the stationary state*; for the approach to stationarity, see Tuljapurkar and Orzack (1980).

The next question is, what conditions apply to the possible values of the vital rates? The rates here are assumed to be always nonnegative, and in addition we assume demographic weak ergodicity (alternatively we assume that the values lie in an ergodic set). This guarantees that the dynamics of (4.1.1) are stable in the following sense. Note that we can rewrite (4.1.1) as an equation for the age structure,

$$Y_{t+1} = X_{t+1}Y_t/(e, X_{t+1}Y_t), \qquad (4.1.2)$$

where we use the scalar product and e is a vector of 1s. The difference between (4.1.1) and (4.1.2) is that the Ys, being vectors of proportions, are constrained so that $(e, Y) = 1$. Now in (4.1.2) pick two distinct initial structures b_0, c_0, and then apply the same random sequence of vital rates to both; call the resulting sequences of structure vectors B_t, C_t, respectively.

Then our ergodicity condition implies that B_t approaches C_t as t increases. This is stability, but of a special sort, since the age structures are stable towards a time-varying limit; *i.e.*, there is some sequence of structures $\hat{Y}_t$, say, and both B_t, C_t approach $\hat{Y}_t$.

We now want to know: is there an analog to the stable age distribution? What is the asymptotic growth rate of population? What is the nature of convergence in the random model? Is there something like a reproductive value?

The answers to these questions are summarized in this chapter and further explored and applied in the rest of the book. First, however, we ask two basic questions. What features of (4.1.1) suggest that it will require a new theory? Why can we not apply insights derived from classical demography and random but non-structured models to get a handle on random demography? The answers to these questions lie in the facts that the dynamics of N are multiplicative and noncommutative, and in addition, the dynamics of Y are nonlinear. From (4.1.1) note that N is determined by a product of random (*i.e.*, randomly chosen) matrices, and that these matrices do not in general commute (*i.e.*, if we switch the order in which the matrices appear, the resulting product will change). It may be a good idea to convince oneself of this by, say, multiplying together two 2×2 Leslie matrices whose subdiagonal elements differ. From (4.1.2) note that the difference equation for Y is nonlinear and thus messier than (4.1.1) for N. In classical demography this difference is irrelevant, but in the random case the moments of Y bear a complicated relationship to those of N and so the linear (4.1.1) does not shed much direct light on the nonlinear (4.2.2).

2   Results for Random Rates

There are many alternative models for random rates, so we cannot except a complete and universal theory. Instead we present results roughly in decreasing order of generality, alternating between stating mathematical results and interpreting them demographically.

2.1   GENERAL RESULTS

We begin with the most general set of assumptions:

ASSUMPTIONS *4.2.1:*

(i) *Demographic weak ergodicity holds in (2.2.1),*

(ii) *The random process generating vital rates is stationary and ergodic,*

(iii) *The logarithmic moment of vital rates is bounded,*

$$\mathsf{E} \log_+ \|X_1\| < \infty, \qquad (4.2.1)$$

where E *indicates an expectation,* $\| \cdot \|$ *is any matrix norm, and*
$\log_+(x) = \max\{0, \log x\}$.

Then we have (Furstenberg & Kesten 1960, Oseledec 1968, Cohen 1977a, Raghunathan 1979, Ruelle 1979):

(A) The long run growth rate of the logarithm of total population, or any part of population, is almost surely given by a number a independent of the initial population vector,

$$a = \lim_{t \to \infty} [\log(c, N_t)]/t \qquad (4.2.2)$$

$$= \lim_{t \to \infty} (\log \|X_t X_{t-1} \ldots X_1\|)/t \qquad (4.2.3)$$

$$= \lim_{t \to \infty} \{E \log(c, N_t)\}/t, \qquad (4.2.4)$$

where c is any vector of bounded nonnegative numbers.

(B) Starting from any initial structure Y_0 the population converges to a (time dependent) stationary random sequence of structure vectors, $\hat{Y}_t$. This limiting sequence is independent of Y_0.

(C) There is a stationary measure which describes the probability distribution of the joint sequence of vital rates and population structure vectors $\{X_1, \hat{Y}_1, X_2, \hat{Y}_2, \ldots\}$.

(D) There are constants ρ_i for $i = 1$ through $i = $ (dimension of N) such that

$$a = \rho_1 \geq \rho_2 \geq \ldots. \qquad (4.2.5)$$

The ρs are determined by the growth rates of exterior powers of the Xs, and are called Liapunov characteristic exponents . For example, let $\|x \wedge y\|$ be the volume of the parallelepiped spanned by vectors, x, y. Choose two nonproportional initial population vectors, say b_0, c_0, and apply (2.2.1) to produce two sequences of random vectors B_t and C_t. Then the almost sure growth rate of the volume spanned by any two vectors is at most

$$a + \rho_2 = \max_{\{b_0, c_0\}} \lim_{t \to \infty} \log \|B_t \wedge C_t\|/t. \qquad (4.2.6)$$

Similar results hold for sums of more exponents. (A notational point: Cohen (1977, etc.) writes $\log \lambda$ for the quantity a.)

We get an interesting general result if we add to assumptions (4.2.1) the

ASSUMPTION 4.2.2: *The random process generating vital rates can be run backwards in time, there being a unique time-reversed process which is stationary and ergodic.*

Then (Ruelle 1979) we have:

(E) Consider the adjoint (time-reversed) process associated with (4.1.2)

$$Z_t = X_t^T Z_{t+1}/(e, X_t^T Z_{t+1}),\qquad(4.2.7)$$

where superscript T indicates a transpose. Suppose we fix a vector at time $t = t_1$, say $w = z_{t_1}$. Then (4.2.7) runs backwards through decreasing values of t, and we have that as $t \rightarrow -\infty$ the resulting vectors Z_t converge to a stationary random sequence of vectors $\widehat{Z}_t$, say, independent of w_0.

2.2 INTERPRETATIONS

The central feature is that a is identified as the almost sure growth rate of population. It is also the average growth rate of the population. As the equations (4.2.2–4) show, the value of a is a function of the random properties of the rates. Note that a is also the average growth rate of any weighted sum of all or part of the population vector (from (4.2.4)).

Property (B) is the random rates counterpart of stability of population structure. Although there is a random limit to which the structures converge, there is no information of the properties of the limit. Property (C) expresses the strong overall convergence of rates plus structures to a statistical stationary state. Property (D) identifies an exponential convergence rate for population structures. All of these properties will take on substance when we become more explicit about the random process generating vital rates.

Property (E) identifies the stochastic analog of a reproductive value and helps to shed some light on the nature of reproductive value as a concept; more on this will follow.

2.3 MIXING AND LOGNORMAL LIMIT THEOREM

In addition to ASSUMPTIONS (4.2.1), let us make:

ASSUMPTION 4.2.3: *The random process generating vital rates is rapidly mixing.*

Technical aspects of the mixing condition are discussed by Furstenberg and Kesten (1960), Billingsley (1968), Tuljapurkar and Orzack (1980), and Heyde and Cohen (1985). Given such mixing, we have:

(F) Write $M_t = (e, N_t)$ for total population size at time t. There is some σ such that the asymptotic distribution of total population is lognormal,

$$\log\{(M_t - at)/\sigma\sqrt{t}\} \rightarrow N(0,1).\qquad(4.2.8)$$

The quantity σ in (4.2.8) determines the asymptotic variance of the logarithm of population size. A limit theorem by Heyde and Cohen (1985) relevant to estimating σ will be discussed in a later chapter on forecasting and projection.

The significance of the lognormal distribution (4.2.8) originally was pointed out by Lewontin and Cohen (1969) for populations without age structure. Suppose that total population number follows the random growth equation

$$M_{t+1} = R_{t+1}M_t$$
$$= R_{t+1}R_t \ldots R_1 M_0.$$

It is clear that $\log M_t$ will be asymptotically normally distributed with mean $t\,\mathsf{E}\,(\log R)$ and a variance which depends on the variance and correlation of the R_ts. One consequence of this is that the average growth rate. $(\log M_t/t)$ for large t, is in general going to be *less* than the growth rate of the average population, because

$$\log \mathsf{E}\,(M_t)/t \longrightarrow \log \mathsf{E}\,(R) \geq \mathsf{E}\,(\log R) = \mathrm{Limit}_{t \to \infty} \frac{1}{t}\mathsf{E}\,\log M_t.$$

This last inequality (Jensen's inequality, Karlin and Taylor 1975) is usually strict. A *second* consequence is that the distribution of M_t is left-skewed, indeed increasingly so for large t. Thus the most probable population sequences will tend asymptotically to fall below the average.

These conclusions all hold in the present case for structured populations. In particular the average growth rate a is the growth rate to be expected for a typical sample path, and it will in general be less than the growth rate of average population. The computation of a is considerably more involved than in the scalar case, but its qualitative importance is the same. See Tuljapurkar and Orzack (1980) for a fuller discussion and numerical examples.

2.4   MARKOVIAN RATES

The key feature here is that statistical stationarity can be captured in a probability distribution function. Make

ASSUMPTION 4.2.4: *The vital rates follow a countable state Markov process.*

Assumptions (4.2.1) and (4.2.3) are still in force. Then (Cohen 1977a,b, Lange 1979)

(G) There is a joint probability distribution of vital rates and population structures; call it $H(t,A,B) = \Pr\{X_t \in A, Y_t \in B\}$. Then as $t \to \infty$ this distribution converges to an equilibrium distribution, say $H^*(A,B)$, which reproduces itself under the action of (4.1.2).

A final extension is to deal with random fertilities in (8.1.1) instead of survival rates. As long as only one fertility varies, or both fertilities vary together, results precisely analogous to those of this section are easily obtained.

General conditions for the age structure to have a smooth or a singular distribution are not known. The state of understanding appears to reflect Hasminskii's (1980, p. 220) comment that the solution of equations such as (8.1.7) is "fraught with difficulties."

2   Random Fertility

I turn now to a 2 age class model for which I obtain an exact *and* analytic distribution of age structure. The results have been applied to the interesting biological question of why delayed flowering might have evolved in biennial plants and to the evolution of diapause and other prereproductive delays (see Chapter 16). The model is

$$N_{t+1} = X_{t+1} N_t, \tag{8.2.1}$$

with

$$X_t = \begin{pmatrix} m_1 F_t & m_2 F_t \\ p & 0 \end{pmatrix}. \tag{8.2.2}$$

Here $m_1 > 0$, $m_2 > 0$, $1 > p > 0$ and $\{F_t, t = 0, 1, \ldots\}$ is a sequence of I.I.D. random variables. I suppose that $(1/F_t)$ has a gamma distribution with probability density function

$$g(w) = (n^n/(n-1)!) \, w^{n-1} e^{-nw}. \tag{8.2.3}$$

The mean and variance of F_t are

$$\begin{aligned}
\mathsf{E}\, F = \langle F \rangle &= \int_0^\infty dw\, g(w)(1/w) \\
&= n/(n-1) \sim 1 + (1/n)
\end{aligned} \tag{8.2.4}$$

$$\begin{aligned}
\mathrm{Var}\, F = \mathrm{Variance}(F) &= \mathsf{E}\, F^2 - \langle F \rangle^2 \\
&= \left\{(n-2)(1-1/n)^2\right\}^{-1} \sim (1/n)
\end{aligned} \tag{8.2.5}$$

where the asymptotic limits are for large n. The parameter n controls the variance of fertility and when $n \to \infty$ we get $F_t \to 1$.

The **average projection matrix** from (8.2.2) is

$$b = \begin{pmatrix} m_1 \langle F \rangle & m_2 \langle F \rangle \\ p & 0 \end{pmatrix} \tag{8.2.6}$$

with dominant eigenvalue λ_0 solving

$$\lambda_0^2 - m_1\langle F\rangle\lambda_0 - m_2 p\langle F\rangle = 0. \tag{8.2.7}$$

For this average matrix, the stable ratio of old to young is $\hat{u} = (p/\lambda_0)$ and so we can write

$$r_0 = \log\lambda_0 = \log(p/\hat{u}). \tag{8.2.8}$$

Also the convergence rate of a population governed by b to the stable state is determined by the subdominant eigenvalue λ_1 of b, and we have

$$r_1 = \log|\lambda_1| = \log(m_2\langle F\rangle p) - r_0. \tag{8.2.9}$$

These two equations will be useful for comparison with the stochastic results to follow.

2.1 EQUATION FOR DISTRIBUTION

The equation for U_t, the ratio of old to young in (8.2.1), is

$$U_{t+1} = \frac{p}{F_{t+1}(m_1 + m_2 U_t)}. \tag{8.2.10}$$

It will be convenient to work with the quantity

$$R_t = (m_2 U_t/m_1), \tag{8.2.11}$$

so that

$$R_{t+1} = \frac{1}{zF_{t+1}} \cdot \frac{1}{(1+R_t)}, \tag{8.2.12}$$

with $z = (m_1^2/m_2 p)$. In this model we have $0 < F_t < \infty$ and so $0 < R_t < \infty$. Assuming that in the steady state R_t has a probability density function $C(x)$, and recalling that (8.2.3) is the density of $(1/F_t)$, we can write

$$C(x) = \int_0^\infty dy\, C(y) \int_0^\infty dw\, \delta\left[x - \frac{w}{z(1+y)}\right] g(w),$$

where $\delta(\cdot)$ is the Dirac delta function. Changing variables to do the integral over w produces an equation for C:

$$C(x) = \int_0^\infty dy\, C(y)zx(1+y)g\left[zx(1+y)\right]. \tag{8.2.13}$$

2.2 DISTRIBUTION

Inserting the explicit (8.2.3) into (8.2.13) yields an integral equation which was (happily) solved by Dyson (1953), and the solution (verifiable by substitution) is

$$C(x) = \kappa^{-1}x^{n-1}(1+x)^{-n}e^{-nzx}, \tag{8.2.14}$$

where κ is a constant which ensures that the area under $C(x)$ is unity,

$$\kappa = \int_0^\infty dx\, x^{n-1}(1+x)^{-n}e^{-nxx} \qquad (8.2.15)$$

Figure 8.2.1 plots C for three different values of n. For $n = 10$ and a coefficient of variation in fertility of 0.3, the distribution of age structure is seen to have substantial variance with a peak quite different from the "stable" value determined by the average vital rates in b.

The smoothness of C allows us to compute expectations easily, in contrast to Section 8.1. Figure 8.2.2 plots the average $\mathsf{E}\,R_t$ as a function of $(1/n)$; Figure 8.2.3 plots the variance of R_t as n changes.

2.3   GROWTH RATE

We can compute a using (4.2.10) which translates here into a double integral. With $M_t =$ (population at time t), (8.2.11) and (8.2.1) show that

$$a = \mathsf{E}\,\log\left(M_{t+1}/M_t\right) = \mathsf{E}\,\log\left[m_1 F_t(1+R_t)+p\right] - \mathsf{E}\,\log\left[m_2+m_1R_t\right] + \log m_2$$

$$= \int dx \int dw\, C(x)g(w)\log\left[\frac{m_1}{w}(1+x)+p\right]$$

$$- \int dx\, C(x)\log\left(m_2+m_1x\right) + \log m_2.$$

However, it is easier to use (8.2.12) in the first line of the above equation and get

$$a = \mathsf{E}\,\log\left(m_2p/m_1R_{t+1}\right) + \mathsf{E}\,\log\left(m_2+m_1R_{t+1}\right) - \mathsf{E}\,\log\left(m_2+m_1R_t\right).$$

In the steady state the last two terms cancel, so we get a single integral

$$a = \log\left(m_2p/m_1\right) - \mathsf{E}\,\log R_t, \qquad (8.2.16)$$

$$= \log\left(m_2p/m_1\right) - \int dx\, C(x)\log x.$$

The form (8.2.16) is very convenient for numerical computation. For analytical work it is easier to use (8.2.12) again and observe that

$$- \mathsf{E}\,\log R_t = -\mathsf{E}\,\log R_{t+1} = \log z + \mathsf{E}\,\log F_{t+1} + \mathsf{E}\,\log\left(1+R_t\right). \quad (8.2.17)$$

From (8.2.3) the reader may show that

$$\mathsf{E}\,\log F_t = \log n - \psi(n) \qquad (8.2.18)$$

where ψ is the logarithmic derivative of the gamma function (Abramowitz and Stegum 1972, Sec. 6.3.1). From the definition of $z(= m_1^2/m_2p)$ and (8.2.16)–(8.2.18), it follows that

$$a = \frac{1}{2}\log\left(\frac{m_2p}{n}\right) + \mathsf{E}\,\log F_t + \frac{1}{2}\log(zn) + \mathsf{E}\,\log\left(1+R_t\right). \qquad (8.2.19)$$
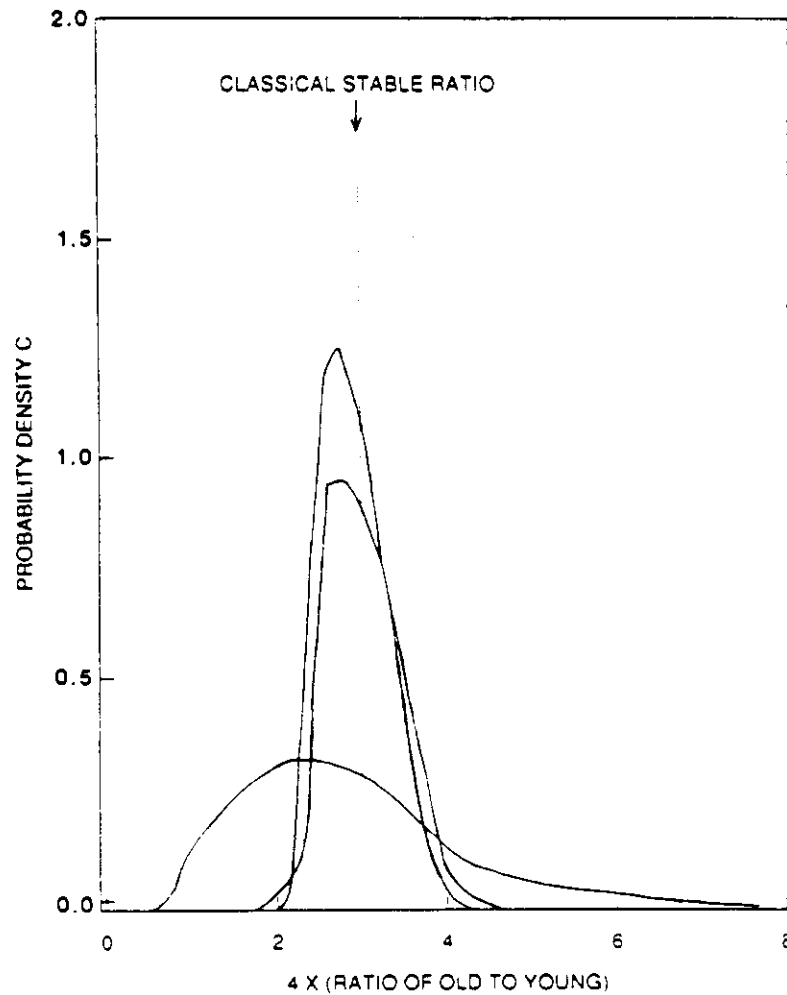
FIGURE 8.2.1. Stationary probability density of scaled age structure as defined in the text. Parameter values are $m_1 = 0.25$, $m_2 = 1$, $p = 0.75$. The classical stable ratio is indicated for vital rates fixed at these parameter values. The most spread-out density is for $n = 10$, the next for $n = 100$, and the most peaked for $n = 100$
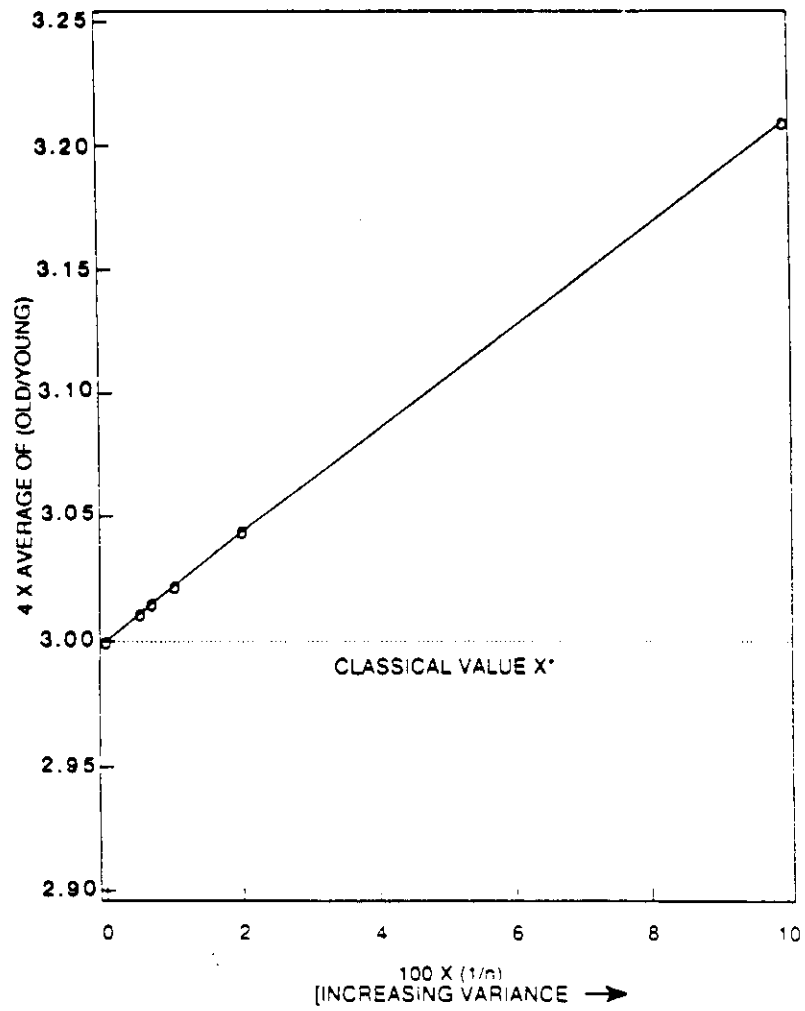
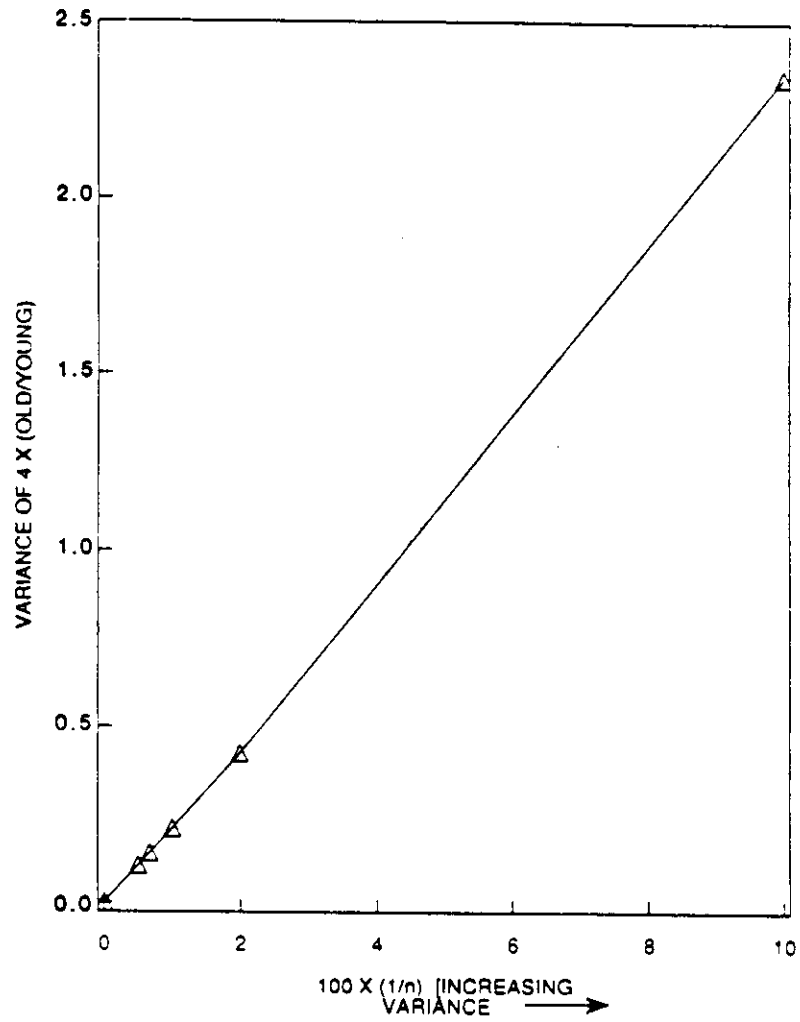FIGURE 8.2.2. Mean age structure for increasing variance in fertility. Parameters as in preceding figure; the classical stable value is shown

14

FIGURE 8.2.3. Variance in age structure for increasing variance in fertility. Parameters as in preceding figure

10

SYNERGY, CONSTRAINTS, CONVEXITY

This book deals with many of the differences between the multidimensional dynamics of structured populations and those of scalar growth models. It is important to identify those features of the structured case which differ markedly from the scalar case. The first two sections below show that the differences can be quite considerable. Section 1 discusses the effect of autocorrelation. Section 2 presents an example where serially uncorrelated random variation raises the growth rate of a population above its possible deterministic growth rate. The third section summarizes a potentially useful result of Cohen concerning the parametric sensitivity of stochastic rates. The last section shows how strong constraints on population vital rates can lead to "scalar" behavior.

1 Autocorrelation

Consider the general projection model $N_{t+1} = X_{t+1} N_t$ and suppose that $b = \mathsf{E} X_t$. There are 3 growth rates relevant to this model. One is a as defined in Section 4.2.1. The second is the growth rate of the average population (*cf.* Chapter 7),

$$\log \mu = \lim_{t \to \infty} \frac{1}{t} \log \mathsf{E} M_t. \tag{10.1.1}$$

The third is the deterministic growth rate given by using the average vital rates, $r_0 = \log \lambda_0 = \log$ (dominant eigenvalue of b). We know (Jensen's inequality) that

$$a \leq \log \mu; \tag{10.1.2}$$

thus, when vital rates are I.I.D. (Section 4.1) we have that

$$a \leq \log \mu = r_0. \tag{10.1.3}$$

In general (*i.e.*, with Markov rates, Chapter 7) serial autocorrelation can complicate matters and we may have

$$a < r_0 < \log \mu \tag{10.1.4}$$

or

$$r_0 < a < \log \mu. \tag{10.1.5}$$

Cohen (1979) provides numerical examples. These effects of autocorrelation are unique to multidimensional structured population models.

2   Synergistic Effects of Environment

Even when there is *no* autocorrelation, structured populations can behave dramatically differently from scalar ones. A striking illustration is provided by situations in which the randomness of the environment makes the difference between population growth and decline.

Consider a population with 2 age classes and suppose that the population's vital rates are given by one of 2 Leslie matrices,

$$A = \begin{pmatrix} 1/4 & 3-x \\ 1/4 & 0 \end{pmatrix}, \tag{10.2.1}$$

or

$$B = \begin{pmatrix} 15/16 - 0.1 & 1/16 + 0.09 \\ 1 & 0 \end{pmatrix}. \tag{10.2.2}$$

Take the environment to change randomly so that in each time interval the population's Leslie matrix is A with probability of p or B with probability $(1-p)$. If we set $x = 0.142857$ and $p = 0.5$ a numerical simulation (of 5000 iterations of the stochastic growth process) yields an estimate $a = +0.1954$ with a sample standard error of $\hat{s} = 0.0047$. Thus, the population should increase with probability one over the long term. Yet computation of dominant eigenvalues of the matrices shows

$$\begin{aligned} \log \lambda_0(A) &= -0.0209, \\ \log \lambda_0(B) &= -0.0087. \end{aligned} \tag{10.2.3}$$

Therefore in the absence of a random environment with matrix A or B fixed forever, the population would decline. We have here a synergistic effect of random variation. Key (1986) suggested this term in the context of a multitype branching process using special kinds of matrices. The example given above is easily generalized to more parameters or dimensions.

An equally important aspect of this example is that it shows decisively that the logarithmic mean dominant eigenvalue (of the underlying matrices) *cannot* accurately describe a, since

$$LM = 0.5[\log \lambda_0(A) + \log \lambda_0(B)] < 0, \tag{10.2.4}$$

whereas $a > 0$. It should also be obvious that this example derives fundamentally from the multidimensional character of the problem, and would not be possible without age structure.

The reader who is curious about the provenance of (10.2.1) and (10.2.2) should note that I started with simple rational members as entries. The phenomenon above is not special in any numerical sense but occurs over a range of values of x. Finally it is possible to deduce a general rule for constructing such examples with many age classes (although I will not discuss it here).

12

GROWTH RATES FOR SMALL NOISE

The long-run growth rate a is central to questions of evolution (Chapter 6), prediction (Chapter 14) and extinction. However, it is only useful if we can describe how vital rates and uncertainty determine a. This is difficult because there is no general formula to compute a for arbitrary vital rates and variability. In addition, the exactly known cases of a (Chapter 8) do not generalize; worse, they reveal singular behavior near parameter limits where demographic ergodicity is lost. One useful and general approach is to develop a systematic approximation to a when the magnitude of random variation is small. This was done by Tuljapurkar (1982b) and the results have since been applied to a number of ecological and demographic problems. The method and some extensions are presented below.

1 Second-Order Expansion of a for General Matrices

In the random-rates model write the matrix of vital rates as a sum of two parts

$$X_t = b + \epsilon H_t, \tag{12.1.1}$$

where

$$b = \mathsf{E}(X_t) \quad \text{and} \quad \mathsf{E}(H_t) = 0. \tag{12.1.2}$$

The average matrix b is assumed to be primitive and have a simple spectral decomposition (as in Section 2.2). As usual, let λ_0, u, v be the dominant eigenvalue and corresponding right and left eigenvectors of b. The parameter ϵ in (12.1.1) measures the magnitude of random variation since the nth moment of $(X_t - b)$ is proportional to ϵ^n. The temporal character of the vital rates is described by moments of variation at one time, such as

$$c(0) = \mathsf{E}(H_t \otimes H_t), \tag{12.1.3}$$

and by covariances across time, such as

$$c(\ell) = \mathsf{E}(H_t \otimes H_{t+\ell}), \quad \ell > 0. \tag{12.1.4}$$

I assume (see Chapter 4) demographic ergodicity and that H_t is a stationary, rapidly mixing stochastic process.

We begin by observing that the stochastic growth rate can be computed as

$$a = \lim_{t \to \infty} \frac{1}{t} E \log(e, X_t X_{t-1} \dots X_1 u)$$

$$= \lim_{t \to \infty} \frac{1}{t} E \log(v, X_t X_{t-1} \dots X_1 u). \qquad (12.1.5)$$

The matrix product in (12.1.5) is now expanded by using (12.1.1) to get

$$X_t X_{t-1} \dots X_1 = (b + \epsilon H_t)(b + \epsilon H_{t-1}) \dots (b + \epsilon H_1) \qquad (12.1.6)$$

$$= b^t + \epsilon \sum_{i=1}^{t} b^{t-i} H_i b^{i-1}$$

$$+ \epsilon^2 \sum_{i=1}^{t-1} \sum_{j=1}^{t-i} b^{t-i-j} H_{i+j} b^{j-1} H_i b^{i-1} + O(\epsilon^3)$$

$$= b^t + \epsilon S_{1t} + \epsilon^2 S_{2t} + 0(\epsilon^3). \qquad (12.1.7)$$

Next compute

$$\log(v, [b^t + \epsilon S_{1t} + \epsilon^2 S_{2t} + O(\epsilon^3)]u)$$

$$= \log(v, b^t u) + \log\left[1 + \epsilon \frac{(v, S_{1t} u)}{(v, b^t u)} + \epsilon^2 \frac{(v, S_{2t} u)}{(v, b^t u)} + 0(\epsilon^3)\right] \qquad (12.1.8)$$

Using the fact that

$$(v, b^t u) = \lambda_0^t (v, u), \qquad (12.1.9)$$

and letting $(v, u) = 1$ as in Chapter 2, continue with (12.1.8) to get

$$\log(v, X_t \dots X_1 u) = t \log \lambda_0 + \epsilon \frac{(v, S_{1t} u)}{\lambda_0^t} + \epsilon^2 \frac{(v, S_{2t} u)}{\lambda_0^t}$$

$$- \epsilon^2 \frac{(v, S_{1t} u)^2}{2\lambda_0^{2t}} + O(\epsilon^3). \qquad (12.1.10)$$

To use (12.1.10) in (12.1.5) we need the following computations

$$\frac{(v, S_{1t} u)}{\lambda_0^t} = \sum_{i=1}^{t} \frac{(v, H_i u)}{\lambda_0}, \qquad (12.1.11)$$

$$\frac{(v, S_{1t} u)^2}{\lambda_0^{2t}} = \sum_{i=1}^{t} \frac{(v, H_i u)^2}{\lambda_0^2} + \sum_{\substack{i=1 \\ i \neq j}}^{t} \sum_{j=1}^{t} \frac{(v, H_i u)(v, H_j u)}{\lambda_0^2}, \qquad (12.1.12)$$

$$\frac{(v, S_{2t} u)}{\lambda_0^t} = \sum_{i=1}^{t-1} \sum_{j=1}^{t-i} \frac{(v, H_{i+j} b^{j-1} H_i u)}{\lambda_0^{j+1}}. \qquad (12.1.13)$$

In (12.1.13) insert the simple spectral decomposition (2.2.10) which says that

$$b^m = \lambda_0^m (uv^T + q^m), \quad m \geq 1, \tag{12.1.14}$$

and get

$$\frac{(v, S_{2t}u)}{\lambda_0^t} = \sum_{i=1}^{t-1} \frac{(v, H_{i+1}H_iu)}{\lambda_0^2} + \sum_{i=1}^{t-1} \sum_{j=2}^{t-i} \frac{(v, H_{i+j}u)(v, H_iu)}{\lambda_0^2}$$

$$+ \sum_{i=1}^{t-1} \sum_{j=2}^{t-i} \frac{(v, H_{i+j}q^{j-1}H_iu)}{\lambda_0^2}$$

$$= \sum_{i=1}^{t-1} \sum_{j=1}^{t-i} \frac{(v, H_{i+j}u)(vH_iu)}{\lambda_0^2} + \sum_{i=1}^{t-1} \sum_{j=1}^{t-i} \frac{(v, H_{i+j}q^{j-1}H_iu)}{\lambda_0^2}$$

$$- \sum_{i=1}^{t-1} \frac{(v, H_{i+1}u)(v, H_iu)}{\lambda_0^2}. \tag{12.1.15}$$

Between the first and second steps we use the fact that $I = uv^T + (I - uv^T)$ where I is the identity matrix.

Now put (12.1.11)–(12.1.15) together into (12.1.5) and take the limit and expectation, using stationarity. The following intermediate steps are worth checking:

$$\lim_{t \to \infty} \frac{1}{t} \mathsf{E} \sum_{i=1}^{t} \frac{(v, H_iu)^2}{\lambda_0^2} = \frac{(v \otimes v)^T c(0)(u \otimes u)}{\lambda_0^2},$$

$$\lim_{t \to \infty} \frac{1}{t} \mathsf{E} \sum_{i=1}^{t-1} \sum_{j=1}^{t-1} \frac{(v, H_{i+j}q^{j-1}H_iu)}{\lambda_0^2} = \sum_{j=1}^{\infty} \mathsf{E}(v, H_{j+1}q^{j-1}H_1u).$$

The final expression for a up to second order in ϵ is

$$a \cong \log \lambda_0 - \epsilon^2 \frac{(v \otimes v)^T c(0)(u \otimes u)}{2\lambda_0^2} + \epsilon^2 \sum_{j=1}^{\infty} \mathsf{E}(v, H_{j+1}q^{j-1}H_1u)$$

$$- \epsilon^2 \mathsf{E}(v, H_2u)(v, H_1u). \tag{12.1.16}$$

2 Serially Independent Random Variation

Focus now on the important case of I.I.D. fluctuations in the vital rates. I will drop the parameter ϵ and simply refer to (ϵH_t) as the deviation. In the absence of serial autocorrelation only the first two terms of (12.1.16) survive and

$$a \simeq \log \lambda_0 - \frac{(v \otimes v)^T c(0)(u \otimes u)}{2\lambda_0^2}. \tag{12.2.1}$$

As one expects, $a < \log \lambda_0$ when $c(0) \neq 0$. It is very informative to rewrite (12.2.1) by making use of the sensitivity analysis of Section 11.1. Recall from there that for the average matrix b one has

$$\frac{\partial \lambda_0}{\partial b_{ij}} = v(i)u(j). \tag{12.2.2}$$

(Here $v^T u = 1$ by suitable normalization). The reader may now deduce that (12.2.1) can be rewritten as

$$a \simeq \log \lambda_0 - \frac{1}{2\lambda_0^2} \sum_{(ij)(k\ell)} \left(\frac{\partial \lambda_0}{\partial b_{ij}}\right) \left(\frac{\partial \lambda_0}{\partial b_{k\ell}}\right) \mathrm{Cov}(ij, k\ell), \tag{12.2.3}$$

where the sum is over $1 \leq i, j, k, \ell \leq n$ and

$$\mathrm{Cov}(ij, k\ell) = \mathsf{E}(H_t)_{ij}(H_t)_{k\ell}. \tag{12.2.4}$$

The sensitivity of a to random variation is therefore measured by squares (and pairwise products) of the sensitivity of λ_0 to average rates. This fact determines the differing effects of random variation in different vital rates.

3   Serially Independent Variation in Age-Structured Populations

Age-structured populations are the motivation for this theory and their projection matrices are Leslie matrices as in Section 2.4. Using the notation of that section, the stochastic growth rate for serially independent fluctuations in all vital rates is

$$
\begin{aligned}
a \simeq \log \lambda_0 &- \frac{1}{2\lambda_0^2} \sum_i \left(\frac{\partial \lambda_0}{\partial f_i}\right)^2 \mathrm{Var}(F_i) \\
&- \frac{1}{2\lambda_0^2} \sum_i \left(\frac{\partial \lambda_0}{\partial p_i}\right)^2 \mathrm{Var}(P_i) - \frac{1}{\lambda_0^2} \sum_{i \neq j} \left(\frac{\partial \lambda_0}{\partial f_i}\right) \left(\frac{\partial \lambda_0}{\partial f_j}\right) \mathrm{Cov}(F_i, F_j) \\
&- \frac{1}{\lambda_0^2} \sum_{i \neq j} \left(\frac{\partial \lambda_0}{\partial p_i}\right) \left(\frac{\partial \lambda_0}{\partial p_j}\right) \mathrm{Cov}(P_i P_j) \\
&- \frac{1}{\lambda_0^2} \sum_{i \neq j} \left(\frac{\partial \lambda_0}{\partial p_i}\right) \left(\frac{\partial \lambda_0}{\partial f_j}\right) \mathrm{Cov}(P_i F_j). \tag{12.3.1}
\end{aligned}
$$

The variance and covariance notation should be transparent. $E.g.$, $\mathrm{Var}(F_i)$ is the variance in fertility at age i while $\mathrm{Cov}(P_i F_j)$ is the covariance between survival rate at age i and fertility at age j.

The results of Sections 2.4 and 11.1 can be combined to obtain important special cases of (12.3.1). I will list the final result in each case and let the reader do her own algebra.

1. *Fluctuations in juvenile survival*, taken to mean survival of the youngest age class. If this survival rate is a random $P_{1t} = p_1 + Z_t$, $E(Z_t) = 0$, $\text{Var}(Z_t) = \sigma^2 = c^2 p_1^2$, then

$$a \cong \log \lambda_0 - \frac{c^2}{2T_0^2} \left(1 - \frac{f_1}{\lambda_0} \right)^2 . \qquad (12.3.2)$$

2. *Uncorrelated fluctuations in all fertilities.* Thus at each age i the fertility at time t is $F_{i,t} = f_i + Z_{it}$, $E(Z_{it}) = 0$, $\text{Var}(Z_{it}) = \sigma_i^2$, $\text{Cov}(Z_{it} Z_{jt}) = 0$ for $i \neq j$. Here

$$a \cong \log \lambda_0 - \frac{\sum_i (\ell_i \lambda_0^{-i} \sigma_i)^2}{2T_0^2} . \qquad (12.3.3)$$

3. *Correlated fertility fluctuations.* Here we take $F_{it} = f_i + Z_{it}$ with $E(Z_{it}) = 0$, $\text{Cov}(Z_{it} Z_{jt}) = \sigma_i \sigma_j$, so that

$$a \cong \log \lambda_0 - \frac{\left(\sum_i \ell_i \lambda_0^{-i} \sigma_i \right)^2}{2T_0^2} . \qquad (12.3.4)$$

There are many important applications of these results, some of which are described in Chapters 14–17 of this book.

4 Higher-Order Expansions and the Loss of Ergodicity

The formulation of Section 12.1 clearly can be extended to higher orders by carrying the expansion (12.1.6) to higher orders in ϵ. The results are instructive although the algebra is not. (Details of the analysis will appear in a forthcoming paper). Here I present the results of a 4th order expansion for the case of I.I.D. random variation in the transition rate from class 1 to class 2. In the age-structured case, this is just the survival rate.

The expansion method through order ϵ^4 yields the result

$$a \cong \log \lambda_0 - \frac{\epsilon^2 \theta^2 \sigma^2}{2\lambda_0^2} + \frac{\epsilon^3 \theta^3 \mu_3}{3\lambda_0^3} - \frac{\epsilon^4 \theta^4 \mu_4}{4\lambda_0^4}$$
$$+ \frac{\epsilon^4 \theta^3 \sigma^4}{\lambda_0^4} w^T (1 - q)^{-1} y$$
$$- \frac{\epsilon^4 \theta^2 \sigma^4}{2\lambda_0^4} (w \otimes w)^T (1 - q \otimes q)^{-1} (y \otimes y). \qquad (12.4.1)$$

A novel feature of this expansion is the appearance of the inverse matrices shown. Recall that q has eigenvalues $(\lambda_\alpha / \lambda_0)$ so $q \otimes q$ has eigenvalues

13

POPULATION STRUCTURE FOR SMALL NOISE

This chapter extends the expansion method of Chapter 12 to the population structure vector Y_t and the reproductive value vector V_t. As a byproduct of this analysis we get information on the growth rate of population over time, and on the serial correlation structure of populations over time in a varying environment. We learn how the history of environmental perturbations is filtered by population response. The first section below deals with the method itself while later sections consider implications of the results.

1 Expansions for Structure and Reproductive Value

The decomposition (12.1.1) and its attendant features from Section 12.1 are the basis for what we do here. The population structure vector Y_t obeys the equation

$$Y_t = M_t Y_0 / (e, M_t Y_0). \qquad (13.1.1)$$

where the matrix M_t is the (now familiar) product of random matrices

$$M_t = X_t X_{t-1} \ldots X_1. \qquad (13.1.2)$$

Similarly the (normalized, $i.e.$, components sum to unity) reproductive value vector obeys the backward-in-time equation

$$V_1 = M_t^T V_{t+1} / (e, M_t^T V_{t+1}). \qquad (13.1.3)$$

The objective here is to use these equations to gain insight into the statistical properties of Y and V. Accordingly I focus on the long-time behavior of these vectors, when the effects of initial conditions have been erased by time. Assuming that demographic weak ergodicity holds for (13.1.1), and therefore also for (13.1.3), we may choose an initial vector that makes calculations convenient, without having to worry about the effects of the particular choice made (at least for steady-state statistical properties).

The choices we make are

$$Y_0 = u, \qquad (13.1.4)$$

and

$$V_{t+1} = v. \qquad (13.1.5)$$

The next step is to use the expansion (12.1.7) in (13.1.1, 3) along with the choices above, and obtain the corresponding expansions of Y_t and V_1 to second-order in the parameter ϵ (which measures the amplitude of environmental fluctuations). The results are:

$$Y_t \simeq u + \epsilon(1 - ue^T)R_{1t} + \epsilon^2(1 - ue^T)[R_{2t} - (e, R_{1t})R_{1t}], \quad (13.1.6)$$

where

$$R_{it} = S_{it}u/\lambda_0^t, \quad i = 1, 2. \quad (13.1.7)$$

Similarly,

$$V_1 \simeq v + \epsilon(1 - ve^T)P_{1t} + \epsilon^2(1 - ve^T)[P_{2t} - (e, P_{1t})P_{1t}], \quad (13.1.8)$$

where

$$P_{it} = S_{it}^T v/\lambda_0^t, \quad i = 1, 2. \quad (13.1.9)$$

In working further with these expressions it is useful to note some properties of the objects $(1 - ue^T) = k$, say, and $(1 - ve^T) = h$. First, direct calculation shows that

$$k^2 = k, and \qquad h^2 = h. \quad (13.1.10)$$

Further, if we apply matrix k to any power of the average vital rate matrix, then the spectral decomposition (see (12.1.14)) shows that

$$\begin{aligned} kb^m &= \lambda_0^m k(uv^T + q^m) \\ &= \lambda_0^m kq^m, \quad m \geq 1. \end{aligned} \quad (13.1.11)$$

Similarly, applying h to the transpose of any power of b shows that

$$h(b^T)^m = \lambda_0^m h(q^T)^m, \quad m \geq 1. \quad (13.1.12)$$

Finally, note that

$$(e, k) = (e, h) = 0 \quad (13.1.13)$$

This last fact is the least significant, and it simply ensures that the vectors Y and V in the expansions have the right normalization. However (13.1.10–12) show that k and h act as projection operators which extract the transient component (remember that $q^m \to 0$ as m increases) from powers of the average vital rate matrix.

2   Properties of Structure and Reproductive Value

The expansion (13.1.7) reveals several facts about Y_t. Recall from the definitions in Section 12.1 that $E(R_{it}) = 0$, since that term is linear in the random deviations H_t. Therefore the average value of Y_t differs from

Lecture Notes in Biomathematics

Managing Editor: S. Levin

85

Shripad Tuljapurkar

Population Dynamics in Variable Environments

Springer-Verlag

New York Berlin Heidelberg London Paris Tokyo Hong Kong

REFERENCES

Billingsley, P. 1968. _Convergence of probability measures._ Wiley.

Box, G.E.P., and Jenkins, G.M. 1970. _Time Series Analysis, Forecasting and Control._ Holden Day

Coale, A.J. 1957. _Cold Spring Harbor Symposium on Quantitative Biology, V. 22, pp. 83-87._

Cohen, J.E. 1977a. _Adv. Appl. Prob._ $\underline{9}$: 18-37

           1979a. _Theor. Pop. Biol._ $\underline{16}$: 159-171.

           1979b. _Math. Proc. Camb. Phil. Soc._ $\underline{86}$: 351-364.

Dyson, F.J. 1953. _Physical Review_ $\underline{92}$: 1331-1338

Furstenberg, H. and Kesten, H. 1960. _Annals Math. Stat._ 31: 457-469

Golubitsky, M., Keeler, E.B., and Rothschild, M. 1976 _Theor. Pop. Biol._ $\underline{7}$: 84-93.

Hajnal, J. 1976. _Math. Proc. Camb. Phil. Soc._ $\underline{79}$: 521-530.

Heyde, C.C. and Cohen, J.E. 1985. _Theor. Pop. Biol_ $\underline{27}$: 120-153.

Hasminskii, R.Z. 1980. _Stochastic Stability of Differential Equations._ Sijthoff & Noordhoff.

...aye, R. and Hargrove, ... Proc. Appl. Prob. ... 607-36?

ee, R.D. 1974. Jour. Amer. Stat. Assoc. 69: 607-614.

Lopez, A. 1961. Problems in Stable Population Theory. Princeton Univ. Press.

Lewontin, R.C. and Cohen, D. 1969. Proc. Nat. Acad. Sci. (USA) 62: 1056-1060.

Karlin, S. and Taylor, H.M. 1975. A First Course in Stochastic Processes. Academic.

Key, E.S. 1987. Prob. Thry. and Related Fields. 75: 97-107.

Kim, Y.J. 1987. Theor. Pop. Biol. 31: 306-322.

Kim, Y.J. and Sykes, Z.M. 1978. Demography 15: 559-569.

Norton, H.T.J. 1928. Proc. London Math. Soc. 28: 1-45.

Oseledec, V.I. 1968. Transac. Moscow Math. Soc. 19. 197-231.

Seneta, E. 1981. Non-negative matrices and Markov chains. Springer-Verlag.

Raghunathan, M.S. 1979. Israel Jour. of Math. 32: 356-367

Ruelle, D. 1979. Advances in Math. <u>32</u>: 68-80.

Tuljapurkar, S. 1982b. Theor. Pop. Biol. <u>21</u>: 141-165.

——— " ———. 1984a. Jour. Math. Biol. <u>19</u>: 335-350.

——— " ——— and Orzack, S. H. 1980. Theor. Pop. Biol. <u>18</u>: 314-342.