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A study of Leslie model under stochastic environments

Kamran Shaukat
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AN ABSTRACT OF THE THESIS OF Kamran Shaukat for the Master of Science in Physics presented August 5, 1981.

Title: A Study of Leslie Model Under Stochastic Environments.

APPROVED BY MEMBERS OF THE THESIS COMMITTEE:


S. D. Tuljapurkar, Chairman


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The prediction and analysis of changes in the numbers of biological populations rest on mathematical formulations of demographic events (births and deaths) classified by the age of individuals. The development of demographic theory when birth and death rates vary statistically over time is the central theme of this work. A study of the standard Leslie model for the demographic dynamics of populations in variable environments is made. At each time interval a Leslie matrix of survival rates and fertilities of a population is chosen according to a Markov process and the

population numbers in different age classes are computed. Analytical bounds are developed for the logarithmic growth rate and the age-structure of a population after long times. For a two dimensional case, it is shown analytically that a uniform distribution results for the age-structure if the survival rate from the first to the second age-class is a uniformly distributed random quantity with no serial autocorrelation. Numerical studies are made which lead to similar conclusions when the survival rate obeys other distributions. It is found that the variance in the survival parameter is linearly related to the variance in the age-structure. An efficient algorithm is developed for numerical simulations on a computer by considering a time sequence of births rather than whole populations. The algorithm is then applied to an example in three dimensions to calculate a sequence of births when the survival rate from the first to the second age-class is a random parameter. Numerical values for the logarithmic growth rate and the logarithmic variance for a population and the probability of extinction are obtained and then compared to the analytical results reported here and elsewhere.

A STUDY OF LESLIE MODEL
UNDER STOCHASTIC ENVIRONMENTS

by
KAMRAN SHAUKAT

A thesis submitted in partial fulfillment of the
requirements for the degree of

MASTER OF SCIENCE

in

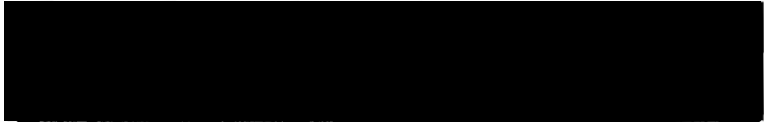
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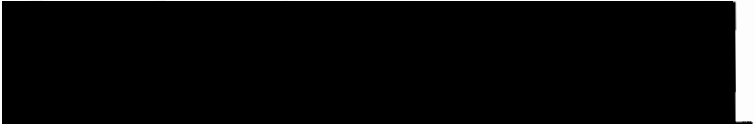
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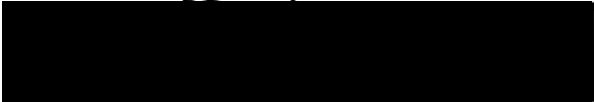
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The members of the Committee approve the thesis of
Kamran Shaukat presented August 5, 1981.


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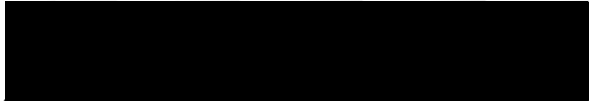

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Kamran Shaukat

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CHAPTER I

INTRODUCTION

The development of sound models for the time trajectory of population numbers, growth rate and extinction probabilities is of prime importance in ecological theory. Since such models are used to predict the environmental consequences of human activities, the strengths, weaknesses and domain of applicability of the models must be clearly understood to avoid costly ecological mistakes.

The foundation of most ecological models is the deterministic model of Malthus (1798) which describes the exponential growth of a single species population. The model was greatly developed in modern times by Lotka (1907), Sharpe and Lotka (1911) and Volterra (1926, 1937). Such models assume an unvarying exponential growth rate which is unreasonable in real communities, albeit, is common in laboratory populations unlimited by nutrients or space. Another shortcoming of Lotka-Volterra type models is that they consider populations as a whole disregarding their internal structure and its effects. For example, the birth and the death rates which are used to estimate the rate of natural increase depend largely on the ages (or sizes) of individuals in a population. Questions about the impact

of infant mortality and the reproductive span, of great interest in human demography, cannot be addressed properly without looking into the age-structure of a population. More complex versions of the basic Lotka-Volterra type models employ continuous time and age variables to account for age-structure. An equivalent class of models employs matrix algebra to describe age-structure in discrete time intervals. Such models use a discrete time variable and a discrete age-scale and have been studied extensively under unvarying environments with age dependent birth and survival rates (Bernardelli, 1941; Lewis, 1942; Leslie, 1945, Keyfitz, 1968, Pielou, 1977). Use of these models permits us to predict the age or size composition of a population after long times along with the population number and the eventual rate of increase. The continuous time models will be referred to as Lotka models; the discrete time versions will be called Leslie models, following Lotka (1907) and Leslie (1945).

Further development in ecological theory depends on more realistic extensions of the deterministic models above to include temporal variability of environments. Changing environmental conditions induce fluctuations in the vital rates of a population so the results of deterministic models are no longer applicable to the dynamics of populations.

Temporal fluctuations in the vital rates of a population can be predictable or random. Predictable variations

at seasonal and other frequencies have been studied by several workers. It has been shown by Skellam (1967), MacArthur (1968), Coale (1972) and Gourley and Lawrence (1977) that periodicity in vital rates results in corresponding variations in population structure. For an arbitrary but known sequence of vital rates which applies over all future times, Lopez (1961) has proven the weak ergodic theorem of demography, i.e., after long times any initial age distribution eventually converges to the same but not necessarily fixed age distribution and the same growth rate.

A more general approach to the problem would be to look at the Leslie model for age or size structured populations in temporally unpredictable environments. The Leslie matrix of vital rates is then randomly determined at each time interval. Following Pollard (1973) and Sykes (1969) the Leslie matrices for a particular realization are assumed to be independent random variables or are chosen according to a Markov chain. Several workers have studied the mean and variance of the population vector (Pollard, 1973; Sykes, 1969; Namkoong, 1972). Weissner (1971) and Athreya and Karlin (1971) have explored the question of asymptotic extinction of a population. Long run growth rates in unpredictable environments have been studied numerically by Boyce (1977) and analytically by Cohen (1976, 1977a, b). Cohen (1977a) has also established the random version of the demographic weak ergodic theorem for Markov sequence of vital

rates. Tuljapurkar and Orzack (1980) have studied the analytical distribution of the asymptotic growth rate of populations, and a given numerical example of a two dimensional stochastic model.

Here further results are developed for variability in survival and mortality schedules under random fluctuations using Monte Carlo techniques and analytical methods. We have focused on the problem of age-structure and its distribution and have obtained various useful results. Next, an efficient algorithm is developed for numerical work on the stochastic Leslie model. The algorithm is applied in three dimensions to study the logarithmic growth rate and its variance, and examine the probability of extinction. The analytical approximations developed in Tuljapurkar (1981) are tested here against numerical calculations.

CHAPTER II

THE BACKGROUND ON POPULATION MODELS IN ECOLOGY

a) The Deterministic Models

The central mathematical model of population due to Malthus (1798) describes a single species growing in an unvarying environment with fixed fertilities and mortalities; this model is the basis for deterministic models of multi-species ecological communities. The differential equation for the Malthusian model of change in population numbers with time is

$$(1) \quad \frac{dx(t)}{dt} = r x(t),$$

where $x(t)$ is population at time t , and r is the net growth rate. The analogous difference equation when time is measured in discrete intervals is

$$(2) \quad N(t+1) = m N(t),$$

where $N(t)$ is the population number at time t and m is the net growth rate in discrete time. Note that for equivalence of these two models, $m = \exp(r)$.

In the above equations, population numbers change exponentially; a trend which cannot continue for long in actual populations which would either disappear or become

infinitely large. Under normal circumstances both these events are quite unlikely and contrary to observation. Ample evidence indicates that many populations regulate their numbers by some density dependent mechanism (Tanner, 1966; Mcbridge, 1966).

Density dependent population control can be incorporated into a growth equation by the addition of a damping term modifying the rate of growth as the population increases. One of the many forms that this damping can take is illustrated by the logistic equation

$$(3) \quad \frac{dx}{dt} = rx(1 - x/k)$$

where k , the carrying capacity, is the maximum number of organisms that the environment can support. The logistic equation fits many population growth experiments well enough to be of considerable practical use. Only two constants must be determined, the intrinsic rate of natural increase and the carrying capacity. Neither of the two quantities can be given in general an exact mathematical or biological definition independently of the eq. (3). Conceptually, the logistic suggests two extremes of evolutionary schemes: (a) evolution toward the fastest possible growth rate: "r-selection"; (b) evolution toward the most efficient use of the environment, resulting in the largest carrying capacity, the "k-selection" (for a discussion see e.g. MacArthur and Wilson, 1967). The utility of the logistic equation

and of the r or k "selection" concept is limited due to the many simplifying assumptions underlying the models.

There is no biological justification for the damping term in eq. (3) to vary with the square of population density. Pielou (1977) suggests we can think of quadratic damping as the first approximation in a Taylor expansion of more general density dependences. Inclusion of higher order terms would allow greater flexibility while curve fitting experimental data (Wangersky, 1978) but might also obscure biological insight.

It is biologically likely that actual populations would not respond instantaneously to changes in their numbers as in the logistic equation. Thus, a time lag between the cause and effect should be introduced into single species growth models. A simple model incorporating time delay is due to Hutchinson (1957). A general form of the equation for the model can be obtained by introducing a discrete time lag into the damping term of equation (3).

$$\frac{dx}{dt} = rx(1 - (x/k))_{t-\tau}$$

where τ is the time lag between cause and effect. Several other forms of the differential equation and corresponding difference equations have been proposed (Ross, 1972; Mazanov, 1973; May, 1973, May, 1974). Lefkovitch (1966) has incorporated delayed responses into a matrix algebra for population growth. The inclusion of time delay has a destabilizing

effect; there is an increase in the kinds of solutions possible. Even under stable environments, oscillations can occur which grow large enough to produce extinction in single species populations.

The logistic equation and other deterministic models discussed here display a monotonic approach to an equilibrium population. If they do show oscillatory behavior as in models with time delay, the fluctuations cannot be entirely explained in biological terms. The difficulty with these models is the assumption that populations live under constant environments. All ecological environments show some periodic or random variability, and such fluctuations eventually affect the patterns of growth of a population.

For this reason, the deterministic models of theoretical ecology, though used extensively in demographic work, do not provide adequate estimates or predict future trends of a population. Since most natural communities exist in environments varying randomly over time, the deterministic models need to be modified to include the temporal variability in the fecundity and mortality schedules. We need to consider the effects of environmental unpredictability on population size, the ultimate rate of increase and the asymptotic stable age distribution.

b) The Stochastic Models

The study of population dynamics under stochastic

environments is more realistic, but often phenomenological considerations lead to mathematically intractable formulations. Perhaps the simplest models take a macroscopic view of the problem and treat population growth as a diffusion process. Rewrite equation (1) as

$$(4) \quad \frac{dx(t)}{dt} = r(t) x(t),$$

where the Malthusian parameter, $r(t)$, is now assumed to be a function of time and takes on values consistent with the variability in environment. $r(t)$ can be assumed to be made of two parts

$$(5) \quad r(t) = \bar{r} + \epsilon(t)$$

where \bar{r} is a constant mean value of the growth rate and $\epsilon(t)$ is a stationary stochastic process. Over long time intervals the process $\epsilon(t)$ can be represented in a coarse-grained way by a δ -correlated white noise

$$(6) \quad \begin{aligned} \langle \epsilon(t) \rangle &= 0 \\ \langle \epsilon(t_1) \epsilon(t_2) \rangle &= 2\beta \delta(t_2 - t_1) \end{aligned}$$

where brackets denote ensemble averages and $\delta(t_2 - t_1)$ is the usual Dirac delta function. Here β is the spectral density for the random fluctuations. With random perturbations model behavior is more complex than in deterministic models.

We now have a first order stochastic differential equation; interest now focuses on the probability of observing a population size of $x(t)$ at time t conditional on a known initial size. $x(t)$ must now be viewed as a realization of a continuous and time homogeneous process. Instead of a stable population we now look for a stable probability distribution of a population. We also need to look at the probability of a population going extinct, since the environmental fluctuations may be strong enough to make the ultimate rate of growth less than unity for some realizations.

If the random fluctuations obey equations (5) and (6), the population size behaves as a Markov diffusion process and can be studied in terms of a Wiener process (Capocelli and Ricciardi, 1974; Tuckwell, 1974). The probability density function $f(x(t) | x(0))$ for $x(t)$ given initial population, $x(0)$ obeys the Kolmogorov forward equation

$$\frac{\partial f(x(t) | x(0))}{\partial t} = -(\bar{r} + \beta) \frac{\partial}{\partial x} (xf) + \beta \frac{\partial^2}{\partial x^2} (x^2 f)$$

where $(\bar{r} + \beta)x$ and $2\beta x^2$ are the drift and variance for the process.

A similar transformation of the logistic equation leads to the stochastic differential equation

$$\frac{dx(t)}{dt} = r(t) x(t) \left(1 - \frac{x(t)}{k}\right), \quad 0 \leq x(t) \leq \infty$$

This equation has been studied by Levins (1969) and May

(1973); Tuckwell (1974) transforms it into an Ornstein-Uhlenbeck process. Results can be immediately obtained for the probability distribution and the extinction probabilities since the process is fully understood analytically. Capocelli and Ricciardi (1974) have derived expressions for the expected first passage time T at some level S and its variance $\sigma^2(S, X(0))$

$$T(S, X(0)) = |\ln(X(0)/S)| / |\bar{r}|$$

$$\sigma^2(S, X(0)) = (2\beta / \bar{r}^2) |\ln(X(0)/S) / \bar{r}|$$

also the most likely value t for the first passage time is

$$\tau = \begin{cases} \ln^2(X(0)/S) / 6\beta, & \bar{r} = 0 \\ -3/2 + [(9/4) + (\bar{r}/2\beta)^2 \ln(X(0)/S)]^{1/2}, & \bar{r} \neq 0 \end{cases}$$

The use of diffusion approximations in the study of ecological models is mathematically convenient but not very realistic. It implies that both death and birth are continuous processes. It also assumes that a gross average rate of growth over the life span of an individual may be meaningfully deduced from the data. Both these assumptions seriously limit the applicability of the model. We know that birth and death processes are discrete and would be more accurately described by a Stochastic difference equation. It is also reasonable to assume that the fertilities

and the survival rates and hence the growth rate of a population is a function of age or size distribution. These considerations lead us to Leslie's model discussed in the next chapter.

CHAPTER III

LESLIE'S MODEL

Earlier we have discussed the need to work with a model that employs a discrete time variable and age structure, giving due weights to the age-specific survivals and mortalities. This approach is also preferable because most available data is in the discrete form and because it coincides with the actuarial practice. Leslie's model is the best known and most detailed of such models.

The Leslie model (1945) considers only one-sex (usually females) in a single closed population divided into age groups corresponding to a discrete unit interval of time. A decision as to the best choice of a unit time interval is usually dictated by the available data. Pollard (1973) shows that there is little difference in the deterministic asymptotic results when different age groupings are used in the case of human populations. The results may not be as satisfactory for other organisms. The model is best suited to a matrix formulation. The general form of a Leslie matrix is

$$\underline{L} = \begin{bmatrix} \underline{A} & \underline{0} \\ \underline{B} & \underline{C} \end{bmatrix}$$

The first row in \underline{A} , a $k \times k$ matrix, contains fertilities $m(i)$ $0, i=1,2,\dots,k$ with $m(k)$ having the last non-zero value. The survival rates for the first k age-classes are on the off-diagonal as indicated:

$$\underline{A} = \begin{bmatrix} m(1) & m(2) & m(3) & \dots & m(k) \\ p(1) & 0 & 0 & \dots & 0 \\ 0 & p(2) & 0 & \dots & 0 \\ \vdots & & & & \\ 0 & \dots & 0 & p(k-1) & 0 \end{bmatrix}$$

\underline{A} is non-negative, irreducible since $m(k)$ does not vanish (Sykes (1969)) and primitive if the greatest common divisor of the indices of the positive elements in the first row is one (Rosenblatt, 1957). Also \underline{A} satisfies the hypotheses of the Perron-Frobenius theory of non-negative matrices.

According to this theory matrix \underline{A} has a positive dominant eigenvalue λ_0 of multiplicity one corresponding to some column eigenvector U and a row eigenvector V' , both of which have positive elements; further λ_0 is greater in absolute size than any other eigenvalue. An excellent account of the properties of \underline{A} is given by Parlett (1970).

It is well known that \underline{A} contains all the important information about \underline{L} . For example, the age groups beyond reproduction do not contribute to the growth rate of the whole population. Hence, without loss of generality \underline{A} can

be used to work out the mechanics of the Leslie model.

Consider the female population in the first k age groups arranged in the form of a k - dimensional vector N_t at any time t . At the end of each time interval $(t, t+1]$, $t=0,1,2,\dots$ a new population vector N_{t+1} is determined by the equation

$$(8) \quad N_{t+1} = \underline{A} N_t$$

Iteration of the above equation yields

$$(9) \quad N_{t+1} = \underline{A}^{t+1} N_0$$

where N_0 is the initial population structure. Since \underline{A} has a positive dominant eigenvalue λ_0 , largest in absolute size, it eventually swamps the effects of other eigenvalues while any initial age distribution asymptotically approaches U , the stable age distribution. Pielou (1969) illustrates the ergodic property nicely in a graph for population trajectories belonging to different Leslie matrices with the same λ_0 . They both converge to the same stable age distribution though they choose different paths depending on higher eigenvalues.

Within the foregoing deterministic description we can incorporate the temporal variability of the environment quite naturally into Leslie theory. Fertilities and survival rates are considered as functions of time. At each time interval $(t, t+1]$, $t=1,2,\dots$ fertilities $m_t(i)$, $i=1,2,\dots,k$

and survival rates $p_t(i)$, $i=1,2,\dots,k$ are contained in a Leslie matrix \underline{X}_t . For any realization of the process the successive Leslie matrices are chosen from a random set to form a Markov sequence of environmental states such that

$$(10) \quad N_{t+1} = \underline{X}_t N_t = \underline{X}_t \underline{X}_{t-1} \cdots \underline{X}_0 N_0$$

Total population at any time t is

$$(11) \quad M_t = \sum_{i=1}^k N_t(i)$$

Define the cumulative growth in total population number in time t to be

$$(12) \quad \Lambda_t = \frac{M_t}{M_0}$$

where M_0 is initial fixed population corresponding to N_0 .

Also since this is a geometric growth model, define the ultimate rate of increase as $\lim_{t \rightarrow \infty} \frac{1}{t} \ln \Lambda_t$. Boyce (1977) has studied the long run growth rates numerically. Cohen (1977) has established the demographic weak ergodic theorem for Markov sequences of vital rates. Tuljapurkar and Orzack (1980) have extended earlier results and looked at the long run distribution of growth rates in fluctuating environments. They establish that the logarithm of the cumulative growth in number is asymptotically normally distributed at long times

$$(13) \quad \ln \Lambda_t \xrightarrow[t \rightarrow \infty]{} \sim N(at, \sigma^2 t)$$

where a, σ^2 are the scaled mean and variance respectively. They have employed the lognormality of cumulative growth rate to explore the probability of extinction analytically and numerically.

CHAPTER IV

BOUNDS FOR POPULATION GROWTH RATE AND AGE STRUCTURE IN VARIABLE ENVIRONMENTS

Assuming for any given environment a reasonable estimate can be made as to the span of variability of each fertility and survival rate for all times such that

$$(14) \quad \begin{aligned} P_{\min}(i) &\leq P_t(i) \leq P_{\max}(i) \\ m_{\min}(i) &\leq m_t(i) \leq m_{\max}(i) \end{aligned}$$

Using these bounds on fertilities and survivals we can construct matrices \underline{X}_{\max} , \underline{X}_{\min} . Then elementwise

$$(15) \quad \underline{X}_{\min} \leq \underline{X}_t \leq \underline{X}_{\max}; \text{ for all } t$$

Using equation (10) it can be shown by iteration

$$(16) \quad \underline{X}_{\min}^t N_0 \leq N_t \leq \underline{X}_{\max}^t N_0$$

Since the inequality is true elementwise, using equations

(11) and (12)

$$(17) \quad \lim_{t \rightarrow \infty} \frac{1}{t} \ln \Lambda_{\min} \leq \lim_{t \rightarrow \infty} \frac{1}{t} \ln \Lambda_t = a \leq \lim_{t \rightarrow \infty} \frac{1}{t} \ln \Lambda_{\max}$$

corresponds to a constant matrix involving $P_{\min}(i)$ and $m_{\min}(i)$. From deterministic theory $N_t \lambda_{\min}^t N_0$ where λ_{\min} is the dominant eigenvalue of \underline{X}_{\min} and the logarithmic growth rate for the process is $\lim_{t \rightarrow \infty} \frac{1}{t} \ln \Lambda_{\min} = \ln \lambda_{\min}$. Similarly

$\lim_{t \rightarrow \infty} \frac{1}{t} \ln \Lambda_{\max} = \ln \lambda_{\max}$ This shows that the long run distribution of logarithmic growth rate is bound by the extremes of values taken by survivals and fertilities. Also, the eventual rate of growth would lie somewhere between λ_{\min} and λ_{\max} .

Another useful inequality provides the bounds on age structure. Consider a Leslie matrix for which all entries are constant except $p_t(1) = p$. p is a random variable with probability density $W(p)$ and bounded by constants p_1 and p_2 , $p_1 \leq p(t) \leq p_2$. Define $U_t = \frac{N_t(2)}{N_t(1)}$, $t = 0, 1, 2, \dots$ the ratio of the second age class to the first at time t . The choice of a new matrix at the end of a time interval $(t, t+1]$ is in effect a choice of a new p . We can write

$$(18) \quad \begin{aligned} U_{t+1} &= f_p(U_t) \\ &= f_p(f_p(\dots f_p(U_0)\dots)) \end{aligned}$$

where $f_p(u)$ is some function of p and U_t determined by the equation for the model. If U_0 at $t=0$ is known then from the bounds on p it can be deduced

$$(19) \quad f_{p_1}(U_0) \leq f_p(U_0) \leq f_{p_2}(U_0)$$

and

$$f_{p_1}(f_{p_1}(U_0)) \leq f_p(f_p(U_0)) \leq f_{p_2}(f_{p_2}(U_0))$$

etc.

If we fix $p = c$, a constant then $N_t \rightarrow \lambda_c^t U$ where λ_c is the dominant eigenvalue and U is the corresponding right eigenvector. After long time we have a stable age distribution which implies $U_t \rightarrow U_c$, a constant. Applying this to equation (18) we have

$$(20) \quad U_{p_1} \leq U_t \leq U_{p_2}, \text{ for all } t.$$

CHAPTER V

A TWO DIMENSIONAL EXAMPLE

Let the survival from first to the second age class be a random variable chosen from some distribution $w(p)$. The basic equation is:

$$(21) \quad \begin{bmatrix} N_{t+1}(1) \\ N_{t+1}(2) \end{bmatrix} = \begin{bmatrix} m(1) & m(2) \\ p & 0 \end{bmatrix} \begin{bmatrix} N_t(1) \\ N_t(2) \end{bmatrix}$$

Here $m(1)$ and $m(2)$ are fertilities of the first and the second age classes and p is the survival rate from the first to the second age class. Define $y_t(1) = N_t(1)/M_t$ and $y_t(2) = N_t(2)/M_t$, the fractions of population in the two age classes and $U_t = \frac{N_t(2)}{N_t(1)}$ as their ratio.

Numerical simulations of such a model to explore the convergence to lognormality and the effects of environmental variance and auto correlation have been reported by Tuljapurkar and Orzack (1980). Here we study the following: Starting from a known distribution $w(p)$ of the survival parameter p how are $y_t(i)$ and U_t distributed after long times? How is the variance in p related to the variance in y_t and U_t ? How is the average of y_t related to average value of p ?

For $m(1) = .85$, $m(2) = 1.0$ and $w(p) \sim \text{triangular } (\beta)$ with

$\bar{p} = 0.4$ Monte Carlo simulations were done on a computer. 500 population trajectories were calculated for the process, each one being 500 generations long. For these trajectories the parameters y_t, U_t were calculated at $t = 500$ and their histograms were plotted. The triangular distribution for p was chosen because it is compact as compared to normal and can be generated more efficiently on a computer. The method to generate the triangular distribution and a Fortran program for the process is given in Appendix A. We find a triangular distribution also results for y_t and U_t (see Figures 1 - 3).

To study the variance and average of y_t and U_t , calculations were made for a number of different values of β about a fixed mean. Figure 4 illustrates the relationship between the variance in p and in $y_t(1)$: An increasing variance in p increases the variance observed in $y_t(1)$. The results are similar for $y_t(2)$ and U_t . With $E(p)$ ($E(\cdot)$ denotes expectation) held fixed, changes in $\text{var}(p)$ did not affect the position of the means of y_t and U_t . Also, $E(U_t)$ and $E(y_t)$ are found to be in excellent agreement with what one would expect from the deterministic theory if p is replaced by its average value.

We also looked at the problem of age structure analytically. From equations (18) and (21) we have

$$(22) \quad f_p(u) = \frac{p}{m_1 + m_2 u} = u', \text{ say}$$

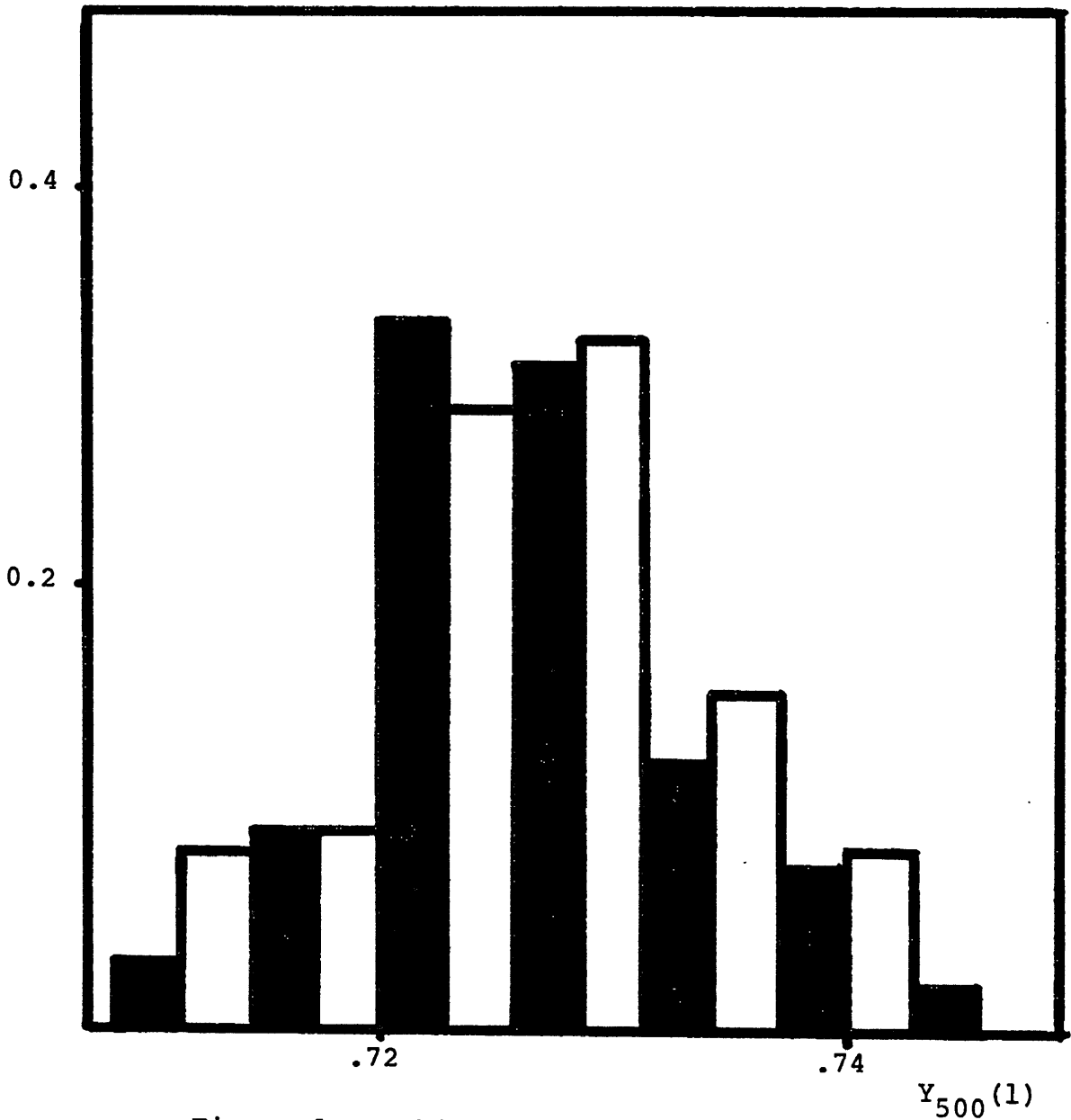


Figure 1. A histogram for the distribution of $Y_{500}(1)$, the fraction of population is the first age class when the survival rate is distributed triangular (.02).

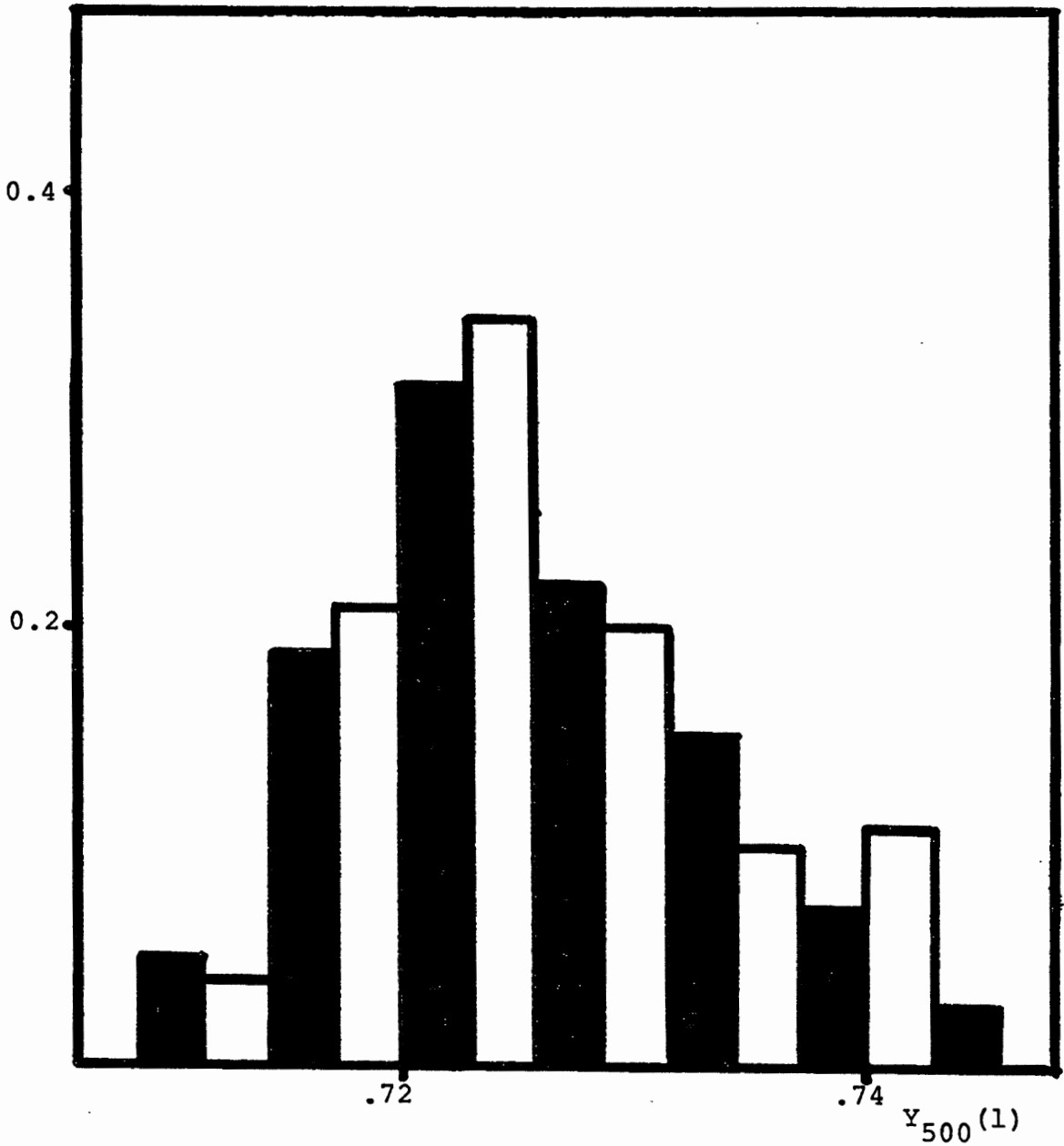


Figure 2. A histogram for the distribution of $Y_{500}(1)$, the fraction of population is the first age class when the survival rate is distributed \sim triangular (.10).

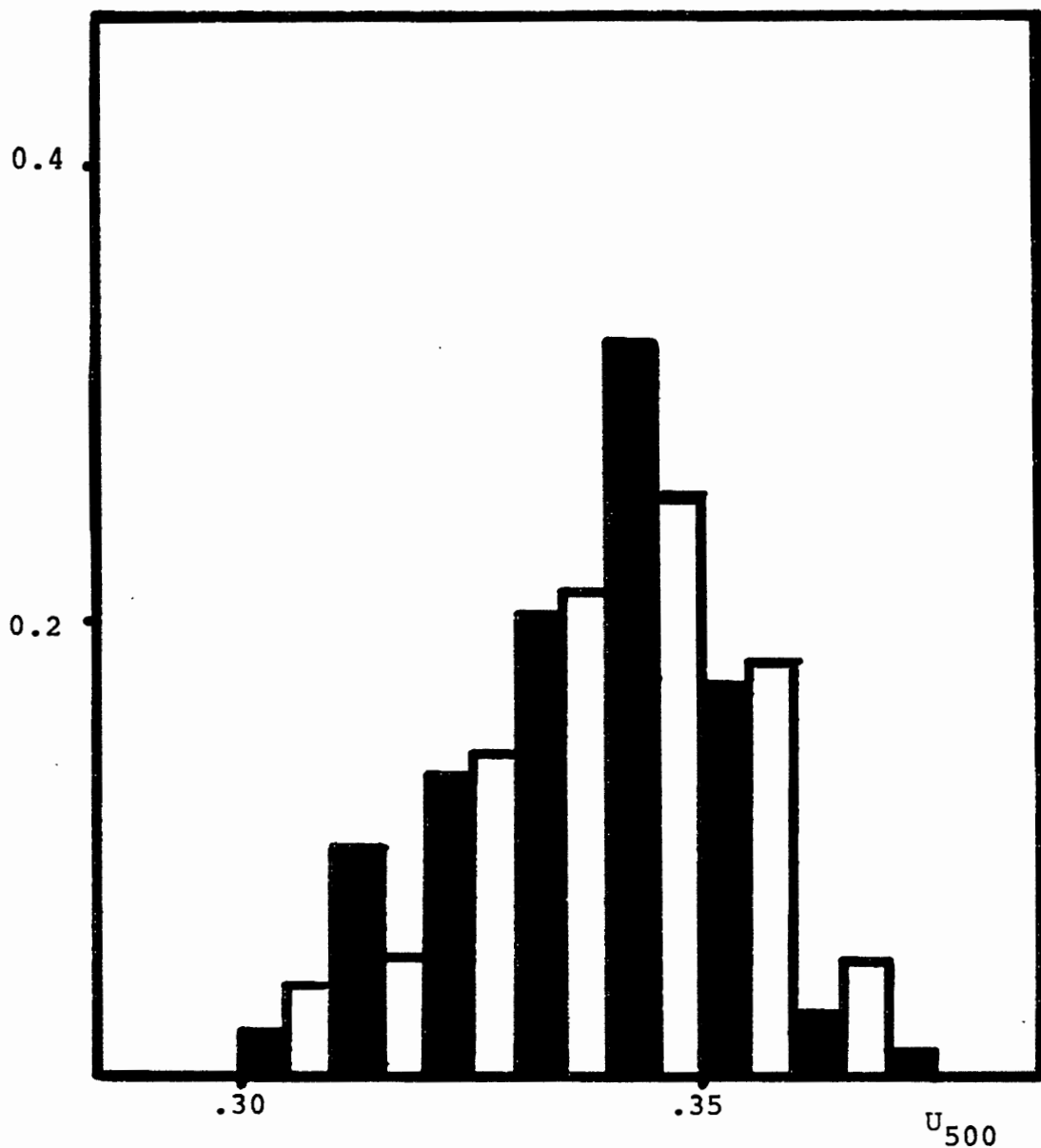


Figure 3. Distribution for U_{500} , the ratio of the second age class to the first, when the survival rate is distributed \sim triangular (0.1).

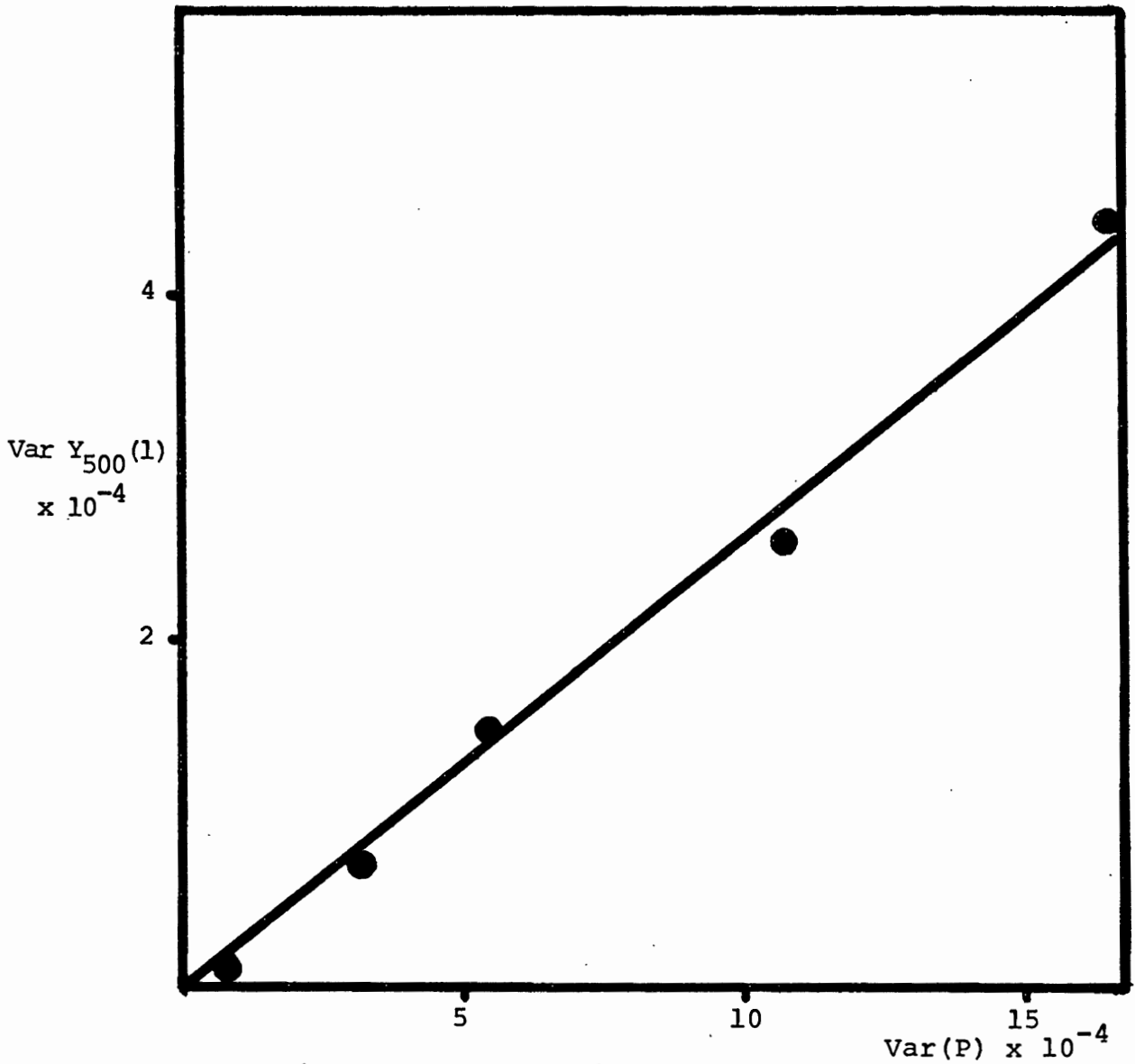


Figure 4. The variance in $Y_{500}(1)$ is plotted as a function of the variance in the survival rate with triangular distribution.

then

$$(23) \quad u = f_p^{-1}(u') = g_p(u') = \frac{p}{m_2 u'} - \frac{m_1}{m_2}$$

Let the stationary distribution of U be

$h(\eta) d\eta = \text{Prob}\{u \in (\eta, \eta+d\eta)\}$ to get the distribution of U' as $h(\xi) d\xi = \text{Prob}\{u' \in (\xi, \xi+d\xi)\}$. Then we have

$$(24) \quad h(\xi) d\xi = \int_I dp w(p) h(\eta) d\eta$$

where I means that for each p we use that η which satisfies $\xi = f_p(\eta)$. So on R.H.S. of equation (24)

$$(25) \quad h(\xi) = \int dp w(p) h(g_p(\xi)) \frac{p}{b\xi^2}, \quad \xi \text{ is fixed on R.H.S.}$$

Rewriting (25) after a change of variables $\eta = g_p(\xi)$,

$$p = (m_1 + m_2 \eta) \xi, \quad dp = b \xi d\eta$$

$$(26) \quad h(\xi) = \int w[\xi(a + b\eta)] h(\eta) (a + b\eta) d\eta$$

A relatively simple result can be obtained if p is uniformly distributed, since then $w(p) = \text{constant}$. As

$\int h(\xi) d\xi = 1$ we have

$$(27) \quad h(\xi) = \frac{1}{u_{p_2} - u_{p_1}}$$

If p belongs to other more complex distributions, the analytical results are not easily extended and it may be necessary to look for a numerical solution to the problem. To investigate the stationary probability distribution numerically, a Markov matrix with row sums equal to unity is constructed by considering a mapping of U_t on U . The algorithm for the process and its implementation in Fortran are given in the Appendix B. As an example we take p distributed uniform on $(.3, .5)$ with other parameters having the same values as described earlier. As expected the results show a uniform distribution for U_t within the analytical range of U_t obtained in the last section.

RESULTS

In summary, we find the following: (1) the age structure distribution closely follows the distribution of the random variable in the Leslie matrix; this random variable is the survival rate in the above two dimensional examples. (2) the variance in age structure is a linear function of the variance in the random variable and (3) the mean age-structure is tied to the predicted deterministic age structure for the average value of the random variable. We expect the results would be true for higher dimensional models.

CHAPTER VI

SIMULATION IN THREE DIMENSIONS

A more efficient and faster algorithm is developed to calculate the population trajectories and relevant statistics on a computer. The process is viewed as a sequence of births in time. Numbers in higher age classes can be computed using the relevant survival rates. Define

$$\Psi_1 = 1 = \Psi_2 ; \Psi_3 = P_2 , \dots , \Psi_i = \prod_2^{i-1} P_i$$

and

$$\chi_i = m_i \Psi_i$$

$$Z_1 = 1 ; Z_2 = P_1(t-1) , \dots , Z_i = P_1(t-i+1)$$

Then the number of births $B(t)$ at time t can be written as

$$(28) \quad N_t(t) = B(t) = \sum_{i=1}^k \chi_i Z_i B(t-i)$$

The above equation assumes the variability in environment affects only the first survival rate. We can write a similar equation for $B(t)$ when other parameters show random variations.

The equation can be iterated to yield a sequence of births of appropriate length provided the births at the first k intervals could be supplied. The latter condition is no more restrictive than the specification of an initial age distribution vector N_0 in the matrix multiplication method. In any case, due to the ergodic property of the process, it is not critical what values are chosen for the first k births.

To work with the equation (28) we need to store $\{B(t)\}_t^{t-k}$, $\{\lambda_k\}_1^k$, and $\{z_i\}_1^{k-1}$; $3k$ quantities in all. Iteration, requires $2k$ multiplies and k adds in each step. This scheme saves substantial storage space and operations. By contrast if matrix methods are employed we need to store k^2+k quantities (a k^2 matrix and a k vector) and require k^2 multiplies and $k(k-1)$ adds in each step.

We also note that the result obtained by Tuljapurkar and Orzack (1980) for the lognormality of t can be easily extended for the birth sequence. Their proof is strict in the sense that the process converges to lognormality element-wise as $t \rightarrow \infty$. Hence, we can conveniently write for the logarithmic growth rate

$$a = \lim_{t \rightarrow \infty} \frac{1}{t} \ln \frac{B_t}{B_0}$$

We used this algorithm for numerical simulations in three dimensions. The main purpose of the study was to

look at the logarithmic expectation and variance of the growth rate in relation to the extent of fluctuations. Also, a numerical test of the analytical results reported by Tuljapurkar (1981) was sought.

In time populations may decline and finally may disappear if the environmental fluctuations are too strong. A stochastic model should be able to predict the possibility of such an event, i.e., the probability of extinction. Since N_0 has nonnegative components in our model, N_t and M_t would always be positive however small (Keiding, 1975). The problem is avoided by defining an extinction level, a pre-assigned number at which populations can be considered extinct. We explore this problem numerically.

EXAMPLE

We study an example in three dimensions due to Boyce (1977) using the algorithm developed earlier. Here $m(1) = 0$, $m(2) = 1.5$, $m(3) = 2.2$ are the fertilities for the three age classes. The survival rate for the second to the third age class $p_2 = 0.25$ is a constant. The survival from the first to the second age class incorporates the random variability of the environment in $p(1) = .6 + \epsilon_1$, where ϵ_1 is uniformly distributed on $(-\beta, \beta)$ with no serial correlation. Also, the number of births at the first three time intervals is: $B(0) = 1000$, $B(1) = 1100$, $B(2) = 1200$. A program for the process is given in the Appendix C.

A sequence of births for 500 time intervals was calculated. A random number generator $\sim U(0,1)$ was first used to decide the sign of variation in p_1 and again for the magnitude of variation. Various statistics were calculated using 200 such birth sequences. Calculations were made for several different β . Estimates of errors were made by doing the experiment a large number of times. Another set of calculations was made for a given β and $E(p_1)$ but different values of $m(3)$. Test calculations were also made for Leslie models appropriate for fish populations with large fecundity (10^5) and very small survival of the first age class (10^{-5}) with essentially the same results.

RESULTS

(1) An increasing value of parameter β decreases the logarithmic average, a and increases the logarithmic variance, σ^2 . A graph between a and σ^2 (Figure 5) shows that the two parameters are linearly related. The intercept on the a -axis provides the expected deterministic result for the logarithmic growth rate.

(2) If β is held fixed and different values are assigned to $m(3)$, we obtain a system of parallel lines for different average values of p_1 in a plot of a vs σ^2 . It shows that a decreasing logarithmic average whether it is due to larger fluctuations or a decreasing fertility increases the logarithmic variance.

(3) The values of a obtained from simulations for small β are remarkably close to the calculated values when the analytical formula reported by Tuljapurkar (1981) is used. We find the formula over-estimates for larger values of β ; as much as by 50% when β is as large as $E(p_1)$. The formulae for variance in Tuljapurkar (1981) provides equally good results for small perturbations; for higher perturbations it underestimates the variance (see Table I).

(4) The probability of extinction at any level (see Figure 7 for numerical values) for a population trajectory decreases rapidly for a given environment with time. The maximum number of births remain fairly stable with increasing β , i.e., some populations grow large even under severe conditions and escape extinction.

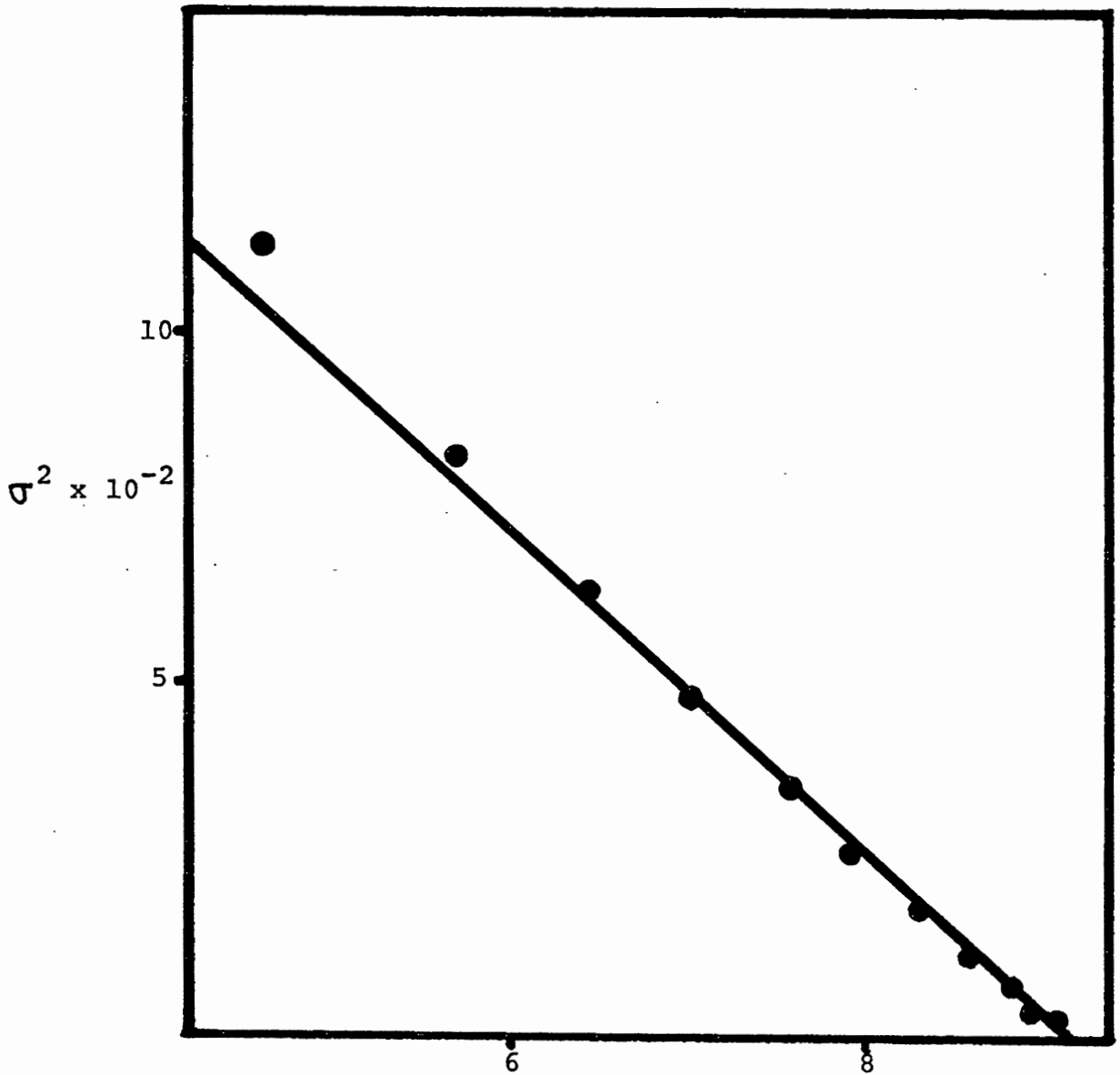


Figure 5. A graph between logarithmic average a and variance σ^2 . $E(p_1) = .6$

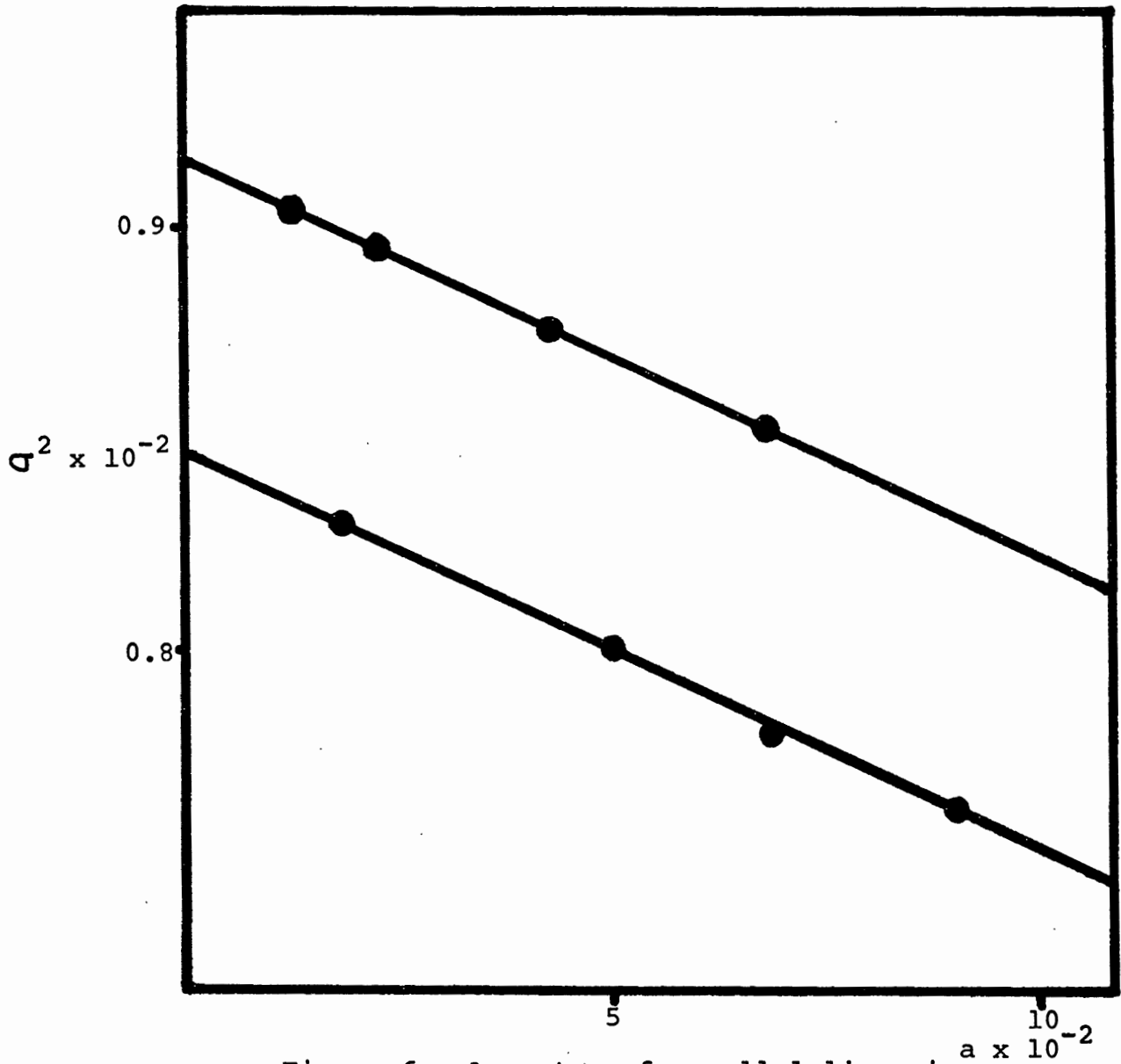


Figure 6. A system of parallel lines in the plot of a^2 vs. a when $E(p_1)$ is fixed but $m(3)$ is allowed to have different values. Here $\epsilon = 0.05$

TABLE I

COMPARISON OF NUMERICAL AND ANALYTICAL VALUES OF a AND σ^2 ¹

Magnitude of Fluctuation (β)	Simulated		Analytical	
	$a \times 10^{-1}$	$\sigma^2 \times 10^{-2}$	$a \times 10^{-1}$	$\sigma^2 \times 10^{-2}$
0.025	0.914	0.011	0.915	0.004
0.050	0.912	0.041	0.914	0.015
0.075	0.911	0.105	0.912	0.038
0.100	0.907	0.179	0.910	0.060
0.150	0.896	0.410	0.902	0.135
0.200	0.880	0.748	0.892	0.240
0.300	0.832	1.80	0.862	0.540
0.400	0.756	3.52	0.820	0.961
0.500	0.643	6.31	0.766	1.50

1. Numerical values are obtained with $E(p_1)=0.6$, $m(1)=0$, $m(2)=1.5$, $m(3)=2.2$ and $p_2=0.25$ corresponding analytical values are calculated using formulas reported in Tuljapurkar (1981).

$$a = \ln \lambda_0 + \frac{\tau^2}{2\lambda_0}$$

and

$$\sigma^2 = \frac{\tau^2}{2\lambda_0}$$

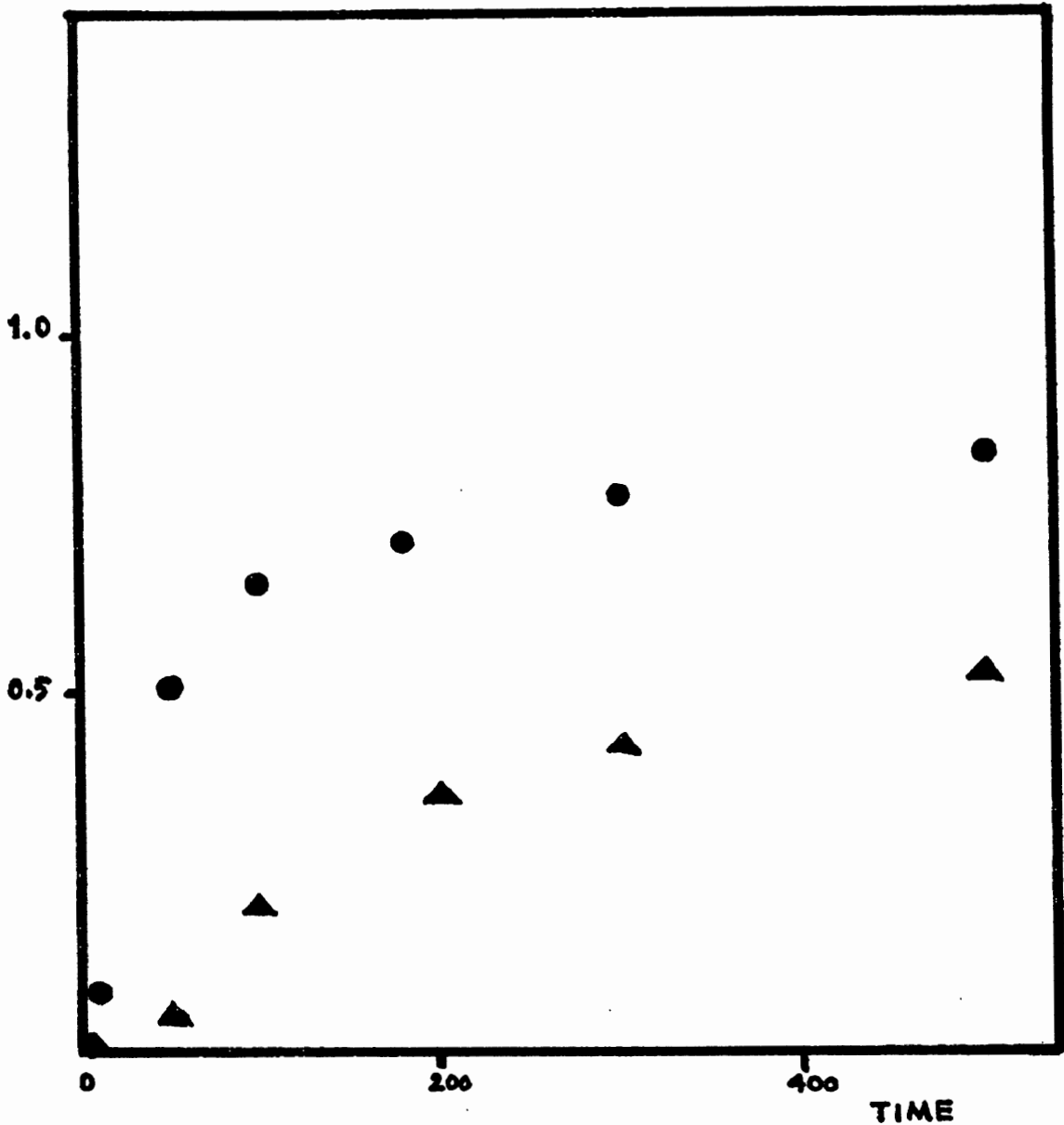


Figure 7. Extinction probability as a function of time. Here $E(p_1) = .5, \beta = .3$. Extinction boundary for is 500 births, for 100 births.

REFERENCES

- Athreya, K. B. and Karlin, S. 1971. On Branching Processes with Random Environments, I: Extinction Probabilities. *Ann. Math. Stat.* 42:1499-1520.
- Bernardelli, H. 1941. Population Waves. *J. Burma. Res. Soc.* 31:1-18.
- Boyce, M. S. 1977. Population Growth with Stochastic Fluctuations in the Life Table. *Theo. Pop. Biol.* 12:366-373.
- Capocelli, R. M. and Ricciardi, L. M. 1974. A Diffusion Model for Pop. Growth in Random Environment. *Theo. Pop. Biol.* 5:28-41.
- Coale, A. J. 1972. The Growth and Structure of Human Populations: A Mathematical Investigation. Princeton University Press, Princeton, N. J.
- Cohen, J. E. 1976. Ergodicity of Age Structure in Populations with Markovian Vital Rates I. Countable States. *J. Amer. Stat. Assoc.* 71:335-339.
- Cohen, J. E. 1977a. Ergodicity of Age Structure in Populations with Markovian Vital Rates II. General States. *Adv. Appl. Prob.* 9:18-37.
- Cohen, J. E. 1977b. Ergodicity of Age Structure in Populations with Markovian Vital rates III. Finite State Moments and Growth Rate; an Illustration. *Adv. Appl. Prob.* 9:469-475.
- Gourley, R. S. and Lawrence, C. E. 1977. Stable Population Analysis in Periodic Environments. *Theo. Pop. Biol.* 11:49-59.
- Hutchinson, G. E. 1957. Concluding Remarks. Cold Spring Harbor Symp. *Quart. Biol.* 22:415-427.
- Keiding, N. 1975. Extinction and Exponential Growth in Random Environments. *Theo. Pop. Biol.* 8:49-63.
- Keyfitz, N. 1968. Introduction to Mathematics of Populations. Addison-Wesley, Reading, Mass.

- Lefkovitch, L. P. 1966. A population Growth Model Incorporating Delayed Responses. *Bull. Math. Biophys.* 28:219-233.
- Leslie, P. H. 1945. On the Use of Matrices in Certain Population Mathematics. *Biometrika* 35:213-245.
- Levins, R. 1969. The Effect of Random Variations of Different Types on Population Growth. *Proc. Nat. Acad. Sci.* 62:1056-1060.
- Lewis, E. G. 1942. On the Generation and Growth of a Population. *Sankhya* 6:93-96.
- Lopez, A. 1961. Problems in Stable Population Theory. Office of Population Research, Princeton University Press, Princeton, N. J.
- Lotka, A. J. 1907. Relation Between Birth Rates and Death Rates. *Science, new series* 26:21-22.
- MacArthur, R. H. and Wilson, E. O. 1967. Island Biogeography. Princeton, N. J., Princeton University Press, p. 203.
- MacArthur, R. H. 1968. Selection for Life Tables in Periodic Environments. *Amer. Natur.* 102:381-383.
- Malthus, T. 1798. An Essay on the Principle of Population. Printed for J. Johnson in St. Paul's Churchyard, London.
- May, R. M. 1973. On Relationships Among Various Types of Population Models. *Am. Nat.* 107:46-57.
- May, R. 1973. Stability and Complexity in Model Ecosystems. Princeton Univ. Press, Princeton, N. J.
- May, R. M. 1974. Biological Populations with Nonoverlapping Generations: Stable Points, Stable Cycles, and Chaos. *Science* 186:645-647.
- Mazanov, A. 1973. On Difference - Difference Growth Equation. *Search* 4:199-201.
- McBride, G. 1966. The Conflict of Crowding. *Discovery* 27:16-19.
- Namkoong, G. 1972. Persistence of Variances for Stochastic, Discrete Time Population Growth Models. *Theo. Pop. Biol.* 3:507-518.

- Parlett, B. 1970. Ergodic Properties of Populations I: The One Sex Model. *Theo. Pop. Biol.* 1:191-207.
- Pielou, E. C. 1977. *Mathematical Ecology*. John Wiley and Sons, New York.
- Pollard, J. H. 1973. *Mathematical Models for the Growth of Human Populations*. Cambridge Univ. Press, New York.
- Rosenblatt, D. 1957. On the Graphs and Asymptotic Forms of Finite Boolean Relation Matrices and Stochastic Matrices, *Naval Res. Logist. Quart.* 4:151-167.
- Ross, G. G. 1972. A Difference Differential Model in Population Dynamics. *J. Theo. Biol.* 37:477-492.
- Sharpe, F. R. and Lotka, A. J. 1911. A Problem in Age Distribution. *Philosophical Magazine* 21:435-438.
- Skellam, J. G. 1967. Seasonal Periodicity in Theoretical Population Ecology. *Proc. of the 5th Berkeley Symp. in Math. Stat. and Prob.* (L. LeCam and J. Neyman, Eds.), Vol. 4, pp. 179-205, Univ. of California Press, Berkeley.
- Sykes, Z. M. 1969. Some Stochastic Versions of the Matrix Models for Population Dynamics. *J. Amer. Stat. Assoc.* 64:111-130.
- Sykes, Z. M. 1969. On Discrete Stable Population Theory. *Biometrics* 25.
- Tanner, J. T. 1966. Effects of Pop. Density on Growth Rates of Animal Pop. *Ecology* 47:733-45.
- Tuckwell, H. C. 1974. A Study of Some Diffusion Models of Population Growth. *Theo. Pop. Biol.* 5:345-357.
- Tuljapurkar, S. D. 1981. Population Dynamics in Variable Environments II. Correlated Environments, Sensitivity Analysis and Dynamics. Submitted: *Theo. Pop. Biol.*
- Tuljapurkar, S. D. and Orzack, S. H. 1980. Population Dynamics in Variable Environments I. Long Run Growth Rates and Extinction. *Theo. Pop. Biol.* 18:314-342.
- Volterra, V. 1926. Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. *Med. Acad. Lincei.*, 2:31-113 (Translation in an appendix to Chapman's *Animal Ecology*. New York, 1931).

Volterra, V. 1937. Principes de biologie mathematique.
Acta Biotheoretica 3:1-36.

Wangersky, P. J. 1978. Lotka-Volterra Population Models.
Ann. Rev. Ecol. Syst. 1978. 9:189-218.

Weissner, E. W. 1971. Multitype Branching Processes in
Random Environments. J. Appl. Prob. 8:17-31.

APPENDIX A

ALGORITHM FOR TRIANGULAR DISTRIBUTION AND FORTRAN PROGRAM FOR STATIONARY DISTRIBUTION

For a triangular distribution

$$f(z) dz = \text{Prob} \{ z \in (z, z+dz) \}$$

where

$$f(z) = \begin{cases} 1/\beta (1 + z/\beta) , & z \leq 0 \\ 1/\beta (1 - z/\beta) , & z \geq 0 \end{cases}$$

with

$$-\beta \leq z \leq \beta$$

The cumulative distribution function is

$$F(z) = \begin{cases} (z+\beta)^2 / 2\beta^2 , & z \leq 0 \\ 1 - (\beta-z)^2 / 2\beta^2 , & z \geq 0 \end{cases}$$

The mean and variance are zero and $\beta^2/6$ respectively. We note the following theorem without proof before we describe the algorithm.

Theorem

Let z be any random variable with cumulative distribution function $F(x) = p [z \leq x]$. Let U be a random variable

uniformly distributed (0,1). Then we can write $z = F^{-1}(U)$.

In the case of triangular distribution, we have

$$(A1) \quad F^{-1}(u) = \begin{cases} \beta (\sqrt{2u} - 1) & , u \leq 1/2 \\ \beta (1 - \sqrt{2(1-u)}) & , u \geq 1/2 \end{cases}$$

To get triangle random variables z , some appropriate β is chosen. On computers very reliable random number generators uniform on (0,1) are available. On Honeywell 66/20 we used FLAT to get a number $U \sim$ uniform (0,1) in each step. We check if U is greater or less than half and accordingly compute z from equation (A1). A Fortran program for the process follows.

```

*** PROGRAM TO COMPUTE HISTOGRAMS FOR POP.
*** NUMBERS AND OTHER PARAMETERS
DOUBLE PRECISION N(2,1),C,NX(2,1),X(2,2),TP(2),F(2,2)
INTEGER G(500),WA(100),WB(100),WC(100),WD(100)
IMPLICIT DOUBLE PRECISION (A-F,O-T,X-Z)
***** INITIAL VALUES FOR PARAMETERS
DO 8 MD=1,2
TP(1)=0.7
TP(2)=.3
RX=.1
F(1,1)=.85
F(1,2)=1.
F(2,1)=.4
F(2,2)=0.
POP=N(1,1)+N(1,2)
DO 50
I=1,2
DO 50
J=1,2
50 X(I,J)=F(I,J)
AY=0.
BY=0.
CY=0.
DY=0.
VAY=0.
VBY=0.
VCY=0.
VDY=0.
DO 3 I=1,500
3 G(I)=0
DO 7 I=1,100
WA(1)=0
WB(1)=0
WC(1)=0
WD(1)=0
7 CONTINUE
POP=N(1,1)+N(2,1)
DO 50
I=1,2
DO 50
J=1,2
50 X(I,J)=F(I,J)
A=0.000000333557711
DO 3 I=1,500
3 G(I)=0
***** NUMBER OF RUN LOOP
SM=0.
AVLM=0.
SQLM=0.
DO 5 M=1,500
IH=500
P=0.5
K=0
L=0
N(1,1)=10.
N(2,1)=10.
***** TIME LOOP BEGINS
30 K=K+1

```

```

**** TRIANGULAR DISTRIBUTION: 6 LINES
Y=FLAT(A)
IF(Y.LT.0.5) GOTO 71
Z=1.-(2.*(1.-Y))**0.5
GOTO 72
71 Z=(2*Y)**0.5-1.
***** RX IS MEASURE OF FLUCTUATION: BETA
72 X(2,1)=0.4+RX*Z
60          DO 80          I=1,2
80          NX(I,1)=0.
DO 90          I=1,2
DO 90          J=1,2
90          NX(I,1)=NX(I,1)+X(I,J)*N(J,1)
DO 100         I=1,2
100         N(I,1)=NX(I,1)
B=N(1,1)+N(2,1)
***** RESCALING OF NUMBERS: 16 LINES
IF(B.GT.1) GO TO 27
IF(K.GT.IH) GO TO 23
IH=K
DO 19 I=K,500
19 G(I)=G(I)+1
23 CONTINUE
IF(B.GT.1/(2.**30.)) GO TO 27
L=L-1
B=B*(2.**30.)
DO 17 I=1,2
17 N(I,1)=N(I,1)*(2.**30.)
27 CONTINUE
IF(B.LT.(2.**30.))GO TO 130
L=L+1
DO 115 I=1,2
115 N(I,1)=N(I,1)/(2.**30.)
B=B/(2.**30.)
130          CONTINUE
IF(K.LT.500)GO TO 30
***** TIME LOOP ENDS
***** CALCULATION OF Y(T),U(T) AND
*****THEIR HISTOGRAMS
FY=N(1,1)/B
AY=AY+FY
VAY=VAY+FY**2
JY=FY*100.
IF(JY.LT100.) GOTO 31
WA(100)=WA(100)+1
GOTO 32
31 WA(JY+1)=WA(JY+1)+1
32 PY=N(2,1)/B
BY=BY+PY
VBY=VBY+PY**2
KY=PY*100
IF(KY.LT.100) GOTO 33
WB(100)=WB(100)+1
GOTO 34

```

```

33 WB(KY+1)=WB(KY+1)+1
34 PY=N(1,1)/N(2,1)
CY=CY+PY
VCY=VCY+PY**2
JY=PY*10
PY=N(2,1)/N(1,1)
DY=DY+PY
VDY=VDY+PY**2
KY=PY*100
IF(KY.LT.100) GOTO 37
WD(100)=WD(100)+1
GOTO 42
37 WD(KY+1)=WD(KY+1)+1
42 CONTINUE
B=(30*L*(DLOG(2))+DLOG(B/POP))/500.
SM=SM+B
SQLM=SQLM+B**2
5 CONTINUE
***** RUN LOOP ENDS
***** CALCULATION OF AVERAGES AND VARIANCES OF
***** PARAMETERS AND PRINT STATEMENTS
YYA=AY/500.
YYB=BY/500.
QQA=CY/500
QQB=DY/500.
VYA=(VAY-AY**2/500.)/499.
VYB=(VBY-BY**2/500.)/499.
VVA=(VCY-CY**2/500.)/499.
VVB=(VDY-DY**2/500.)/499.
AVLM=SM/500.
VAR=500.*(SQLM-SM**2/500.)/199.
PRINT 140,AVLM,VAR,(G(I),I=1,500)
PRINT 122,WA,WB,WC,WD
122 FORMAT(/5(5X,20I3//))
QL=DEXP(-AVLM*DLOG(POP)/VAR)
PRINT 150,QL
150 FORMAT(/,5X,"EXTINCTION LOWER BOUND",5X,D15.7)
PRINT 153,YYA,YYB,QQA,QQB,VYA,VYB,VVA,VVB
153 FORMAT(/5X,"MEAN Y(T),U(T)"/4(5X,D15.7//)//5X,
"VARIANCE Y(T),U(T)"/4(5X,D15.7//))
140 FORMAT(///20X,"AVERAGE LM",5X,D23.16,/,20X,"VARIANCE",7X,
D23.16,/,/,5X,"CUMMULATIVE EXTINCTION",/,20(5X,15I4/))
8 CONTINUE
STOP
END

```

APPENDIX B

ALGORITHM FOR STATIONARY DISTRIBUTION AND ITS FORTRAN IMPLEMENTATION

Let U and p be bounded as indicated: $x_1 \leq U \leq x_2$ and $p_1 \leq p \leq p_2$. The intervals (x_1, x_2) and (p_1, p_2) are divided into convenient intervals:

$$\epsilon = (x_2 - x_1) / N \quad ; \quad N \text{ intervals } I_\alpha, \alpha = 1, 2, \dots, N$$

with
$$\mu(I_\alpha) = \text{Prob} \{ U \in I_\alpha \}$$

and
$$\eta = (p_2 - p_1) / M \quad ; \quad M \text{ intervals } S_i, i = 1, 2, \dots, M$$

with p_i as midpoints of S_i

Now for each p_i we calculate

$$z_1 = f(p_i, x_1 + (\alpha - 1)\epsilon)$$

$$z_2 = f(p_i, x_1 + \alpha\epsilon)$$

the maximum and minimum value of U_1 for every α . $[z_1, z_2]$ would map on several $I(\beta)$, $\beta = 1, 2, \dots, N$. Calculate $C_{\alpha\beta}(i)$ = fraction of $[z_1, z_2]$ in $I(\beta)$. This gives $\underline{C}(i)$ a $N \times N$ matrix for all values of α and β . Since we do this for every p_i we get a set of m matrices $\underline{C}(i)$

calculate

$$E[C] = \sum_{i=1}^M \underline{C}(i) \nu(S_i)$$

where

$$\nu(S_i) = \text{Prob} \{ p \in S_i \}, \quad i=1,2,\dots,M$$

$E[\underline{C}]$ is Markov since $C_{\alpha\beta}(i) \geq 0$, $\sum_{\beta} C_{\alpha\beta}(i) = 1$

The probability measure for the mapping of U_1 on U_0 is

$$\begin{aligned} \mu^{(1)}(I_{\beta}) &= \sum_{i,\alpha} \mu(I_{\alpha}) C_{\alpha\beta}(i) \nu(S_i) \\ &= \mu' E[\underline{C}] \end{aligned}$$

The probability density vector for u_t is

$$\mu^{(t)} = \mu' E[\underline{C}]^n \propto \pi'$$

where $\pi' E[\underline{C}] = \pi'$, the left eigenvector of $E[\underline{C}]$. A Fortran implementation of the algorithm follows.

```

*****PROGRAM TO COMPUTE STATIONARY DISTRIBUTION:KSTAT
IMPLICIT DOUBLE PRECISION (A-H,O-Z)
DIMENSION B(56,56),C(100,100),PI(56),CC(56,56)
QM1=.85
QM2=1.
X1=0.
X2=1.
P1=.3
P2=.5
***** INTERVAL LENGTHS
E1=(X2-X1)/200.
E2=(P2-P1)/50.
DO 11 I=1,56
11 PI(I)=1.
DO 12 I=1,100
DO 12 J=1,100
12 C(I,J)=0.
DO 6 I=1,50
PP=P1+(I-.5)*E2
DO 4 J=40,95
*****BOUNDS ON MAPPING
Z1=PP/(QM1+QM2*(X1+(J-1)*E1))
Z2=PP/(QM1+QM2*(X1+J*E1))
Z1=Z1*200.
Z2=Z2*200.
AL=ABS(Z2-Z1)
K1=IFIX(Z1)+1
K2=IFIX(Z2)+1
IF(K1-K2) 8,8,9
8 C(J-39,K2-39)=C(J-39,K2-39)+1.
GOTO 4
9 C(J-39,K2-39)=C(J-39,K2-39)+(K2-Z2)/AL
IF((K1-K2).LT.2) GOTO 3
DO 5 M=K2+1,K1
5 C(J-39,M-39)=C(J-39,M-39)+(E1*200.)/AL
3 C(J-39,K1-39)=C(J-39,K1-39)+(Z1+1-K1)/AL
4 CONTINUE
6 CONTINUE
***** PRINTING OF C(I,J)
DO 15 I=1,56
PRINT 51,(C(I,J),J=1,100)
51 FORMAT(10(5X,10(F4.2,2X))/)
15 CONTINUE
DO 18 I=1,56
DO 18 J=1,56
18 CC(I,J)=ABS(C(I,J)/50.)
DO 33 I=1,56
PRINT 52,(CC(I,J),J=1,56)
52 FORMAT(5(5X,10(F4.2,2X))/)
33 CONTINUE
*****ITERATION FOR CC(I,J)
MM=0
7 MM=MM+1
DO 2 I=1,56

```

```
DO 2 J=1,56
2 B(I,J)=0.
DO 19 I=1,56
DO 19 K=1,56
DO 19 J=1,56
19 B(I,K)=B(I,K)+CC(I,J)*CC(J,K)
DO 31 I=1,56
DO 31 J=1,56
31 CC(I,J)=B(I,J)
XX=CC(1,10)/CC(1,11)
YY=CC(2,10)/CC(2,11)
IF(ABS(XX-YY).LT.10**(-5)) GOTO 21
IF(MM.LT.30) GOTO 7
21 SN=0.
DO 34 I=1,56
PRINT 53,(CC(I,J),J=1,56)
53 FORMAT(5(2X,6(D9.2,2X)/)/)
34 CONTINUE
PRINT 49,MM
49 FORMAT(5X,"POWER OF 2:",3X,I3)
DO 23 J=1,56
23 SN=SN+CC(1,J)
DO 22 I=1,56
22 PI(I)=(CC(1,I)/SN)*1000.
PRINT 50,PI
50 FORMAT(5X,"LEFT EIGEN VECTOR"/56(5X,D23.16/))
STOP
END
```

APPENDIX C

A Fortran program to calculate birth sequences and relevant statistics is given beginning on the next page.

```

*****POPULATION TRAJECTORIES & EXTINCTIONS: KBTHU
INTEGER G(50),H(5)
IMPLICIT DOUBLE PRECISION (A-F,O-T,X-Z)
**** SEED: DD
CC=42317765.77
DD=3456721.001
***** FERTILITIES
ZZ=0.
DO 1 MA=1,5
  DXM=0.
  DXX=-10.
  QM2=1.5
  QM3=2.20
  ***** PROBABILITIES
  P1=0.5
  P2=0.25
  DO 3 I=1,50
    3 G(I)=0
    *** BAD WEATHER COUNTER: IR
    SM=0.
    AVL=0.
    SQLM=0.
    XMAX=0.
    XMIN=1000.
    XMAS=-10.
    XMIS=100.
    ZZ=ZZ+.025
    ** RUN LOOP BEGIN
    DO 5 M=1,200
      ***** COUNTERS
      DO 4 I=1,5
        4 H(I)=0
        IR=0
        K=0
        L=0
        *****BIRTHS BT'S
        BT3=1000.
        BT2=1096.
        BT1=1201.
        ***** P1 AT TIME T-2,T-1
        P1T1=P1
        P1T2=P1
        *****BIRTHS AT TIME ZERO
        BZ=QM2*P1*BT2+QM3*P2*P1*BT3
        BTX=BT2
        BTY=BT1
        BTZ=BZ
        ***** TIME LOOP BEGIN
        30                                     K=K+1
        Y=FLAT(DD)
        BT=QM2*P1T1*BTY+QM3*P2*P1T2*BTX
        P1T2=P1T1
        IF(Y.LE.0.5) GOTO 51
        Z=FLAT(CC)

```

```

P1T1=P1+ZZ*Z
GOTO 63
51 Z=FLAT(CC)
P1T1=P1-ZZ*Z
IR=IR+1
63 CONTINUE
*****HISTOGRAMS
IF(L.NE.0) GOTO 23
IF(BT.GT.1000) GOTO 27
IF(H(1).EQ.1) GOTO 21
H(1)=1
G(1)=G(1)+1
21 CONTINUE
IF(BT.GT.500) GOTO 27
IF(H(2).EQ.1) GOTO 22
G(2)=G(2)+1
H(2)=1
22 CONTINUE
IF(BT.GT.300) GOTO 27
IF(H(3).EQ.1) GOTO 24
G(3)=G(3)+1
H(3)=1
24 CONTINUE
IF(BT.GT.100) GOTO 27
IF(H(4).EQ.1) GOTO 25
G(4)=G(4)+1
H(4)=1
25 CONTINUE
IF(BT.GT.10) GOTO 27
IF(H(5).EQ.1) GOTO 23
G(5)=G(5)+1
H(5)=1
23 CONTINUE
***** SCALING SEGMENT: 12 LINES
IF(BT.GT.1/(2.**30.)) GO TO 27
L=L-1
BT=BT*(2.**30.)
BTY=BTY*(2.**30.)
BTX=BTX*(2.**30.)
BTZ=BTZ*(2.**30.)
27 CONTINUE
IF(BT.LT.(2.**30.))GO TO 130
L=L+1
BTY=BTY/(2.**30.)
BTX=BTX/(2.**30.)
BT=BT/(2.**30.)
BTZ=BTZ/(2.**30.)
130 CONTINUE
IF(K.NE.10) GOTO 31
G(6)=K
DO 41 I=1,5
41 G(6+I)=G(6+I)+H(I)
31 CONTINUE
IF(K.NE.50) GOTO 32

```

```

G(12)=K
DO 42 I=1,5
42 G(12+I)=G(12+I)+H(I)
32 CONTINUE
IF(K.NE.100) GOTO 33
G(18)=K
DO 43 I=1,5
43 G(18+I)=G(18+I)+H(I)
33 CONTINUE
IF(K.NE.200) GOTO 34
G(24)=K
DO 44 I=1,5
44 G(24+I)=G(24+I)+H(I)
34 CONTINUE
IF(K.NE.300) GOTO 35
G(30)=K
DO 45 I=1,5
45 G(30+I)=G(30+I)+H(I)
35 BTX=BTY
BTY=BTZ
BTZ=BT
IF(K.LT.500)GO TO 30
  ***TIME LOOP END
BX=(30*L*(DLOG(2.))+DLOG(BT/BZ))/501.
XMAS=DMAX1(XMAS,BX)
XMIS=DMIN1(XMIS,BX)
XMAX=DMAX1(XMAX,(30*L*DLOG(2.))+DLOG(BT))
XMIN=DMIN1(XMIN,(30*L*DLOG(2.))+DLOG(BT))
SM=SM+BX
13 SQLM=SQLM+BX**2
PRINT 106,B,L,IR
106 FORMAT(5X,"MT:SCALE",5X,D23.16,5X,2I5)
5 CONTINUE
  ** RUN LOOP END
PRINT 191,(G(I), I=1,5)
191 FORMAT(/5X,"EXT. LEVEL:1000,500,300,100,10"/5(5X,I4)/)
PRINT 192,(G(I), I=6,35)
192 FORMAT(5X,"TIME",10X,"EXT. LEVEL 100,..."/5(5X,6I6/))
AVLM=SM/200.
VAR=500.*(SQLM-SM**2/200.)/199.
PRINT 140,AVLM,VAR
PRINT 122,WA,WE,WC,WD
122 FORMAT(//5(5X,20I3//))
140 FORMAT(///20X,"AVERAGE LM",5X,D23.16,///,20X,
"VARIANCE",7X,D23.16///)
QL=DEXP(-AVLM*DLOG(BZ)/VAR)
PRINT 150,QL
PRINT 153,YYA,YYB,QQA,QQB,VYA,VYB,VVA,VVB
153 FORMAT(//5X,"MEAN Y1,.."/4(5X,D23.16//)5X,
"VAR VY1,.."/(5X,D23.16//)
150 FORMAT(//,5X,"EXTINCTION LOWER BOUND",5X,D23.16)
PRINT 143,XMAX,XMIN,XMAS,XMIS
143 FORMAT(//5X// "N.LOG OF MAX&MIN POP & LOG AV",/
4(5X,D23.16//))

```

1 CONTINUE
STOP
END