VARIANCE OF LIFETIME REPRODUCTIVE SUCCESS: ESTIMATION BASED ON DEMOGRAPHIC DATA

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Abstract.—Variance of lifetime reproductive success is not a well-defined parameter; it is a function of the way a life cycle is defined. Therefore, comparisons of such variance across studies and taxa will only be valid if the life cycles employed are complete (i.e., an entire generation), precisely defined (e.g., egg to egg or adult to adult), and identical. Given a well-defined life cycle, we present methods for obtaining estimates of the variance of lifetime reproductive success among individuals using demographic data. The estimates are based on the assumptions of no selection and negligible covariance between life span and reproductive effort. The techniques can be used to investigate the effects of alternate life histories on the distribution of reproductive success in a population, as well as to obtain estimates of effective population size. They may also provide a null model for investigations of selection. Some theoretical and empirical results are presented. A method for obtaining confidence intervals for the estimates is described.

There has been considerable interest in recent years in lifetime reproductive success (LRS) and its distribution among members of a population. For example, two volumes reviewing empirical data on reproductive success in natural populations have appeared (Clutton-Brock 1988; Newton 1989a). Theoretical reasons for this interest are clear: differences in reproductive success among individuals are the stuff of natural selection, the magnitude of the variance of LRS sets an upper limit on the magnitude of selection (see, e.g., Arnold and Wade 1984; Arnold 1986), and the ratio of variance to mean LRS affects the effective size of a population (Crow and Kimura 1970). The latter has become considerably interesting in computations associated with maintaining genetic variation in managed populations of threatened species. In addition, there has been a resurgence of long-term population studies associated with empirical questions in behavior and sociobiology; examination of data from these investigations have led researchers to consider patterns in the distribution of reproductive success among individuals and the processes leading to them (Newton 1989b; Partridge 1989).

It is quite difficult to measure LRS in natural populations. In small organisms, such as many invertebrates, various stages of the life cycle may not be readily visible to observers, or the individuals may be too small to mark and recapture. For larger organisms, such as many vertebrates, individuals may still be too

small to observe during part of their life cycle. Additionally, life cycles for some vertebrates may be quite long compared to the average length of a field project. Consequently, estimates of LRS, measured through a complete life cycle (e.g., recruited breeding adults per breeding adult) are usually not available for constructing the distribution of actual reproductive success in a population. Thus, it would be useful to have a method for estimating this distribution, or its moments, from data that are readily available.

In this article, we develop equations for estimating the variance of LRS from commonly available demographic data. Naturally, assumptions are required. In addition, we present some examples using data from natural populations and discuss some general results. Finally, the robustness of the estimates is briefly explored using simulations.

THEORETICAL CONSIDERATIONS

Our objective is to obtain estimates of the variance among individuals in lifetime reproductive success, V_{LRS}, based on minimum data. There are few studies of any organism in which a population has been studied for sufficient time and in a sufficiently intensive fashion that lifetime values of reproductive success are known for enough individuals to estimate the variance of the distribution. Nevertheless, it may be possible to obtain estimates of the magnitude of V_{LRS} based on fewer data. Here we develop two approaches to this problem; first, we obtain an analytical solution at the expense of making a number of restricting assumptions. Second, we develop an exact solution that avoids some of these assumptions but without a closed form; that is, this latter solution will be a deterministic computation of the convolution of distributions.

Analytical Solution

Consider the following: suppose that breeding adults have some distribution of reproductive life span, with a mean X_L and a variance V_L. Further suppose that, in any given year in which these individuals breed, there obtains a distribution of reproductive success, which we will call fecundity, with a mean X_F and a variance V_F. Now consider the production of offspring by an individual in this population as a process in which a random number of offspring, F_i, drawn from the above distribution of fecundity, are produced each year, i, of the individual's reproductive life. The extent of that individual's life is a random variable, L, drawn from the distribution of reproductive life spans. Then the sum

$$\sum_{i=1}^{L} F_i$$

is itself a random variable, and the distribution of these sums is the distribution of LRS of individuals in the population. Note that the sum is a random summation of random variables; this type of stochastic process is known as a random sum. If the F_i's are independently drawn from a single distribution, and if they are independent of L, then the mean and variance of this distribution are the mean

and variance of LRS of the population, respectively, and have values

$$X_{\mathrm{LRS}} = X_{\mathrm{F}} X_{\mathrm{L}} \tag{1}$$

and

$$V_{\mathrm{LRS}} = X_{\mathrm{F}}^2 V_{\mathrm{L}} + X_{\mathrm{L}} V_{\mathrm{F}}. \tag{2}$$

Equation (1) is derived by Papoulis (1965, eq. [8-58]) and stated by Feller (1968, p. 301, problem 1). Equation (2) can be found explicitly stated in Feller (1968, p. 301, problem 1). It can be derived easily from equation (8-59) of Papoulis (1965) using the definition of variance as the difference between the expectation of the square of a random variable and the squared expectation of the same random variable. Our equation (2) differs from that used by some authors (e.g., Brown [1988]) in the treatment of a slightly different problem, that of variance partitioning. This difference in approaches is discussed in the Appendix.

With the above assumptions, one could obtain an estimate of variance of LRS given estimates of the mean and variance of reproductive life spans and reproductive success within years. Unfortunately, however, one often does not even have the requisite estimates of reproductive success for a single year.

Variance of reproductive success will differ depending on which stage of an organism's life cycle is taken as a point of reference. Consider, for example, the hypothetical organism in figure 1. Suppose that every adult in a population produces 10^8 gametes during its lifetime, 10^2 of which become eggs, 10 of which become fledglings, and 1 of which becomes a breeding adult; then V_{LRS}, measured as breeding adults produced by breeding adults, is zero. However, measured as fledglings produced by fledglings, this variance is nine; as gametes produced by gametes, the variance is even larger; for example, $V_{\mathrm{LRS}} \approx 10^8$ (i.e., $10^8 - 1$ gametes produce zero gametes during their entire lives, but one produces 10^8). Consequently, if estimates of V_{LRS} are to be compared among populations, taxa, field studies, and so forth, the estimates must be obtained for a complete life cycle and with reference to the same end points of that cycle.

With regard to equations (1) and (2), one ought to have estimates of fecundity in terms of adults produced per adult or eggs produced per egg and so on. But one often does not have such estimates of mean or variance of fecundity because one rarely is able to follow individuals through an entire life cycle. Most estimates of the distribution of fecundity will consist of numbers of eggs, hatchlings or litter sizes, or fledglings or dispersers, per adult. Nevertheless, with some additional assumptions, it may still be possible to obtain an estimate of V_{LRS}.

Suppose one has an estimate of the mean and variance of some measure of reproductive success for less than an entire life cycle, for example, fledged young birds produced by adults during their lifetime. Because there is usually substantial mortality between fledging and becoming a breeding adult in most species of birds, these moments will be poor estimators of the mean and variance for a full life cycle. However, one might assume that the mean LRS of a population should be approximately two, rather than the estimate obtained for a partial life cycle, for instance, fledglings, X_{PRS}. With such an assumption the corrected estimate of
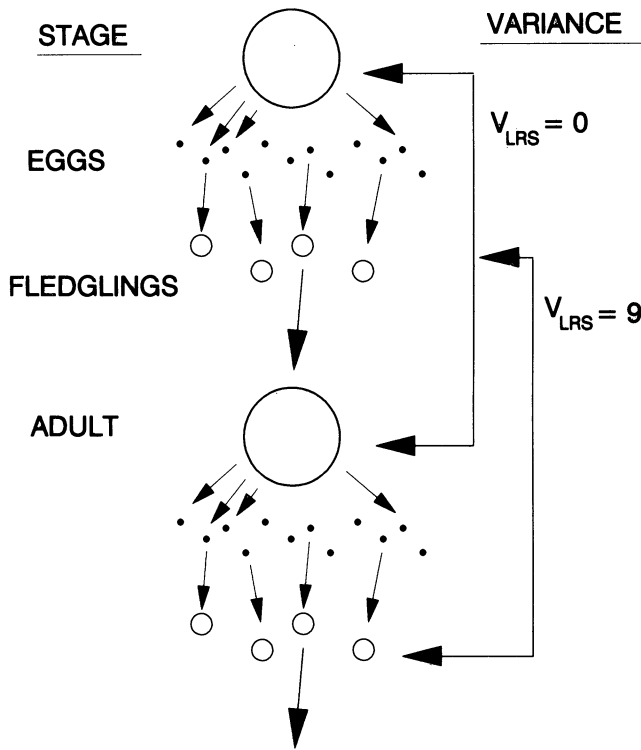
FIG. 1.—Variance of lifetime reproductive success (V_{LRS}) among individuals in a population is a function of the chosen end points of the life cycle. Here every adult individual in a hypothetical population produces 10^2 eggs that result in 10 fledglings and eventually one adult and so on; V_{LRS} among adults from generation to generation is zero. Since only one of 10 fledglings produces an adult that in turn produces 10 fledglings, V_{LRS} among fledglings is nine.

X_{LRS} is two, or pX_{PRS}, where, in this case, $p = 2/X_{PRS}$. A corrected estimate of V_{LRS} can also be obtained through an extension of this idea.

Expressions (1) and (2) contain formulas for the mean and variance of LRS in terms of the mean and variance of fecundity within a breeding season. Fecundity must be measured as the production of individuals at the end point of the reference cycle. Thus, we need to obtain an expression for X_F and V_F in terms of a combination of measures of fitness that are observable, coupled with subsequent random mortality that reduces the expected X_{LRS} to two; this must be accomplished in such a way that entire individuals live or die: the proper model for this mortality—from point of observed measure of fecundity to recruited breeder—is another stochastic process in which each individual lives or dies with a probability p. This process can be viewed as a series of Bernoulli trials with mean

$$p = 2/X_{PRS}$$

and variance

$$V_p = p(1 - p).$$

As before, this process can be viewed as a random sum.

Consider the random variable $\mathbf{M}$, measured fitness (e.g., clutch size), with mean X_M and variance V_M, and the random variable $\mathbf{S_i}$, survival of individual i from the measured stage of the life cycle to breeding status, with mean p and variance $p(1 - p)$. Then the sum

$$\sum_{i=1}^{\mathbf{M}} \mathbf{S_i}$$

is the sum over the measured fitness of the random variable survival of each unit propagule. This is the fecundity, as defined above, for that breeding season or bout. Again as above, if we assume the survival probabilities of offspring are independent of each other and of the litter size, then this stochastic process has mean and variance

$$pX_M \quad \text{and} \quad p^2 V_M + X_M V_p,$$

respectively. Substitution of these expressions in equations (1) and (2) leads to overall formulas for the mean and variance of LRS in terms of observable variables, X_L, V_L, X_M, and V_M, and a measure of survival rate, p, which can be adjusted so that overall X_{LRS} is two. In particular,

$$X_{LRS} = pX_L X_M \tag{3}$$

and

$$V_{LRS} = p^2 X_M^2 V_L + p^2 X_L V_M + X_L X_M V_p. \tag{4}$$

If one did have information on survival rate to adulthood, then p and V_p ought to be replaced by the appropriate empirical estimates of these two parameters.

Numerical Solution

A major restriction of these equations is the assumption that the distribution of reproductive success is independent of age and that every individual starts breeding at the same age. Neither of these may be true; in birds, for example, fecundity frequently increases with age (Saether 1990). In a species such as the lesser snow goose, first breeding may occur at ages two through four, and average production of fledglings increases through age seven. Therefore, we developed a computer program to obtain estimates of the distribution, and hence variance, of LRS for such situations.

In this approach the exact distribution of offspring is found deterministically. This is implemented by computing the distribution of offspring for individuals in their first year of breeding using the appropriate fecundity schedule. The survival schedule is consulted to obtain the fraction that die; the lifetime distribution of fecundity of those dying is known and saved. The fraction that survive are in

their second year of breeding; the appropriate fecundity schedule is used to appor-
tion their total fecundity over the first 2 yr. Then survival rate for the second year
is used to determine the fraction of these advancing to a third year of breeding and
the fraction whose lifetime fecundity is added to the distribution of fecundity of
those dying after the first year; this procedure is continued iteratively. Eventually,
the lifetime distribution of offspring is found for the entire cohort. Because the
distribution of offspring is usually in terms of eggs, fledglings, and so forth, Ber-
noulli trials must again be used to estimate reproductive success for an entire life
cycle. As above, survival of offspring can be adjusted so that a cohort just re-
places itself. This is done by taking the fraction of individuals producing N sub-
adult offspring and computing the proportion that would have had each of the N,
$N - 1$, $N - 2$, and so forth, possible numbers of adult offspring given the
necessary survival rate and a binomial expansion. Because a different fecundity
distribution may be used for each year of breeding and the fraction of individuals
breeding may be varied from zero to one, this approach allows more realistic
estimates of the distribution of lifetime fecundity than does the analytical ap-
proach. It also, however, requires more data. Once the lifetime distribution of
adult progeny is found, the variance can be computed.

RESULTS AND DISCUSSION

The equations derived above enable one to obtain estimates of variance among
individuals in LRS given information on survival rate, fecundity, and so forth.
However, two major assumptions are common to the analytical equations as well
as to the deterministic computation. First, because fecundity and life span are
sampled from single distributions, we assume that there is no selection among
individuals. Second, we assume that there is no covariance between survival rate
and fecundity or among fecundities in succeeding years. If significant selection
or covariances of this sort occur in natural populations, then there might be a
systematic bias in the estimates obtained using our methods. Whether the bias
would be positive or negative would depend on the sign of the covariance. A
positive covariance between survival rate and fecundity or among successive
fecundities across years is equivalent to differential selection (phenotypic or ge-
netic; see, e.g., Arnold and Wade 1984) among individuals. A negative covariance
would be interpreted as a cost of reproduction. Positive and negative covariances
would result in our equations underestimating and overestimating, respectively,
the true variance. We know of no compelling evidence for the generality of such
covariation in nature.

Following this line of reasoning, one might view our results as producing a
null, stochastic model (without selection), somewhat similar to an idea of Suther-
land (1987). Observed data on variance of LRS could be compared to that esti-
mated with our models, and inferences about selection might be made. Unfortu-
nately, however, large sample sizes would be necessary to achieve any power.
Some forms of selection (e.g., sexual) might be expected to increase variance of
reproductive success, but others, such as some forms of stabilizing selection,
could reduce it. In addition, our models also could be used to test for the types

TABLE 1

Observed and Analytical Estimates of Variance of Lifetime Reproductive Success (V_{LRS}) from a Long-Term Study of a Natural Population of the Mexican Jay (Aphelocoma ultramarina)

Life Cycle	Observed* V_{LRS}	Demographic Parameters				Analytical V_{LRS}
		X_L†	V_L†	X_F‡	V_F‡	
Nestling to nestling	12.32 (4.84–21.07)	.39	1.87	2.07	2.85	9.12
Breeding adult to breeding adult	2.11 (1.07–3.29)	3.35	5.61	.29	.41	1.86

* Bootstrapped 95% confidence interval in parentheses.
† Mean and variance of reproductive life span.
‡ Mean and variance of fecundity.

of covariance between reproduction and life span discussed above. Again, one might test for such effects using cases in which variance of LRS is known; the observed variance could be compared to the variance predicted using the equations above. Such data also could be used to test all the various assumptions of our equations. Unfortunately, few such data exist.

We were unable to locate any published examples of both actual distributions of LRS through a complete, well-defined life cycle, as well as distributions of year-to-year survival and yearly distributions of some measure of reproductive success. A few long-term studies clearly involve such data (e.g., Clutton-Brock 1988), but published complete data sets are apparently few. However, we were able to use unpublished data from a long-term (22-yr) study of behavior and demography of a Mexican jay population from southeastern Arizona (Brown and Brown 1981). A set of data was available that included life spans, yearly numbers of nestlings produced, and yearly numbers of recruited breeders produced for individuals from the population. From this single set of data we were able to estimate the actual mean and variance of LRS for the jays, as well as the means and variances of breeding life span and yearly fecundity. We were able to do this for both a nestling-to-nestling life cycle and a breeding recruit–to–breeding recruit cycle. From the estimates of the mean and variance of reproductive life span and yearly fecundity, we computed an analytical estimate of V_{LRS} for comparison with the observed value (table 1).

As discussed above, variance of reproductive success is a function of the life cycle chosen as reference; for these data the nestling-to-nestling cycle encompasses approximately five to six times as much variance as the adult-to-adult cycle. For both cycles, the analytical estimate of V_{LRS} underestimates the observed variance but is well within the empirical 95% confidence interval obtained by bootstrapping (1,000 times) over individuals. The magnitude of the underestimation is 14% and 35% for the adult and nestling cycles, based on sample sizes of 62 and 329, respectively. Although the sample for the nestling cycle is substantial, it includes a large majority of nestlings that die long before obtaining breeding status. Our results seem reasonably accurate, given a sample size of one study. The bootstrap result suggests the underestimation is consistent with sampling error; however, the result is also consistent with a moderate amount of positive
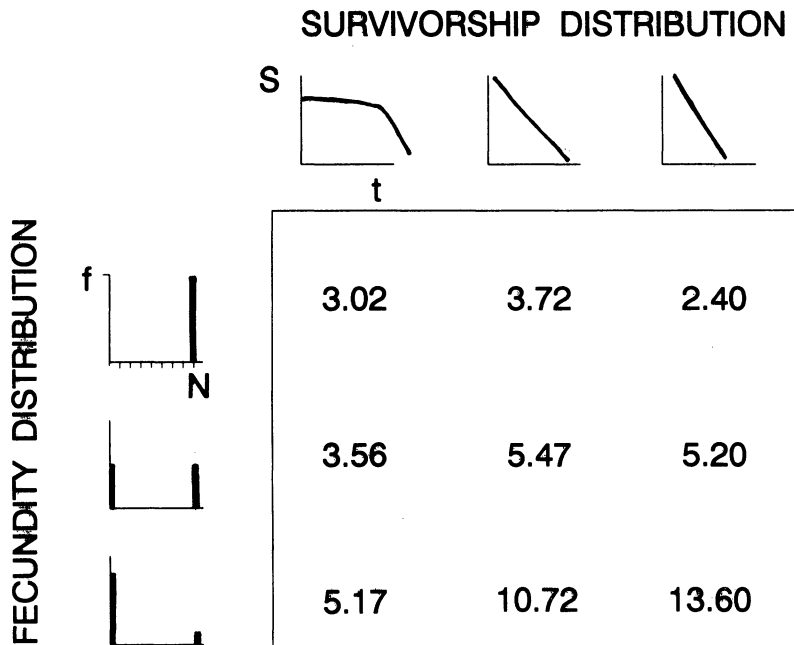
SURVIVORSHIP DISTRIBUTION

FIG. 2.—Expected variance of lifetime reproductive success (V_{LRS}) for hypothetical populations as a function of varying survival rate and yearly fecundity distributions. Year-to-year survival (S_x) of breeding individuals decreases across the top; *left,* Type I survival schedule with S_x of 0.9; *middle,* Type II schedule with S_x of 0.5; *right,* extreme Type II with S_x of 0.2. Fecundity distribution within years becomes more skewed from top to bottom; *top,* all individuals produce identical numbers of offspring; *middle,* 50% probability of complete nest failure; *bottom,* 80% probability of nest failure. Probability of survival of offspring to adulthood is adjusted with Bernoulli trials so that E(LRS) = 2.

covariation in the population, involving survival rate and fecundity, as explained above.

Given analytical equations for variance in reproductive success, one can investigate how different patterns of life expectancy and fecundity affect patterns of this variance. For example, in figure 2 we examine the interaction of three more or less realistic patterns of survival for vertebrate organisms with three patterns of fecundity. From left to right across the top of the figure are life expectancy distributions showing increasing mortality during the period of reproduction. The first is an example of Deevey's (1947) Type I survival curve; the second and third are Type II curves (exponential distributions). On the ordinate are increasing patterns, from top to bottom, of variance of within-year reproductive success. At the top all individuals produce the same number of offspring; next is a bimodal distribution with equal numbers of individuals succeeding and failing; at the bottom a minority of the population produces all the offspring. These patterns might apply to males of monogamous, mildly polygynous, and lekking species, respectively. Binomially distributed survival was applied to the offspring so that all combinations of patterns resulted in an expectation of two recruits per breeding

individual. The corresponding variance among individuals in these theoretical populations are shown in the figure. Variance of LRS increases as the distribution of within-year reproductive success becomes heteroscedastic; this is most pronounced for organisms with higher variance of survival rate. These results are not counterintuitive but do illustrate how the analytical equations might be used to investigate the effects of alternative life-history traits on, for example, effective population size.

As a more empirically based example of the use of the analytical equations, we present estimates in table 2 of variance of LRS for four species of birds with varying life-history patterns. These results are based on data reported in the literature from long-term studies of natural populations. In all cases, the variance is for the life cycle defined as first-time breeding adult to first-time breeding adult. Two of the species are extremely long-lived pelagic birds with single-egg clutches. The other two are relatively short-lived species, but their ratios of variance to mean annual fecundity differ strikingly. Interestingly, when mean productivity is adjusted to two, the variances are rather similar for the four species. Thus, life-history patterns this different do not greatly affect variance of lifetime reproduction. The expected variances, however, are approximately twice the mean reproductive success—not consistent with a binomial or Poisson process.

It is straightforward to use the estimates of variance to compute effective population size. For example, if the size of a population is approximately constant, then

$$N_e = (4N_c - 4)/(V_{LRS} + 2)$$

(Crow and Kimura 1970, table 7.6.4.1, separate sexes). If N_c, census size, is large, then

$$N_e/N_c \approx 4/(V_{LRS} + 2).$$

For the prairie warbler data presented in table 2, V_{LRS} was estimated as 4.45 when the average progeny number was 2.0. For this example, then, the ratio of effective to census size is about 0.62; the effect of the demography and fecundity schedules is to reduce the effective size of the population by 40%. Because the variance used here was for an adult-to-adult life cycle, this ratio applies to a census of adults. If the census were taken in terms of eggs, immatures, and so on, one would have to use the appropriate variance of LRS for the cycle corresponding to the empirical census count. One could also modify the formulas in Crow and Kimura (1970) and Crow and Denniston (1988) for more complicated situations in which population size is not constant, different effective numbers are needed, or the sex of offspring is known.

In addition to the analytical solution, we have described a deterministic estimate of the distribution of LRS that allows one to relax the assumptions of a single age of first breeding and a constant fecundity schedule throughout a cohort's lifetime. The method requires a computer program and more data than are usually obtained. However, the additional details of the demography schedules may appreciably affect estimates of variance of LRS. As an example, consider the lesser snow goose (table 3). In this species only half the individuals start

TABLE 2

EXPECTED VARIANCE AMONG INDIVIDUALS OF LIFETIME REPRODUCTIVE SUCCESS FOR FOUR SPECIES OF BIRDS

SPECIES	BREEDING LIFE SPAN		ANNUAL FECUNDITY		Progeny Survival Rate	$\hat{V}_{LRS}$	SOURCE
	$\hat{X}_L$	$\hat{V}_L$	$\hat{X}_F$	$\hat{V}_F$	$(\hat{p})$		
Yellow-nosed albatross (Diomedea chlororhynchus)	10.65	74.97	.53*	.25	.35	4.27	Weimerskirch et al. 1987
Northern fulmar (Fulmarus glacialis)	19.72	111.08	.41*	.24	.25	2.94	Hatch 1987
Eastern screech owl (Otus asio)	2.65	3.98	4.43†	.71	.17	3.98	Van Camp and Henny 1975; Ricklefs 1983
Prairie warbler (Dendroica discolor)	2.80	4.30	2.47*	3.59	.29	4.45	Nolan 1978

* Fledglings.
† Eggs.

TABLE 3

ESTIMATES OF SURVIVAL AND BREEDING PROBABILITIES AND OBSERVED FREQUENCY DISTRIBUTION OF
FECUNDITY BY AGE FOR THE LESSER SNOW GOOSE (*ANSER CAERULESCENS*)

	AGE					
	0	1	2	3	4	4+
Survival probability	.46	.76	.76	.76	.81	.81
Breeding probability	.00	.00	.50	.86	1.00	1.00

	CLUTCH SIZE AT HATCHING							
	0	1	2	3	4	5	6	7
Age:								
2	3	0	3	9	3	1	0	0
3	4	4	6	17	29	11	1	0
4	12	2	8	25	25	14	5	0
5	5	1	4	22	37	35	3	2
6	3	1	3	24	36	25	10	0
7	4	0	2	11	35	21	3	0
Total	31	8	26	108	165	107	22	2

breeding at age two, 86% are breeding at age three, and all individuals have started to breed at age four (Cooke and Rockwell 1988); the mean clutch size increases from age two to seven and then remains approximately constant (Rockwell et al. 1983). One can ignore these subtleties and assume all individuals commence breeding at age two and that their fecundity distribution is constant with age and equal to the distribution pooled over ages. With those assumptions, the analytical estimate of V_{LRS} is 5.22, assuming the expectation of LRS is two. If instead, the actual distribution of LRS is computed using a variable age of onset of breeding and increasing fecundity with age, then one obtains an estimate of V_{LRS} of 6.82. For this example from a natural population, the effect of the complexities is to increase the variance by 30%.

The results obtained from both the analytical solution and the computer simulation are deterministic. They represent the expected variance of LRS for an infinite population assuming the distributions or moments used in the calculations are parametric values. Clearly this will not be the case for data derived from natural populations. Thus, it would be appropriate to have confidence limits on the estimates of V_{LRS} obtained with our methods. Unfortunately, this is not a simple problem because the sampling distribution for the variance (eq. [4]) is unknown. An alternative approach is to evaluate the robustness of the estimates by random sampling from a known distribution.

We investigated the effect of limited data on estimates of variance with a Monte Carlo simulation. We used an arbitrary but simple demographic schedule (table 4); life expectancy and offspring number in each of the years of life were stochastic variables with known distributions. The parametric expectation (1.126) and

TABLE 4

An Example of a Simple Demographic Schedule for Survival
and Breeding Propensity

Age (x)	Survival Probability (s_x)	Cumulative Survival (l_x)	Breeding Probability (b_x)
0	.50	1.00	0
1	.50	.50	1.0
2	.00	.25	1.0
3	. . .	0	. . .

Note.—For this schedule, probability of fecundity $P(F)$ for all
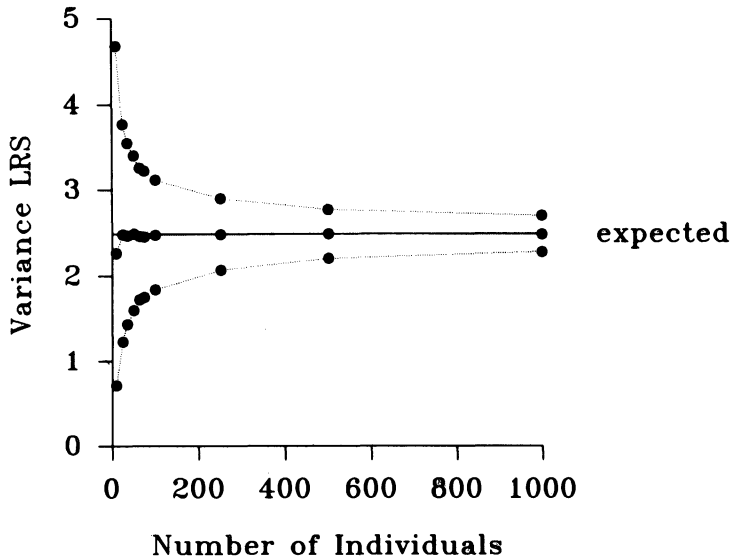numbers of offspring (0–3) is .25.

Fig. 3.—Empirical mean and 95% confidence intervals of variance of lifetime reproductive
success for simulated populations of varying sizes with the demographic parameters of table
4. Mean and confidence interval based on 1,000 Monte Carlo simulations at each population
size.

variance (2.490) of LRS are easily computed. One thousand iterations of variously
sized samples of individuals were drawn from the distributions, and an estimate
of V_{LRS} was computed from each sample; for the 1,000 estimates at each sample
size (10, 25, 35, 50, 64, 75, 100, 250, 500, and 1,000), the empirical mean and 95%
confidence interval for V_{LRS} are plotted in figure 3. For very small samples, 25
and fewer, estimates of variance of LRS may be off by a factor of two; for
samples up to 100 or so, estimates of variance may diverge from the parametric
value by about a third; as samples approach 500 to 1,000, 95% of the estimates
are within 10%–20% of the parametric value. Not surprisingly, relatively large

samples, by field study standards, are necessary to obtain estimates of variance with even a little precision.

Many field studies do not follow individuals for complete lifetimes. Rather a number of adults may be watched for several years, that is, through part of their potential life span, and a number of clutches will be observed. In such cases, the variable with the most limited sample size probably will have the greatest influence on the sampling error of V_{LRS}. As figure 2 indicates, both life expectancy pattern as well as fecundity distribution have a significant effect on V_{LRS}. It is clearly desirable to base estimates of V_{LRS} on samples of at least several score observations of individual year-to-year survival and an equal number of clutches. In addition, it is desirable to compute an explicit estimate of confidence through a bootstrap analysis or a Monte Carlo simulation such as the one described here.

APPENDIX

RANDOM SUMS AND PRODUCTS OF RANDOM VARIABLES

We have shown that for an iteroparous organism the lifetime reproductive success (LRS) of an individual is the sum of its reproductive successes for each of the breeding episodes that occur during its lifetime. Thus, the individual probability events, which result in the overall distribution of LRS of the population, are the sums, over the number of reproductive bouts, of the numbers of offspring produced during each bout, that is

$$\sum_{i=1}^{L} F_i ,$$

where L is the random variable representing number of reproductive episodes during the individual's lifetime and F_i is its fecundity in the ith breeding episode. If the F_i's are independent and identically distributed and are independent of L, then for the population of such individuals

$$V_{LRS} = X_F^2 V_L + X_L V_F .$$

In developing an algorithm for decomposing empirical estimates of V_{LRS} into variance components, Brown (1988) relied on Goodman's (1960) equation for the variance of the product of two random variables, for example L and F,

$$V_{LF} = X_F^2 V_L + X_L^2 V_F + Q(L, F) .$$

The last term represents joint variation. This equation is inappropriate for the problem of variance of LRS, however. The value of an individual probability event in a product of random variables formulation is the product of, say, lifetime L and fecundity F. Thus, for example, one sample event in this space is an individual lives 3 yr and has five offspring; the value of this event is 3×5, or 15. A possible biological interpretation of this event might be that the individual has five offspring in each of its 3 yr. Most real organisms,

however, produce different numbers of recruits in their various breeding attempts, simply because of yearly environmental variance. At any rate, a process that separately samples from a distribution of reproductive successes during each breeding episode will not have the same variance as one in which identical numbers of offspring are produced during each reproductive episode.

The magnitude of the difference in variance is seen in the comparison of the variance of a random sum versus Goodman's formula for the variance of a product of random variables, that is,

$$V_{\text{SUM}} = X_F^2 V_L + X_L V_F \quad \text{versus} \quad V_{LF} = X_F^2 V_L + X_L^2 V_F + Q(\mathbf{L}, \mathbf{F}).$$

Interestingly, the expectations of the two processes are identical, $X_L X_F$. The second term in the equation for the variance of the product of two random variables will be greater or less than the corresponding term for the variance of a random sum depending on the value of the mean lifetime (actually the number of breeding bouts). If this expectation is greater than one, then the first two terms of the product variance will exceed the actual variance and, in a variance components decomposition, result in the inference of a negative covariance, even if one does not exist. If the expectation of breeding bouts were less than one, then a positive covariance would be inferred.

Another way of viewing the difference between the two approaches is that the analytical random sum method starts with the assumption that the variance of reproductive success in the population is because of environmental variation common both among individuals and across years. In the product of random variables approach, an initial assumption is that the variance in the population is because of consistent among-individual differences and that there is no among-breeding-attempt variability within individuals. Thus, any actual within-individual among-year variation is interpreted as a covariance and not an environmental component of variation.

LITERATURE CITED

Arnold, S. J. 1986. Limits on stabilizing, disruptive, and correlational selection set by the opportunity for selection. American Naturalist 128:143–146.
Arnold, S. J., and M. J. Wade. 1984. On the measurement of natural and sexual selection: theory. Evolution 38:709–719.
Brown, D. 1988. Components of lifetime reproductive success. Pages 439–453 in T. H. Clutton-Brock, ed. Reproductive success. University of Chicago Press, Chicago.
Brown, J. L., and E. R. Brown. 1981. Extended family system in a communal bird. Science (Washington, D.C.) 211:959–960.
Clutton-Brock, T. H. 1988. Reproductive success. University of Chicago Press, Chicago.
Cooke, F., and R. F. Rockwell. 1988. Reproductive success in a lesser snow goose population. Pages 237–250 in T. H. Clutton-Brock, ed. Reproductive success. University of Chicago Press, Chicago.
Crow, J. F., and C. Denniston. 1988. Inbreeding and variance effective population numbers. Evolution 42:482–495.
Crow, J. F., and M. Kimura. 1970. An introduction to population genetics theory. Harper & Row, New York.
Deevey, E. S., Jr. 1947. Life tables for natural populations of animals. Quarterly Review of Biology 22:283–314.
Feller, W. 1968. An introduction to probability theory and its application. Vol. 1. 3d ed. Wiley, New York.
Goodman, L. A. 1960. On the exact variance of products. American Statistical Association Journal 55:708–713.
Hatch, S. A. 1987. Adult survival and productivity of Northern Fulmars in Alaska. Condor 89:685–696.
Newton, I. 1989a. Lifetime reproduction in birds. Academic Press, San Diego, Calif.

————. 1989*b*. Synthesis. Pages 441–469 *in* I. Newton, ed. Lifetime reproduction in birds. Academic
        Press, San Diego, Calif.
Nolan, V., Jr. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*. American
        Ornithologists Union, Lawrence, Kans.
Papoulis, A. 1965. Probability, random variables, and stochastic processes. McGraw-Hill, New York.
Partridge, L. 1989. Lifetime reproductive success and life-history evolution. Pages 421–440 *in* I.
        Newton, ed. Lifetime reproduction in birds. Academic Press, San Diego, Calif.
Ricklefs, R. E. 1983. Comparative avian demography. Current Ornithology 1:1–32.
Rockwell, R. F., C. S. Findlay, and F. Cooke. 1983. Life history studies of the lesser snow goose
        (*Anser caerulescens*). I. The influence of age and time on fecundity. Oecologia (Berlin)
        56:318–322.
Saether, B.-E. 1990. Age-specific variation in reproductive performance of birds. Current Ornithology
        7:251–283.
Sutherland, W. J. 1987. Random and deterministic components of variance in mating success. Pages
        209–219 *in* J. W. Bradbury and M. B. Andersson, eds. Sexual selection: testing the alterna-
        tives. Wiley, Chichester.
Van Camp, L. F., and C. J. Henny. 1975. The screech owl: its life history and population ecology in
        northern Ohio. North American Fauna 71:1–65.
Weimerskirch, H., J. Clobert, and P. Jouventin. 1987. Survival in five southern albatrosses and its
        relationship with their life history. Journal of Animal Ecology 56:1043–1055.

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