The Statistical Analysis of Population Growth Rates Calculated from Schedules of Survivorship and Fecundity

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THE STATISTICAL ANALYSIS OF POPULATION GROWTH RATES CALCULATED FROM SCHEDULES OF SURVIVORSHIP AND FECUNDITY[1]

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Abstract. Population growth rates can be estimated from sample cohort schedules of survivorship and fecundity, but the variation inherent in these estimates has received little attention. We define an ideal population such that it is completely described by the probabilities governing age-specific survival and reproduction. We define the lifetime contribution of an individual to population growth in a manner analogous to Fisher's (1930) reproductive value. The mean of these individual contributions is equal to the finite rate of increase for the population. We then investigate the properties of sample cohorts drawn from an ideal population. Estimates of population growth rates that are based on sample cohorts are shown to be biased. The magnitude of the bias decreases as the number of individuals used to construct the sample schedules of survivorship and fecundity is increased. This relationship conflicts with the statistical desirability of maximizing the number of estimates of the population growth rate. Bias can be reduced by pooling individual schedules to calculate a single estimate of the growth rate of the population within which individual contributions are defined. When cohort size is small, we recommend a modified jackknifing procedure for further reducing bias. To demonstrate the application of these methods, we obtain a 95% confidence interval for a rate of increase based on a sample cohort of aphids.

Key words: bias; demography; estimation; jackknife; population growth; rate of increase; reproductive value; stable-age equation.

INTRODUCTION

The comparative study of population growth rates can suggest environmental and genetic factors that influence the distribution and abundance of organisms (e.g., Birch 1953*a*, 1953*b*). Age-specific schedules of survivorship and fecundity provide a basis for calculating rates of population growth (Lotka 1925, Fisher 1930, Leslie 1945, 1948, Goodman 1968, Michod and Anderson 1980). It is unfortunate that the variation inherent in estimates of population growth rates has received only limited attention (Keyfitz 1968), and has been generally ignored by ecologists.

The purpose of this paper is to explore the statistical properties of population growth rates calculated from schedules of survivorship and fecundity. First, we consider ideal populations for which the true probabilities governing age-specific survival and reproduction are known. The finite rate of increase is shown to equal the mean lifetime contribution of individuals to population growth. We provide a formulation for the variance associated with this mean contribution. Second, we investigate the properties of sample cohorts drawn from ideal populations. Estimates of population growth rates based on sample cohort schedules of survivorship and fecundity are shown to be biased. We compare several methods of estimation using the criteria of accuracy, power, fairness, and facility.

There are widespread differences in demographic

notation. Because our emphasis is statistical, we follow the convention of using the Greek alphabet to indicate population parameters and the Roman alphabet to indicate observations and sample statistics. We have chosen symbols to make the presentation of this paper as logical as possible, and we have ignored usage that, though widespread, might be confusing in the context of this paper.

Lotka (1925) has shown that if age-specific schedules of survivorship and fecundity remain constant through time, a population will approach a stable age distribution, regardless of its initial age distribution. Lotka (1925) and Fisher (1930) considered schedules of survivorship and fecundity wherein age is a continuous variable. Many subsequent demographers (e.g., Goodman 1968) have treated age as a discrete variable. There are several justifications for the latter approach. Many organisms reproduce at discrete intervals (e.g., seasonally). Even with organisms whose breeding is effectively continuous, observations are restricted to discrete intervals. If intervals between observations are sufficiently short, the discrete approach closely approximates the continuous approach (Leslie 1945).

The finite rate of increase of a population, ϕ, can be calculated from age-specific schedules of survivorship and fecundity in the following manner (Goodman 1968, Michod and Anderson 1980). Let σ_x be the proportion of all females in age-class 0 that survive to age-class x. Let β_x be the mean number of female offspring born to all females in age-class x, excluding offspring that do not survive to enter age-class 0 (at which time the
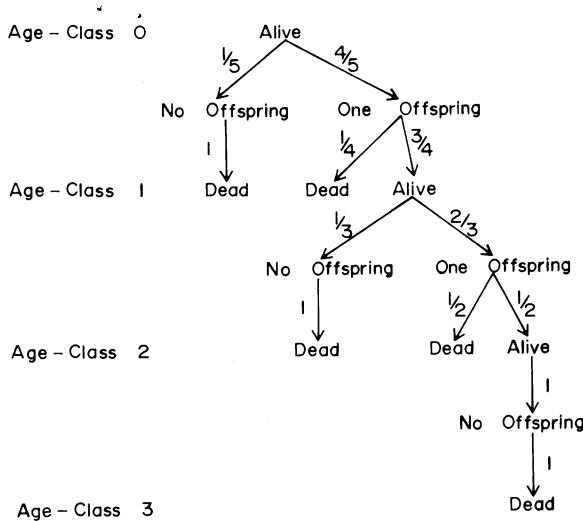
FIG. 1. Example of an ideal population. The probabilities governing age-specific survival and reproduction are presented as a branching process. Note that there are five possible sequences, or lives, and that each of these lives is equally probable for any female entering age-class 0. All offspring are female and survive to enter age-class 0.

female parents would enter age-class $x + 1$). Then the finite rate of increase can be calculated iteratively from the stable-age equation

$$1 = \sum_{x=0}^{\infty} \phi^{-(x+1)} \sigma_x \beta_x. \tag{1}$$

It is not necessary to calculate explicitly the stable age distribution; however, the stable age distribution is implicit in this formulation.

Age-specific survivorships and fecundities are averages, and there will be variation among individuals in their contribution to population growth. Therefore, a complete understanding of population growth requires a probabilistic, rather than a deterministic, approach. Unlike those used in most other stochastic population models (e.g., Pollard 1966), our units of chance are not demographic events (i.e., births and deaths), but instead are individual lives.

ANALYSIS AND RESULTS

Ideal populations

We define an *ideal population* as the statistical universe whose parameters we seek to infer by sampling a cohort of individuals and observing age-specific survivorships and fecundities. We define a *life* as the temporal sequence of survival and reproduction experienced by an individual. The probabilities governing survival and reproduction for individuals of all ages uniquely determine the frequencies of all lives within an ideal population. These probabilities are constant through time, so that the ideal population possesses a stable age distribution. The rate of increase for an ideal population is obtained by Eq. 1.

An example of an ideal population is shown in Fig. 1. The probabilities of survival and reproduction for females of all ages are presented as a branching process. In this example, there are five equally probable sequences, or lives; this can be verified by computing the product of all probabilities leading to each end point. We define π_i as the probability of experiencing life i for any female entering age-class 0. Note that no heritable variation among individuals is implied; differences in individual contributions to population growth are assumed to be stochastic.

Schedules of survivorship and fecundity can be drawn up for each life, just as they can for the population as a whole. However, in schedules for individual lives, survivorships and fecundities are restricted to integer values. The survivorship of an individual of life i to age-class x is S_{xi}. The fecundity of an individual of life i in age-class x is B_{xi}. Note that if $S_{xi} = 0$ then $B_{xi} = 0$. Since population fecundity β_x is defined per female alive in age-class x, then

$$\beta_x = \sum_i \pi_i B_{xi} / \sigma_x.$$

Table 1 shows the survivorship and fecundity schedules for each life and for the population, from the example in Fig. 1.

Fisher (1930:27) asked: "To what extent will [individuals in age-class x], on the average, contribute to the ancestry of future generations?" Fisher demonstrated that the value of an offspring produced at age $x + 1$ must be discounted by a factor of ϕ relative to an offspring produced at age x. This discounting is in recognition of the fact that a later offspring constitutes a smaller fraction of a growing population (Fisher 1930, Roughgarden 1979). Fisher defined this age-specific reproductive value in a relative fashion, such that the reproductive value for age-class 0 equals one.

We ask: to what extent will individuals experiencing life i, on the average, contribute to the ancestry of future generations? We define the lifetime contribution of an individual to population growth, ϕ_i, as the sum of an individual's fecundities discounted by the population's growth rate. That is,

$$\phi_i = \sum_{x=0}^{\infty} \phi^{-x} B_{xi}. \tag{2}$$

By virtue of our choice for the negative exponent in Eq. 2, the mean of the individual lifetime contributions equals the finite rate of population growth:

$$\sum_i \pi_i \phi_i = \phi.$$

See Proof 1 in the Appendix. The contributions for the lives defined by our example of an ideal population are shown in Table 1. It is a simple matter to compute the true population variance of these lifetime contributions:

$$\text{var}(\phi_i) = \sum_i (\phi_i - \phi)^2 \pi_i.$$

TABLE 1. Schedules of survivorship and fecundity for each life and for the population defined by the probabilities in Fig. 1.

Life i	π_i	S_{0i}	B_{0i}	S_{1i}	B_{1i}	S_{2i}	B_{2i}	S_{3i}	ϕ_i	F_i
1	.2	1	0	0	0	0	0	0	0	0
2	.2	1	1	0	0	0	0	0	1	1
3	.2	1	1	1	0	0	0	0	1.8708	1.6180
4	.2	1	1	1	1	0	0	0	1.8708	1.6180
5	.2	1	1	1	1	1	0	0	1.8708	1.6180
Population		1	.8	.6	.6667	.2	0	0	1.1483	1.0472

In our example, the mean lifetime contribution of individuals to population growth (i.e., the finite rate of increase) is ≈ 1.1483, with a variance of ≈ 0.4813.

Many natural populations do not even approximate ideal populations, and it may be difficult to observe populations in their natural setting. It is more often convenient to sample individuals not from all age-classes, but from a set of new offspring. These offspring form a cohort, and their lives are observed under a specified set of conditions. Therefore, let us now turn our attention away from calculating the mean lifetime contribution and its variance for an ideal population, and consider the problem of estimating these parameters from a sample cohort.

Sample cohorts

One of the basic principles of inductive statistics is that the strength of an inference about some population parameter increases with the number of independent sample observations. Yet ecological researchers are subject to limited resources, including the availability of experimental organisms. Therefore, obtaining many estimates of the rate of increase, each based on a few individuals, will be a more powerful estimation procedure (i.e., provide more degrees of freedom) than obtaining a few estimates, each based on many individuals. When constructing schedules of survivorship and fecundity from a sample cohort, individual lives can be observed independently, given proper experimental design. A plausible methodology is to compute a rate of increase for each individual, F_i, based on its schedule of survivorship and fecundity:

$$1 = \sum_{x=0}^{\infty} F_i^{-(x+1)} B_{xi},$$

which is identical to

$$F_i = \sum_{x=0}^{\infty} F_i^{-x} B_{xi}. \tag{3}$$

(It is better to compute the finite rate of increase than the instantaneous rate of increase, since the latter will be undefined for any individual who dies without reproducing.) As Smith (1963:657) notes, "This rate applies to an imaginary stable-age-distribution population of individuals all exactly like the one followed."

We can compute a finite rate of increase F_i for any life. The values of F_i for each of the lives defined by the probabilities in Fig. 1 are given in Table 1. Drawing a sample cohort from any ideal population, the expected mean value for the F_i is

$$E(\bar{F}) = \sum_i \pi_i F_i;$$

recall that π_i is the probability of experiencing life i for individuals sampled from age-class 0. In our example, there are five equally probable lives, and the expected mean of the F_i is ≈ 1.0472. Note that this does not equal the true population finite rate of increase, ϕ, which is ≈ 1.1483. In fact, the mean of these individual rates is a biased estimator of the population rate; the definition of an unbiased estimator is that "the mean of its sampling distribution is exactly equal to the value of the parameter being estimated" (Blalock 1972:202). This bias occurs in samples drawn from all but the most trivial ideal populations (e.g., wherein all females experience identical lives), and may be positive or negative depending on the ideal population.

Let us also compare the variance in the F_i with the variance in the ϕ_i. Consider an ideal population in which there are two lives, such that $\phi_1 > \phi_2$. Individuals with the higher ϕ_1 are subject to more severe discounting, when calculating F_i, than are individuals with the lower ϕ_2. That is,

$$\phi_1 \geq F_1 > \phi > F_2 \geq \phi_2.$$

See Proof 2 in the Appendix. Therefore, a set of F_i will be less variable than a corresponding set of ϕ_i, i.e., $\text{var}(F_i) < \text{var}(\phi_i)$. Underestimating the variance among individual lives wrongly inflates one's confidence in an estimate of ϕ based on observed F_i. Not only is the mean of the F_i a biased estimator of the finite rate of increase, but the variance of the F_i is too small.

Just as it was possible to compute a rate of increase based on one life, we can compute a rate of increase corresponding to any combination of lives. Let N be the number of individuals in a sample cohort. Let $\bar{S}_x$ and $\bar{B}_x$ be the average age-specific survivorships and fecundities, respectively, within the sample. Then we can estimate the finite rate of increase iteratively using

$$1 = \sum_{x=0}^{\infty} F_N^{-(x+1)} \bar{S}_x \bar{B}_x, \tag{4}$$

TABLE 2. Individual and cohort schedules of survivorship and fecundity for a sample of 18 aphids.

Individual	S_{0i}	B_{0i}	S_{1i}	B_{1i}	S_{2i}	B_{2i}	S_{3i}	B_{3i}	S_{4i}	B_{4i}	S_{5i}	B_{5i}	S_{6i}	B_{6i}	S_{7i}	B_{7i}
1	1	0	1	0	1	0	1	3	1	4	1	5	1	2	1	1
2	1	0	1	0	1	2	1	6	1	1	1	1	1	3	1	2
3	1	0	0	...	0	...	0	...	0	...	0	...	0	...	0	...
4	1	0	1	0	1	0	1	4	1	2	1	2	1	2	1	1
5	1	0	1	0	1	0	1	0	1	2	1	1	0	...	0	...
6	1	0	0	...	0	...	0	...	0	...	0	...	0	...	0	...
7	1	0	1	0	1	2	1	5	1	3	1	3	1	1	1	1
8	1	0	0	...	0	...	0	...	0	...	0	...	0	...	0	...
9	1	0	1	0	1	0	1	7	1	2	1	3	1	3	1	0
10	1	0	1	0	1	5	1	7	1	5	1	5	1	2	1	2
11	1	0	1	0	1	1	1	5	1	6	1	3	1	1	1	0
12	1	0	1	0	1	7	1	6	1	6	1	6	1	3	1	3
13	1	0	1	0	1	1	1	6	1	3	1	3	1	1	0	...
14	1	0	1	0	1	0	1	4	1	7	1	2	1	4	1	3
15	1	0	1	0	1	0	1	6	1	4	1	5	1	0	0	...
16	1	0	1	0	0	...	0	...	0	...	0	...	0	...	0	...
17	1	0	1	0	1	0	1	3	1	2	1	3	1	1	1	3
18	1	0	1	0	1	0	1	0	1	2	1	2	1	2	1	0
Cohort																
$\bar{S}_x$	1		.8333		.7778		.7778		.7778		.7778		.7222		.6111	
$\bar{B}_x$		0		0		1.2857		4.4286		3.5000		3.1429		1.9231		1.4545

where F_N is the sample estimate of ϕ. Given any ideal population, the joint probability of each possible combination of N lives can be calculated from the probabilities of the constituent lives, assuming random sampling from age-class 0. In Fig. 2, the expected value for F_N is given for sample cohorts of one, two, three, four, five, and six individuals drawn from the ideal

FIG. 2. Bias in the estimation of ϕ for samples of various sizes drawn from the ideal population shown in Fig. 1. Shown above are $E(F_N) = \bullet$ and $NE(F_N) - (N - 1) E(F_{N-1}) = \triangle$.

population shown in Fig. 1. Use of the stable-age equation, for any finite sample cohort, generates a biased estimate of the true rate of increase of the ideal population. The magnitude of the bias decreases as the number of individuals used to construct the sample schedules of survivorship and fecundity is increased. This relationship conflicts with the statistical desirability of maximizing the number of independent estimates of the parameter ϕ.

What is the source of this bias? The problem is similar to that of estimating a population variance from sample observations. The average of the squared deviations is a biased estimator of the true population variance (Fisher 1920), because the squared deviations cannot be calculated independently of the mean. The bias in the stable-age equation arises because the discounting factors (i.e., ϕ^{-x}) cannot be estimated independently of the age-specific survivorships and fecundities using sample cohort data.

Compare Eqs. 2 and 3. The lifetime contribution of an individual, ϕ_i, is defined only within the context of an ideal population which has a specified rate of growth ϕ. The rate of increase calculated for an individual, F_i, is a poor estimate of the lifetime contribution of that individual, since it utilizes minimal information about the growth rate of the population.

Say that we have observed the lives of a sample cohort of N individuals. F_N is a more accurate estimator of ϕ than is $\bar{F}$, by virtue of the relationship between bias and sample cohort size. Moreover, F_N gives a better estimate of the discounting factor applicable to an individual's contribution than does the rate of increase calculated from that individual. Therefore, we can estimate the lifetime contribution of an individual to population growth, F'_i, using F_N as a
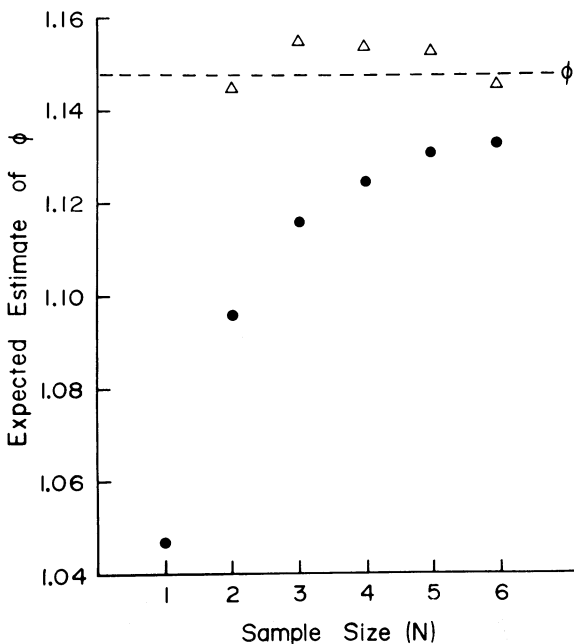
TABLE 2. Continued.

S_{8i}	B_{8i}	S_{9i}	B_{9i}	S_{10i}	B_{10i}	S_{11i}	B_{11i}	S_{12i}	B_{12i}	S_{13i}	B_{13i}	F_i	F'_i	F^*_i	F''_i
1	1	0	...	0	...	0	...	0	...	0	...	1.6719	1.6268	1.6702	1.6309
1	0	1	0	1	0	1	0	0	...	0	...	1.8283	2.3465	1.8350	2.3525
0	...	0	...	0	...	0	...	0	...	0	...	0	0	1.3068	0
1	0	1	0	0	...	0	...	0	...	0	...	1.6061	1.3498	1.6073	1.3533
0	...	0	...	0	...	0	...	0	...	0	...	1.2298	.3231	1.3773	.3239
0	...	0	...	0	...	0	...	0	...	0	...	0	0	1.3068	0
1	0	1	0	1	0	1	0	0	...	0	...	1.8393	2.4199	1.8520	2.4261
0	...	0	...	0	...	0	...	0	...	0	...	0	0	1.3068	0
0	...	0	...	0	...	0	...	0	...	0	...	1.7624	2.0707	1.7722	2.0759
1	1	1	0	0	...	0	...	0	...	0	...	2.1528	4.3808	2.3120	4.3919
1	0	0	...	0	...	0	...	0	...	0	...	1.8282	2.4146	1.8516	2.4207
0	...	0	...	0	...	0	...	0	...	0	...	2.2585	5.1301	2.4908	5.1431
0	...	0	...	0	...	0	...	0	...	0	...	1.8027	2.2506	1.8133	2.2563
1	2	1	1	0	...	0	...	0	...	0	...	1.7683	2.1530	1.7922	2.1585
0	...	0	...	0	...	0	...	0	...	0	...	1.7716	2.1262	1.7851	2.1316
0	...	0	...	0	...	0	...	0	...	0	...	0	0	1.3068	0
1	0	0	...	0	...	0	...	0	...	0	...	1.5785	1.2224	1.5781	1.2255
1	0	1	0	1	0	1	0	1	0	0	...	1.3549	.4850	1.4124	.4863
.5000		.3333		.1667		.1667		.0556		0			$F_N = 1.6833$		
	.4444		.1667		0		0		0		...				

common discounting factor:

$$F'_i = \sum_{x=0}^{\infty} F_N^{-x} B_{xi}.$$

The mean of these estimated contributions is equal to the estimated finite rate of population growth, i.e., $\overline{F'} = F_N$. As N is increased, F_N approaches ϕ, and each F'_i approaches ϕ_i. Therefore, the variance associated with the F'_i will approach the true variance of the ϕ_i in the ideal population.

When the bias of an estimator is some monotonically decreasing function of sample size, as it is for F_N, a statistical technique known as the "jackknife" can be used to generate a new estimator that is less biased. Keyfitz (1968) suggested the applicability of this technique to estimating demographic parameters. If F_N is the estimate of ϕ based on a sample cohort of N lives, let F_{-i} be the estimate of ϕ based on that sample omitting life i. Then the "pseudovalue" F^*_i is defined by

$$F^*_i = NF_N - (N - 1)F_{-i},$$

and the mean of the N pseudovalues is an estimator of ϕ. The expected value of this mean is

$$E(\overline{F^*}) = NE(F_N) - (N - 1)E(F_{N-1}).$$

The expected values for $\overline{F^*}$ for samples of two, three, four, five, and six lives, drawn from the ideal population in Fig. 1, are shown in Fig. 2. Jackknifing reduces the bias in estimating ϕ, as anticipated.

Unfortunately, the variance among the pseudovalues is an underestimate of var(ϕ_i), just as var(F_i) was. See Proof 3 in the Appendix. We can circumvent this problem by defining another estimate of an individual's lifetime contribution, F''_i, which takes into ac-

count the reduced bias of $\overline{F^*}$ relative to $\overline{F'}$:

$$F''_i = F'_i(\overline{F^*/F'}).$$

$\overline{F''}$ is identical to $\overline{F^*}$, but the F''_i provide a fairer estimate of the true variation among individual contributions to population growth.

AN APPLICATION

In order to clarify computations required by the various methodologies, we focus on the problem of obtaining a 95% confidence interval for an estimate of ϕ based on a sample cohort of 18 aphids (*Uroleucon rudbeckiae*). Each aphid's survival and reproduction were observed daily, but we have collapsed the data into 5-d age-classes to facilitate calculations for this example. The individual schedules of survivorship and fecundity are shown in Table 2; sample statistics are presented in Table 3. The relative merits of the methodologies will be summarized in the Discussion.

Estimating ϕ with $\overline{F}$

1) Calculate the rate of increase F_i for each individual:

$$1 = \sum_{x=0}^{\infty} F_i^{-(x+1)} B_{xi}.$$

2) Compute the sample mean and variance of the F_i:

$$\overline{F} = \sum_i F_i / N$$

$$\text{var}(F_i) = \sum_i (F_i - \overline{F})^2 / (N - 1).$$

Estimating ϕ with $\overline{F'}$

1) Calculate sample cohort survivorships and fecundities for all ages:

TABLE 3. Summary from application presented in Table 2. Confidence intervals assume values are normally distributed. $t_{.05} = 2.110$; df $= 17$.

	Mean	Variance	95% confidence interval
F	1.3585	0.6129	0.9692–1.7478
F'	1.6833	2.1476	0.9545–2.4121
F^*	1.6876	0.1132	1.5203–1.8549
F''	1.6876	2.1586	0.9569–2.4183

$$\overline{S}_x = \sum_i S_{xi}/N$$

$$\overline{B}_x = \sum_i B_{xi}/(N\overline{S}_x).$$

2) Calculate the sample cohort rate of increase F_N:

$$1 = \sum_{x=0}^{\infty} F_N^{-(x+1)}\overline{S}_x\overline{B}_x.$$

3) Calculate each individual's contribution, F'_i, to the cohort rate of increase:

$$F'_i = \sum_{x=0}^{\infty} F_N^{-x}B_{xi}.$$

4) Compute the sample mean and variance of the F'_i:

$$\overline{F}' = \sum_i F'_i/N$$

$$\mathrm{var}(F'_i) = \sum_i (F'_i - \overline{F}')^2/(N - 1).$$

Estimating ϕ with $\overline{F^*}$

1) Calculate F_N as above.
2) Remove one individual from the sample cohort. Compute survivorships, fecundities, and rate of increase for this subset of $N - 1$ individuals, denoting the new rate of increase by F_{-i}.
3) Calculate the pseudovalue F^*_i:

$$F^*_i = NF_N - (N - 1)F_{-i}.$$

4) Repeat steps 2 and 3 for each individual, generating N pseudovalues.
5) Compute the sample mean and variance of the F^*_i:

$$\overline{F^*} = \sum_i F^*_i/N$$

$$\mathrm{var}(F^*_i) = \sum_i (F^*_i - \overline{F^*})^2/(N - 1).$$

Estimating ϕ with $\overline{F''}$

1) Calculate the F'_i, $\overline{F}'$, and $\overline{F^*}$ as above.
2) Calculate each individual's contribution, F''_i, to the cohort rate of increase:

$$F''_i = F'_i(\overline{F^*}/\overline{F}').$$

3) Compute the sample mean and variance of the F''_i:

$$\overline{F''} = \sum_i F''_i/N$$

$$\mathrm{var}(F''_i) = \sum_i (F''_i - \overline{F''})^2/(N - 1).$$

DISCUSSION

The rate of a population's growth under specified conditions can be estimated from schedules of survivorship and fecundity based on a sample cohort. Eq. 4 provides an estimator, F_N, of the finite rate of increase ϕ, which is widely used by population biologists. It is unfortunate that use of this estimator yields no information about the variation among the observations used to generate an estimate, and hence the estimator is not suitable for statistical analysis. In the preceding pages, we have presented four other estimators of ϕ, each of which is the mean of N values calculated from the independently observed lives of N organisms. These estimators can be compared in terms of four desirable characteristics: (1) accuracy, i.e., smallest bias associated with the estimator; (2) power, i.e., most degrees of freedom; (3) fairness, i.e., accuracy of the estimated variance among individuals; and (4) facility, i.e., fewest number of iterative solutions required.

$\overline{F}'$ is a more accurate estimator of ϕ than is $\overline{F}$. Both $\overline{F}'$ and $\overline{F}$ yield $N - 1$ degrees of freedom. However, the variance among the F_i is an underestimate of the true variation among individual contributions to population growth. All of the F'_i can be calculated with a single iterative solution, while N iterative solutions are required to obtain all of the F_i. By all of these criteria, $\overline{F}'$ is equal or superior to $\overline{F}$ as an estimator of the finite rate of increase.

$\overline{F^*}$ and $\overline{F''}$ produce identical estimates of ϕ. Both $\overline{F^*}$ and $\overline{F''}$ have $N - 1$ associated degrees of freedom, and both require $N + 1$ iterative solutions. Because of a superior estimate of the variance among individual contributions, the F''_i are preferable to the F^*_i.

$\overline{F''}$ gives a more accurate estimate of ϕ than does $\overline{F}'$. Both methodologies allow $N - 1$ degrees of freedom, and both give fair estimates of the variation among individuals. Only one iterative solution is necessary to calculate all of the F'_i, while $N + 1$ are required to compute all of the F''_i. Because the bias of either estimator is likely to be quite small for even moderate sample sizes, we recommend general usage of the readily calculable F'_i. However, for small sample cohorts, the additional computational effort required for $\overline{F''}$ is justified by the reduced bias in estimating ϕ.

So far we have only considered the problem of estimating ϕ for a population, although this is clearly related to the problem of comparing estimates among populations. Consider the null hypothesis that the finite growth rates of two populations are equal, i.e., $\phi_A = \phi_B$, vs. the alternative that the population rates

are not equal. When estimating individual contributions, should we assume a common discounting factor, or should we compute separate discounting factors for each sample? If the null hypothesis is true, use of a common discounting factor is appropriate and should yield a common estimate of ϕ (with less bias than if separate discounting factors were used, each based on a smaller sample size). If the null hypothesis is false, the expected difference between the sample mean contributions will be greater if a common discounting factor is used. In either case, use of a common discounting factor increases the likelihood of supporting the correct hypothesis.

In the first use of the methodology recommended in this paper, we (Service and Lenski, *in press*) used a total of only 144 aphids (*Uroleucon rudbeckiae*). Yet we demonstrated several significant differences in rates of increase which support the hypothesis that diversity can be maintained by differential success in a heterogeneous environment. The use of individual contributions provides an accurate, powerful, fair, simple, and intuitive methodology for statistically analyzing population growth rates estimated from sample cohort schedules of survivorship and fecundity. It is important to apply rigorous statistical criteria to inferences based on rates of increase, especially given the explosion of ecological and evolutionary theory whose validation rests on the comparative study of such rates.

LITERATURE CITED

Birch, L. C. 1953a. Experimental background to the study of the distribution and abundance of insects. I. The influence of temperature, moisture and food on the innate capacity for increase of three grain beetles. Ecology 34:698–711.

———. 1953b. Experimental background to the study of the distribution and abundance of insects. II. The relation between innate capacity for increase in numbers and the abundance of three grain beetles in experimental populations. Ecology 34:712–726.

Blalock, H. M., Jr. 1972. Social statistics. McGraw-Hill, New York, New York, USA.

Fisher, R. A. 1920. A mathematical examination of the methods of determining the accuracy of an observation by the mean error, and by the mean square error. Monthly Notices of the Royal Astronomical Society 80:758–770.

———. 1930. The genetical theory of natural selection. Oxford University, Oxford, England.

Goodman, L. A. 1968. An elementary approach to the population projection-matrix, to the population reproductive value, and to related topics in the mathematical theory of population growth. Demography 5:382–409.

Keyfitz, N. 1968. Introduction to the mathematics of population. Addison-Wesley, Reading, Massachusetts, USA.

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika 33:183–212.

———. 1948. Some further notes on the use of matrices in population mathematics. Biometrika 35:213–245.

Lotka, A. J. 1925. Elements of physical biology. Williams and Wilkins, Baltimore, Maryland, USA.

Michod, R. A., and W. W. Anderson. 1980. On calculating demographic parameters from age frequency data. Ecology 61:265–269.

Pollard, J. H. 1966. On the use of the direct matrix product in analysing certain stochastic population models. Biometrika 53:397–415.

Roughgarden, J. 1979. Theory of population genetics and evolutionary ecology: an introduction. Macmillan, New York, New York, USA.

Service, P. M., and R. E. Lenski. *In press*. Aphid genotypes, plant phenotypes, and genetic diversity: a demographic analysis of experimental data. Evolution.

Smith, F. E. 1963. Population dynamics in *Daphnia magna* and a new model for population growth. Ecology 44:651–663.

APPENDIX

Proof 1

$$\sum_i \pi_i \phi_i = \sum_i \pi_i \sum_{x=0}^{\infty} \phi^{-x} B_{xi} = \sum_i \sum_{x=0}^{\infty} \phi^{-x} \pi_i B_{xi}.$$

By definition,

$$\beta_x = \sum_i \pi_i B_{xi}/\sigma_x,$$

so that

$$\sigma_x \beta_x = \sum_i \pi_i B_{xi}.$$

Therefore,

$$\sum_i \pi_i \phi_i = \sum_{x=0}^{\infty} \phi^{-x} \sigma_x \beta_x = \phi.$$

Proof 2

Given $\phi_1 > \phi_2$. Since ϕ is the mean of the ϕ_i (see Proof 1), then $\phi_1 > \phi > \phi_2$.
By definitions,

$$\sum_{x=0}^{\infty} F_1^{-(x+1)} B_{x1} = 1,$$

and

$$\sum_{x=0}^{\infty} \phi^{-x} B_{x1} = \phi_1.$$

Dividing the latter equality by ϕ, we obtain

$$\sum_{x=0}^{\infty} \phi^{-(x+1)} B_{x1} = \phi_1/\phi > 1 = \sum_{x=0}^{\infty} F_1^{-(x+1)} B_{x1}.$$

Negative exponents reverse an inequality, so if $\phi \geq F_1$, then

$$\phi^{-(x+1)} \leq F_1^{-(x+1)}$$

for all $x \geq 0$. This clearly violates the preceding inequality, so F_1 must be $>\phi$.
By definitions,

$$\sum_{x=0}^{\infty} F_1^{-x} B_{x1} = F_1,$$

and

$$\sum_{x=0}^{\infty} \phi^{-x} B_{x1} = \phi_1.$$

We have shown that $F_1 > \phi$, so that by the rule of negative exponents, F_1 must be $\leqslant \phi_1$.

By parallel arguments, $\phi > F_2 \geqslant \phi_2$.

Proof 3

By definitions,

$$F^*_i = NF_N - (N - 1)F_{-i},$$

and

$$\overline{F^*} = \sum_i F^*_i/N = NF_N - (N - 1)\overline{F}_{-i}.$$

Therefore, the sample variance of the F^*_i is

$$\mathrm{var}(F^*_i) = \sum_i (F^*_i - \overline{F^*})^2/(N - 1)$$

$$= \sum_i \{(N - 1)(\overline{F}_{-i} - F_{-i})\}^2/(N - 1)$$

$$= (N - 1) \sum_i (\overline{F}_{-i} - F_{-i})^2.$$

The variance of the F_{-i} is given by

$$\mathrm{var}(F_{-i}) = \sum_i (F_{-i} - \overline{F}_{-i})^2/(N - 1).$$

Therefore,

$$\mathrm{var}(F^*_i) = (N - 1)^2 \mathrm{var}(F_{-i}).$$

Recall that each F_{-i} is based on $N - 1$ observations, and furthermore that all pairs of F_{-i} share, by definition, all but one of these $N - 1$ observations. Therefore,

$$\mathrm{var}(F_{-i}) \simeq (N - 1)^{-2} \mathrm{var}(F_i),$$

and

$$\mathrm{var}(F^*_i) \simeq \mathrm{var}(F_i).$$