CONFIDENCE LIMITS FOR POPULATION PROJECTIONS
WHEN VITAL RATES VARY RANDOMLY

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ABSTRACT

Due to unpredictable future environmental changes, population growth is more realistically viewed as a stochastic than a deterministic process. Environmental variablity is modeled by allowing the population's survival and fecundity rates to be correlated random variables. The expected future population vector and its variance-covariance matrix are computed. The projected total future population size is approximately log-normally distributed, but confidence limits for future population size can be more accurately computed from the distribution of the realized factor of increase. Numerical examples illustrate how the calculation of confidence limits for future population size and of the probability that the population will increase in size can be applied to the management of living resources.

The predicted size of an age-structured population can be projected if its initial size, age distribution, and vital rates are known (e.g., Leslie 1945; Keyfitz 1968). Such population projections are commonly used in fisheries and wildlife management when age-specific fecundity and mortality rates are available. However, there is uncertainty in such projections. First, we rarely know vital rates exactly; rather, we have estimates of the true rates, and these estimates are subject to sampling and other types of errors. Second, the true rates themselves are not constant with time. Environmental conditions are always changing, and the vital rates would be expected to change in response. To an extent, the changes of conditions may themselves be forecast and incorporated into a population model. Some changes, however, are unpredictable, and these changes give rise to fluctuations in the vital rates which make our estimates of population size for some future time less certain. Nevertheless, it may still be possible to make probabilistic predictions about future population size given some statistical knowledge about the fluctuating vital rates.

In this paper we limit ourselves to consideration of the second of these problems, projecting age-structured populations when mortality and fecundity rates vary randomly with time. Recently this topic has been of interest and controversy in a more theoretical context (Boyce 1977; Cohen 1979a, b; Daley 1979; Tuljapurkar and Orzack 1980; Tuljapurkar 1982; Slade and Levenson 1982). In spite of earlier results to the contrary (Boyce 1977), analyses (Sykes 1969; Cohen 1977), and simulations (Slade and Levenson 1982) have shown that when vital rates fluctuate randomly with no serial correlation, the expectation of population size at a future time will be exactly equal to the population size projected using the mean vital rates in a deterministic projection. For application in fisheries and wildlife management, the problem is that the distribution of future population sizes will often be strongly skewed. This skew means that the mean and variance of future population size, even if known, are not sufficient to characterize the distribution and, in particular, not sufficient to compute confidence limits for total population size. In this paper we examine two transformations of this skewed distribution which approximate a normal distribution, and evaluate the accuracy of confidence limits computed from these transformations.

As pointed out by several of the authors cited above and earlier by Lewontin and Cohen (1969) for a non-age-structured population, stochastic effects can cause the modal or most likely population trajectory to decline to extinction, even though the expected or mean population size is growing at a geometric rate. Clearly, if we are to use population projections in fisheries and wildlife management, we should be concerned about the effects of natural variability on the results of our projections. In response to this concern, we have written two com-

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puter programs for stochastic population projections which can serve as research and management tools. Here we illustrate the utility of these programs with numerical examples, compare our results with recent theoretical analyses, and discuss the implications of these results to the management of living resources.

METHODS

Sykes (1969) presented three models for incorporating stochasticity into population projections. He concluded that the observed variability in human demographic projections was best described by his third model, in which the elements of the Leslie matrix (the effective fecundity rates and the survival rates) are random variables, each with a specified mean and variance, and with specified covariances between them. The model does not allow for serial covariance in vital rates between successive time periods.

Let n_t be a population vector of ω age classes at time t. The stochastic projection model is

$$n_{t+1} = (A + \Delta_t)\, n_t, \qquad t = 0, 1, 2, \ldots$$

where A is a constant projection matrix of mean vital rates and Δ_t is a matrix of random deviations whose elements have a specified covariance structure $\{\mathrm{Cov}(\Delta_i, \Delta_j)\}$ but which are uncorrelated in time. Let

$$N_t = \sum_{i=1}^{\omega} n_{ti}$$

be the total population size at time t. It is convenient to normalize the projected population to the initial population size and consider the distribution of the ratio N_t/N_0. The mean and variance of this ratio are given by

$$E(N_t/N_0) = E(N_t)/N_0$$

$$= \sum_{i=1}^{\omega} E(n_{ti})/N_0$$

and

$$\mathrm{Var}\,(N_t/N_0) = \mathrm{Var}\,(N_t)/N_0^2$$

$$= \sum_{i=1}^{\omega} \sum_{j=1}^{\omega} \mathrm{Cov}\,(n_{ti},n_{tj})/N_0^2.$$

From Sykes (1969, equations 19 and 20), the mean and variance of the population vector are given by

$$E(n_t) = \{E(n_{ti})\} = A^t n_0$$

and

$$\mathrm{Var}\,(n_t) = \{\mathrm{Cov}\,(n_{ti},n_{tj})\}$$

$$= \sum_{k=0}^{t-1} A^{t-1-k} \left\{ \sum_{\alpha=1}^{\omega} \sum_{\beta=1}^{\omega} \mathrm{Cov}\,(\Delta_{i\alpha}, \Delta_{j\beta}) \right.$$

$$\left. [\mathrm{Cov}\,(n_{k\alpha},n_{k\beta}) + E(n_{k\alpha})E(n_{k\beta})] \right\} \; A'^{t-1-k}$$

where A' is the transpose of A and where the curly brackets indicate that the expression inside them is the ith element of the vector or the ijth element of the matrix considered.

Tuljapurkar and Orzack (1980) predict that for large t, N_t/N_0 will be lognormally distributed. The mean and variance of the normally distributed variable $\log(N_t/N_0)$ are calculated from the mean and variance of the lognormally distributed variable N_t/N_0 by

$$E[\log(N_t/N_0)] = \log[E(N_t/N_0)] - \left\{ \frac{\mathrm{Var}[\log(N_t/N_0)]}{2} \right\}$$

and

$$\mathrm{Var}\,[\log(N_t/N_0)] = \log \left\{ \frac{\mathrm{Var}\,(N_t/N_0)}{[E(N_t/N_0)]^2} + 1 \right\}$$

(Aitchison and Brown 1957). We have found in simulations that the distribution of the realized factor of increase $(N_t/N_0)^{1/t}$ is approximately normal. Based on the assumption that the realized factor of increase is normally distributed, the mean and variance of $(N_t/N_0)^{1/t}$ are computed from the mean variance of N_t/N_0 by methods given in Appendices 1 and 2.

Using the formulae of Sykes (1969), the mean and variance of each age class in the future population can be computed analytically. Confidence intervals for the total population size and for the realized factor of increase, and an estimate of the probability that the future population will be larger than the starting population, are computed based on the assumption that either $\log(N_t/N_0)$ or $(N_t/N_0)^{1/t}$ is normally distributed.

We can also simulate the growth of an age-structured population under fluctuating environmental conditions. At each time period, a new set of fecundity and survival rates, the elements of the Leslie matrix, are chosen and used to project the population. Each fecundity and survival rate is a normally distributed random variable with specified mean, variance, and covariance with every other fecundity and survival rate. The projection, starting from the

same initial population vector, may be replicated a given number of times. From these replicated projections, the mean, variance, and covariances of the population vector are computed, together with statistics on a variety of other demographic parameters. The distributions of the final population size and the realized factor of increase are tabulated.

The computer programs to accomplish these stochastic projections are called, respectively, SPP (Stochastic Population Projection) and SLT (Stochastic Life Table simulation). Program listings and guides to the use of both programs are given in Ger-

dynamics of the population are given in Table 2 (taken from Goodman 1981: table 1) and confer a population growth rate of about 8% per year. The initial age vector in this case was chosen to be the stable age distribution with a total of 100,000 females. Values for the standard deviations in vital rates in Table 2 were selected by choosing reasonable values for their coefficients of variation. Correlations in vital rates were assumed to be 0.9 between fecundities at different ages, 0.9 between survival rates at different ages, and 0.5 between all fecundities and survival rates.

TABLE 1.—Initial population vector, mean vital rates, and covariance matrix of vital rates for a three age-class population projection. In the covariance matrix, F refers to fecundity rate, P to survival rate, and numbers to age classes.

Age class	Initial population size	Mean fecundity rate	Mean survival rate		Covariance matrix					
					F1	F2	F3	P1	P2	P3
1	100	0.1	0.7	F1	0.0010	0.0020	0.0020	0.0005	0.0005	0.0
2	80	1.0	0.9	F2		0.0050	0.0045	0.0010	0.0010	0.0
3	50	0.4	0.0	F3			0.0050	0.0010	0.0010	0.0
	230			P1				0.0050	0.0045	0.0
				P2					0.0050	0.0
				P3						0.0

rodette et al. (1983). Although lengthy, these programs are suitable for use on many microcomputers.

Numerical Examples

Two numerical examples are presented to verify various analytic results and to illustrate the use of programs SPP and SLT in a management context.

The first example is a simple artificial life table with three age classes. The mean vital rates and the covariance matrix for the vital rates are given in Table 1. This example was used to compare the predicted mean and variance in projected population size based on Sykes' (1969) formulae with the actual mean and variance from the simulation. The example was also used to test the assumption that ultimate population sizes will be lognormally distributed, and in particular whether accurate confidence limits for the tails of the distribution can be made based on this assumption.

The second example is based on a real population. A northern fur seal, *Callorhinus ursinus*, population is projected using vital rates consistent with a phase of rapid growth which occurred earlier in this century. The mean vital rates which govern the

TABLE 2.—Initial population vector, means, and standard deviations (S.D.) of vital rates for a fur seal population projection used as a numerical example in the text. Mean rates are taken from Goodman (1981: table 1). Each age class represents 1 yr, and only the female portion of the population is tabulated. The initial population vector is in the stable age distribution with a total of 100,000 females.

Age class	Initial population size	Mean fecundity rate	S.D.	Mean survival rate	S.D.
1	17,618	0.0000	0.0000	0.8786	0.0439
2	14,312	0.0000	0.0000	0.8786	0.0439
3	11,627	0.0050	0.0003	0.8837	0.0442
4	9,500	0.0151	0.0008	0.8888	0.0444
5	7,807	0.2631	0.0132	0.9039	0.0090
6	6,525	0.3693	0.0185	0.9191	0.0092
7	5,545	0.4250	0.0213	0.9342	0.0093
8	4,789	0.4604	0.0230	0.9443	0.0094
9	4,182	0.4756	0.0238	0.9494	0.0095
10	3,671	0.4705	0.0235	0.9443	0.0094
11	3,205	0.4655	0.0233	0.9292	0.0093
12	2,753	0.4554	0.0228	0.9039	0.0090
13	2,301	0.4402	0.0220	0.8786	0.0088
14	1,869	0.4250	0.0213	0.8484	0.0085
15	1,466	0.4048	0.0202	0.8029	0.0080
16	1,089	0.3794	0.0190	0.7524	0.0075
17	757	0.3542	0.0177	0.6918	0.0069
18	484	0.3187	0.0159	0.6262	0.0063
19	280	0.2833	0.0142	0.5454	0.0055
20	141	0.2479	0.0124	0.4494	0.0045
21	59	0.2024	0.0101	0.3282	0.0033
22	18	0.1467	0.0073	0.1009	0.0010
23	2	0.0657	0.0033	0.0000	0.0000
Total	100,000				

RESULTS

Example 1.

The results of the stochastic projection by program SPP are presented in Table 3. The second column shows the expected (mean) population vector for each time step. The mean population vector is obtained by projecting with the mean vital rates. The covariance matrix for the population vector gives, on the diagonal, the variances of each age class and, above the diagonal, the covariances between age classes.

The calculations using Sykes' formulae concur with the results of the Monte Carlo simulation of a stochastic population projection, taking the entries of the life table as time-varying random variables (program SLT). In Tables 4 and 5 the results of the simulation are presented. The means and covariances of the vital rates actually achieved on this particular run of program SLT are shown in Table 4 and are close to the specified rates given in Table 1. By comparing the results in Table 5 with those of time step 6 in Table 3, we see that the results of the simulation (SLT) and the analytic solution (SPP) agree closely.

The distribution of the ratio of the final population size to the initial population size is shown as a histogram in Figure 1A. The curve is skewed to the right,

TABLE 3.—Results of the stochastic projection of the population, given in Table 1, through 6 time steps (program SPP). The columns labeled "95% C.L." give the lower and upper 95% confidence limits for total population size and for the realized factor of increase relative to the initial population. The last column gives the probability P that the final population size will be greater than the initial population size.

Time step	Expected population vector	Covariance matrix			Total population Mean	Total population Lower 95% C.L. Upper 95% C.L.	Factor of increase Mean	Factor of increase Lower 95% C.L. Upper 95% C.L.	P
0	100 80 50				230				
1	110 70 72	142.5	18.0 50.0	14.4 36.0 32.0	252	215 289	1.096	0.934 1.258	0.8764
2	110 77 63	261.5	48.4 131.0	73.5 46.1 65.3	250	197 307	1.041	0.925 1.156	0.7545
3	113 77 69	365.3	94.4 189.7	154.1 68.7 136.4	259	193 335	1.039	0.934 1.134	0.7856
4	116 79 69	485.5	158.2 244.9	219.9 99.0 184.2	264	187 356	1.033	0.950 1.116	0.7808
5	119 81 71	559.6	230.8 307.5	287.1 141.7 231.0	271	184 378	1.031	0.957 1.105	0.7910
6	121 83 73	736.2	309.8 367.0	366.2 189.7 283.5	277	182 400	1.029	0.961 1.096	0.7990

TABLE 4.—Means, variances, and covariances of vital rates achieved during a Monte Carlo projection of the population given in Table 1 (program SLT). Values were computed on the basis of 30,000 vectors of vital rates. F refers to fecundity rate, P to survival rate, and numbers to age classes. Values in this table should be compared with the "target" values in Table 1.

	Mean	Covariance matrix $F1$	$F2$	$F3$	$P1$	$P2$	$P3$
$F1$	0.10016	0.00101	0.00202	0.00201	0.00049	0.00045	0.0000
$F2$	1.00027		0.00505	0.00453	0.00100	0.00092	0.0000
$F3$	0.39998			0.00502	0.00099	0.00091	0.0000
$P1$	0.69992				0.00501	0.00414	0.0000
$P2$	0.89744					0.00435	0.0000
$P3$	0.00000						0.0000

TABLE 5.—Results of the Monte Carlo simulation of the 6 time-step projection of the population whose age structure and vital rates are given in Table 1 (program SLT). Sample size for the simulation was 5,000 trials. Results in this table should be compared with the "predicted" values in the last row of Table 3. Here P is the proportion of final population sizes greater than the initial population size.

Time step	Mean population vector	Covariance matrix			Mean total population	Mean factor of increase	P
6	121 83 73	741.3	314.7 371.7	369.8 187.6 281.5	277	1.029	0.7954

as anticipated. Both the logarithmic transformation (Fig. 1B) and the root transformation (Fig. 1C) appear to normalize the distribution. When the cumulative frequency distributions are plotted on normal probability scales (dots in Fig. 1), however, the root transformation appears superior to the logarithmic. The dots in Figure 1C are nearly linear, indicating that the distribution is close to normal.

In Table 6 the accuracy of the 95% confidence limits for the total population size computed by the logarithmic and root transformations is compared for projections of 2, 5, and 10 time steps, using the same numerical example. Program SLT calculates the proportion of final populations which fall above and below the computed upper and lower confidence limits. We expect that 2.5% of the cases should fall above the upper limit and 2.5% below the lower limit if the 95% confidence interval has been correctly estimated. Table 6 shows that both the logarithmic and the root transformations do a fair job of estimating the 95% confidence limits. The root transformation, however, appears more accurate in this example, as well as in other examples we have tried, when the number of time steps is small. When the number of time steps is large (50-100), both transformations produce normally distributed variables.

Since the root transformation gave the most accurate results for short projections, we used this transformation in program SPP to compute a confidence interval on total population size. More details of the
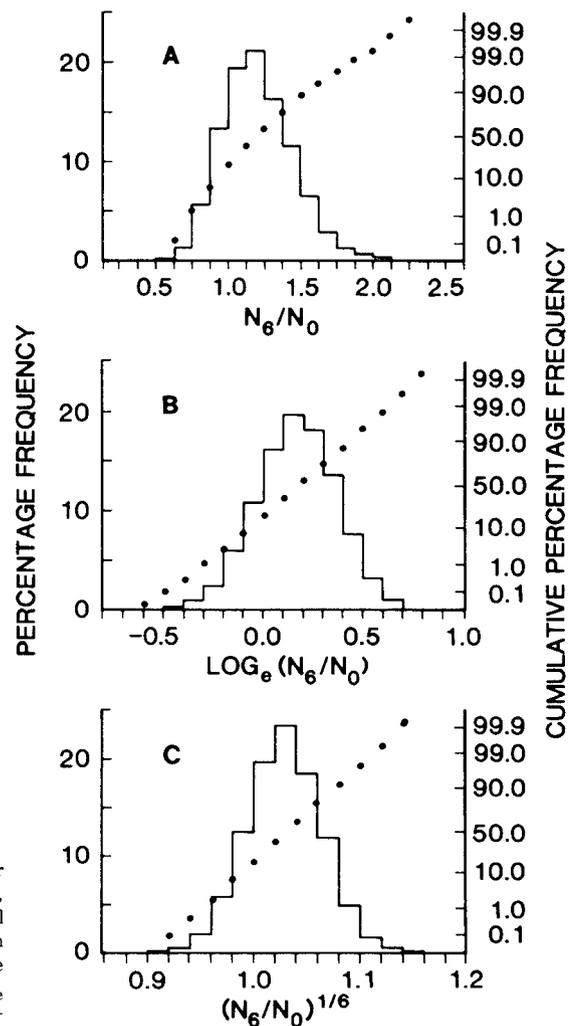
FIGURE 1.—Distributions of future total population size under variable conditions. Histograms show the percentage frequency, and dots the cumulative percentage frequency plotted on a normal probability scale, for 5,000 stochastic projections of the population given in Table 1 for six time steps. A. Distribution of N_6/N_0, the final population size divided by the initial. B. Distribution of $\log_e (N_6/N_0)$. C. Distribution of $(N_6/N_0)^{1/6}$, the realized factor of increase.

TABLE 6.—Accuracy of the 95% confidence limits (C.L.) on population size estimated by the logarithmic and root transformations of the distribution of total population size. For each transformation, the estimated lower and upper confidence limits are shown for projections of the population given in Table 1 for 2, 5, and 10 time steps. The columns labeled "Proportion beyond C.L." give the actual proportion of 10,000 stochastic projections using program SLT which fall below the estimated lower limit and above the estimated upper limit for each transformation. Each set of projections was replicated 3 times. The root transformation estimates the 95% confidence interval on population size more accurately, especially for short projections.

| No. of time steps to projection | | Transformation | | | |
| | | Logarithmic | | Root | |
		Estimated 95% C.L.	Proportion beyond C.L.	Estimated 95% C.L.	Proportion beyond C.L.
2	Lower	199	0.0311	197	0.0256
			0.0317		0.0255
			0.0295		0.0231
	Upper	309	0.0160	307	0.0204
			0.0181		0.0214
			0.0199		0.0228
5	Lower	187	0.0290	184	0.0251
			0.0285		0.0242
			0.0318		0.0260
	Upper	380	0.0227	378	0.0245
			0.0219		0.0235
			0.0215		0.0235
10	Lower	178	0.0266	175	0.0238
			0.0280		0.0252
			0.0286		0.0257
	Upper	489	0.0226	486	0.0234
			0.0211		0.0221
			0.0217		0.0226

example projection are shown in the columns on the right side of Table 3. The mean and the 95% confidence interval for the total population size and for the realized factor of increase are given for each time step. As the population vector approaches the stable age distribution, the ratio between successive mean total population sizes approaches the asymptotic value 1.0240. The mean realized factor of increase shown in Table 3, which is computed relative to the initial population, does not converge on this asymptotic value; nor can the mean realized factor of increase be computed from the ratio of the mean final population size to the initial population size. Instead, the mean and variance of the realized factor of increase are computed by methods described above.

The probability that the total population size will have increased over its initial value is also shown for each time step in the last column of Table 3. In this particular example, since we did not begin with the stable age distribution, this probability decreases at first and then increases. As a further check, program SLT computes the proportion of cases in which the final population was greater than the initial popula-

tion, and this answer (0.7954, Table 5) is close to the probability computed analytically by program SPP assuming that the realized factor of increase is normally distributed (0.7990, Table 3). Given a population whose age structure and dynamics conform to the values given in Table 1, therefore, we can make the statement that there is an 80% chance that the population will be larger 6 time steps from now and a 20% chance that it will be smaller.

Example 2.

The results of the stochastic projection of the northern fur seal population by program SPP are given in Table 7 and Figure 2. Table 7 shows that after 5 yr, the expected (mean) number of 9-yr-olds, for example, is 6,188 with a standard deviation of 333. The expected total population size is 147,982 with a standard deviation of 8,832. The mean and standard deviation of the realized factor of increase are 1.0812 and 0.0129, respectively; from these values we compute the 99% confidence interval on population size to be from 126,410 to 171,930. Note

TABLE 7.—Results of the 5-yr stochastic projection of the northern fur seal population, based on the age structure and vital rates given in Table 2. Probability that the final population > initial population = 0.999 +.

Age class	Expected population size	Standard deviation
1	26,071	1,672
2	21,179	1,619
3	17,205	1,519
4	14,058	1,402
5	11,553	1,280
6	9,655	972
7	8,205	720
8	7,087	516
9	6,188	333
10	5,432	121
11	4,743	106
12	4,075	92
13	3,406	76
14	2,767	62
15	2,170	49
16	1,611	36
17	1,121	25
18	717	16
19	415	9
20	209	5
21	87	2
22	26	1
23	2	0.05
Total	147,982	

	Total population	Factor of increase
Lower 99% C.L.	126,410	1.0480
Expected value (mean)	147,982	1.0812
Upper 99% C.L.	171,930	1.1145

specify the statistics of the variation in the age-specific vital rates. Realistically, we do not expect there to be be many examples where the statistics of the variation in vital rates are genuinely known with substantial precision, for these rates are difficult to measure in natural populations. Nevertheless, in an imperfect world, management decisions must be made with imperfect data. A considerable component of the uncertainty in a population prediction will be owing to the phenomena treated in this paper. Thus, even the use of very rough guesses at the statistics of the variation in the age-specific vital rates, in order to estimate confidence intervals in a population projection, is preferable to neglecting this source of variation entirely. At the very least, incorporation of speculative estimates in this applied context will allow the exploration of "what if" questions in a fashion that can indicate priorities for future data gathering.

In many fish and aquatic invertebrate species, there is an enormous variation in the success of year classes. In such cases the population dynamics may be dominated by the overwhelming abundance of one

that, as will generally be the case, the confidence interval for total population size is not symmetric about the mean value.

In the last line of Table 7, the probability of an increased population is shown to be very close to 1.0. In other words, it is virtually certain that the population will have increased in size after 5 yr. Figure 2 presents the results for total population size graphically. The 95% and 99% confidence limits computed by program SPP are shown for each time step. The confidence limits grow nearly geometrically.

DISCUSSION

Fishery and wildlife management often involves predictions of population size, and, owing to imperfect knowledge of the world, these predictions are uncertain. Accordingly, a practical analysis attaches estimates of confidence intervals for any given prediction. The programs described in this paper carry out the computation of confidence intervals for projections of age-structured populations, if we can

FIGURE 2.—Confidence limits for future total female population size for the northern fur seal, based on the schedule of vital rates in Table 2. The solid line plots the mean population trajectory.

or two cohorts. The environmental factors which lead to such huge variations in recruitment are as yet imperfectly understood for most species. In order to predict future population sizes, the year-to-year variation could be incorporated into the variances of the effective fecundity terms in the first row of the Leslie matrix. This will lead to enormous (but realistic) confidence limits for predicted future population sizes of such stocks. A more fruitful use of the results of this paper, however, would be to separate recruitment uncertainty from survival uncertainty and to calculate a confidence interval on future population size given recruitment success for a particular cohort. Among harvested species such a conditional forecast could be used to incorporate environmental variation into management recommendations.

In keeping with the fact that applied management may often depend on very elementary quantities, we also calculate a particularly important special statistic of the distribution of projections–the probability that the population will increase under the specified conditions. In the first example, the probability of an increased population was found to be about 0.8. In the second example, the fur seal population projection, there is a higher probability that the population will increase. Starting with the female population of 100,000, the calculations indicate 99% certainty that the population will have increased to between 126,410 and 171,930 in 5 yr.

Our simulations of stochastic population growth differ from previous efforts by Boyce (1977) and Slade and Levenson (1982) by allowing all vital rates to vary simultaneously, rather than only one at a time, and by permitting correlations among the vital rates to be specified. In the stochastic growth models of Cohen (1977, 1979a) and Tuljapurkar and Orzack (1980), at each time step the population finds itself in one of several possible environments. Within each environment vital rates are fixed. By contrast, here we model a single variable environment whose conditions, as reflected in the population's vital rates at any point in time, are never precisely duplicated. The results of Example 1 verify the results for the mean and variance of future population vectors and show that the mean and variance for total ultimate population size can be computed from Sykes' formulae. Our results confirm the conclusions of Cohen (1977), Tuljapurkar and Orzack (1980), and Slade and Levenson (1982) that the expected mean value of a stochastic population projection with no serial correlation in vital rates is equivalent to the value projected deterministically from mean vital rates. Cohen (1979a, b)

and Tuljapurkar (1982) address the more general question of serial correlation in vital rates.

All of the work cited above has been concerned with the state of the population at a time in the future much greater than will generally be useful in management. In this paper we have examined the stochastic behavior of the population at a shorter time in the future. Example 1 has verified that the distribution of ultimate population sizes from stochastic population projections is approximately lognormal (Tuljapurkar and Orzack 1980). From the perspective of fitting the tails of this distribution for a small number of time steps t, however, it appears better to assume that the $1/t$th power of the distribution is normally distributed. In either case the distribution of ultimate population sizes is skewed (with long tails at the higher values), and the skew becomes more pronounced as t increases. An important property of such a distribution is that the most likely or modal population value will always be smaller than the mean. How much smaller depends on the number of time steps t, and on the variances and covariances among the survival and fecundity rates.

An interesting theoretical and practical problem is to find a descriptor of population growth under stochastic conditions which characterizes the skewed distribution of ultimate population size. Cohen (1979a) has proposed two measures of long-run population growth: λ, the ensemble average of realized factors of increase; and μ, the factor of increase needed to realize the ensemble average of final population sizes. The first is a measure based on growth rates, while the second is based on population sizes (Cohen 1979b). The average realized factor of increase calculated here is analogous to λ. If the Leslie matrix of mean vital rates is known, μ is easily calculated as the dominant eigenvalue of that matrix. The problem, as we have seen, is that under stochastic conditions the mean of the population sizes is not very informative and may, in fact, be misleading. Tuljapurkar (1982) has proposed a growth measure α which leads to the approximate median population size. The two measures proposed here–namely, $E[(N_t/N_0)^{1/t}]$ and $E[\log(N_t/N_0)]$–are close approximations to the rate of growth leading to the modal population size. As such, they may loosely be said to describe the most probable trajectory of the population under stochastic conditions.

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APPENDIX 1.

Calculation of the mean and variance of the realized factor
of increase, assuming it is normally distributed.

Let λ, the realized factor of increase, be defined as the tth root of the ratio of the population size at time t to the initial population size:

$$\lambda = \left(\frac{N_t}{N_0}\right)^{1/t}$$

or

$$\lambda^t = \frac{N_t}{N_0}$$

Let μ be the mean and ν the variance of λ. The mean and variance of λ^t are given by formulae in the Methods section. The problem is to find the mean and variance of λ.

Let $F(\mu,\nu)$ be a function which gives the tth moment of λ:

$$F(\mu,\nu) = E(\lambda^t).$$

Similarly let $G(\mu,\nu)$ be a function which gives the variance of λ^t in terms of the tth and $2t$th moments of λ:

$$G(\mu,\nu) = E(\lambda^{2t}) - [E(\lambda^t)]^2.$$

Now assume that λ is normally distributed. Appendix 2 gives a recursive algorithm which allows any moment of a normally distributed variate to be calculated. From the tth and $2t$th moments of λ, the functions F and G can be computed from the equations above. Generally, F and G will be tth and $2t$th order polynomials in μ and ν. Then, with F and G known, we have a system of two equations

$$F(\mu,\nu) - E(\lambda^t) = 0$$
$$G(\mu,\nu) - \mathrm{Var}(\lambda^t) = 0$$

in two unknowns. Given initial estimates of μ and ν, a two-variable version of Newton's method, or any similar iterative technique, can be used to converge on a simultaneous solution.

APPENDIX 2.

A recursive algorithm for computing the higher order moments of the normal distribution.

The moment generating function for the normal distribution is

$$M_x(t) = e^{\mu t + \frac{vt^2}{2}}$$

where μ is the mean and v is the variance of the normal variate x. The nth moment of x is found by evaluating, at $t = 0$, the nth derivative of $M_x(t)$ with respect to t. The nth differentiation with respect to t leads to the series

$$(\mu + vt)^n M_x(t) + \ldots + A(\mu + vt)^\alpha v^\beta M_x(t) + B(\mu + vt)^{\alpha-2} v^{\beta+1} M_x(t) + \ldots,$$

which, evaluated at $t = 0$, gives

$$\mu^n + \ldots + A\mu^\alpha v^\beta + B\mu^{\alpha-2} v^{\beta+1} + \ldots,$$

where A and B are coefficients and α and β are exponents such that $\alpha + 2\beta = n$. The next $[(n + 1)\text{th}]$ differentiation of the middle terms gives

$$A(\mu + vt)^{\alpha+1} v^\beta M_x(t) + A\alpha(\mu + vt)^{\alpha-1} v^{\beta+1} M_x(t)$$

$$+ B(\mu + vt)^{\alpha-1} v^{\beta+1} M_x(t) + B(\alpha - 2)(\mu + vt)^{\alpha-3} v^{\beta+2} M_x(t)$$

$$= \ldots + (A\alpha + B)(\mu + vt)^{\alpha-1} v^{\beta+1} M_x(t) + \ldots$$

which, evaluated at $t = 0$, gives

$$\ldots + (A\alpha + B)\mu^{\alpha-1} v^{\beta+1} + \ldots.$$

Thus the coefficient of each term of the series of the $(n + 1)$th moment can be computed from the two terms in the series of the nth moment "before" and "after" it. The exponents of μ and v follow the regular pattern shown.

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