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# Effective Population Size and Lifetime Reproductive Success

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**Abstract:** *The mean and variance of lifetime reproductive success,  $E_{LRS}$  and  $V_{LRS}$ , influence the ratio of effective to census population size,  $N_e/N_c$ . Because the complete data needed to calculate  $E_{LRS}$  and  $V_{LRS}$  are seldom available, we provide alternatives for estimating  $N_e/N_c$  from incomplete data. These estimates should be useful to conservation biologists trying to compute the effective size of a censused population. An analytical approach makes assumptions regarding the process influencing offspring survival. We provide a method for examining the validity of those assumptions and show that particular violations can result in either over- or underestimates. When the assumptions are violated or when more data are available, we suggest estimating  $N_e/N_c$  using computer simulations of models based on individuals. We examine how such simulations can be used to estimate  $N_e/N_c$  using an individual-based model for Lesser Snow Geese (*Anser caerulescens*). We demonstrate that such estimates can be biased unless the simulations are based on complete cohorts and samples of known age. We show that because the estimate of  $N_e/N_c$  depends on the stage of the reproductive cycle used as a point of reference in the model, the census population size  $N_c$  must be based on the same stage to provide unbiased estimates of  $N_e$ .*

Tamaño poblacional efectivo y el éxito reproductivo vitalicio

**Resumen:** *La media y la varianza del éxito reproductivo vitalicio ( $E_{LRS}$  y  $V_{LRS}$ ) influyen el cociente entre tamaño poblacional efectivo y el tamaño censal  $N_e/N_c$ . Dado que los datos completos necesarios para calcular  $E_{LRS}$  y  $V_{LRS}$  están raramente disponibles, nosotros proveemos alternativas para estimar  $N_e/N_c$  a partir de datos incompletos. Estas estimaciones deberían ser útiles para los biólogos de la conservación que tratan de computar el tamaño efectivo de una población censada. Una aproximación analítica utiliza supuestos acerca del proceso que influye la supervivencia de la progenie. Nosotros proveemos de un método para examinar la validez de esos supuestos y mostramos violaciones particulares que resultan en sobreestimaciones o subestimaciones. Cuando los supuestos son violados o cuando más datos están disponibles, nosotros sugerimos estimar  $N_e/N_c$  utilizando simulaciones de modelos basados en individuos. Examinamos como tales simulaciones pueden ser usadas para estimar  $N_e/N_c$  utilizando un modelo basado en individuos para el ganso (*Anser caerulescens*). Demostramos que tales estimaciones pueden estar sesgadas a menos que las simulaciones estén basadas en cohortes completas y muestras de edades conocidas. Mostramos que dado que la estimación de  $N_e/N_c$  depende del estado del ciclo reproductivo usado como punto de referencia en el modelo, el tamaño poblacional censal ( $N_c$ ) debe estar basado en el mismo estado a efecto de proveer estimaciones de  $N_e$  no sesgadas.*

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## Introduction and Background

Effective population size ( $N_e$ ) is central to many issues in conservation biology. For example, effective population

size determines the rate of loss of heterozygotes in a population and is thus necessary for calculating a minimum viable population size that avoids inbreeding depression or that maintains specified levels of additive genetic variance (Lande & Barrowclough 1987). Because in many cases we either know the census population size ( $N_c$ ) and need the effective size, or we can compute

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a necessary effective size and need to project the census size, it would be useful to be able to convert between them (Nunney 1994).

Effective population size is known to be affected by factors such as sex ratio, mating system, fluctuations in population size, overlapping generations, and differences among families in the number of offspring recruited into the population. The potential effect of the last factor is clear in Crow and Kimura's (1970) formulation (EQN 7.6.2.17 in Table 7.6.4.1):

$$N_e = \frac{(N_{t-2} \cdot \bar{k}) - 2}{\bar{k} - 1 + (V_k/\bar{k})}, \quad (1)$$

where  $N_{t-2}$  is the census size of a closed population with non-overlapping generations at time  $t-2$  and  $\bar{k}$  and  $V_k$  are the mean and variance of recruited progeny per parent. Although this formulation assumes that sexes are separate, it does not assume that their contributions to  $\bar{k}$  and  $V_k$  are equal. If we assume that the population size is not changing rapidly and is reasonably large, so that  $N_t \cong N_{t-2} \gg 2$ , and if we define  $N_t$  as the census size of the population,  $N_c$ , we can rewrite equation 1 as

$$\frac{N_e}{N_c} \cong \frac{\bar{k}}{\bar{k} - 1 + (V_k/\bar{k})}. \quad (2)$$

The ratio of effective to census population size clearly depends on the mean and variance of recruited progeny per parent. Although this formulation is based on non-overlapping generations, the results of Hill (1972, 1979) show that the dependency is more general. He demonstrated that the effective size of a population with overlapping generations is equal to that of one with nonoverlapping generations that has the same number of individuals entering the population each generation and the same variance in lifetime reproductive success. Lande and Barrowclough (1987) note that the mean and variance of lifetime reproductive success must be used for  $\bar{k}$  and  $V_k$  when estimating  $N_e$  for populations with overlapping generations.

Unfortunately, the mean and variance of lifetime reproductive success are usually poorly known, if known at all, because it is difficult to obtain complete lifetime information on the reproductive success of members of natural populations (Barrowclough & Rockwell 1993). Most investigations provide only annual estimates of adult survival and reproductive success, usually measured simply as clutch, brood, or litter size. Although these may be adequate for investigations of short-lived organisms with non-overlapping generations, they are inadequate for longer-lived species. Few published empirical studies provide estimates of the rate at which the offspring are recruited into the population as breeding adults, and still fewer provide variances for those rates. Most studies implicitly assume a Poisson distribution of offspring recruitment, although available data suggest this is a poor assumption (Barrowclough & Rockwell

1993). For many birds, for example, the variance of lifetime reproductive success is greater than the mean. Not accounting for this would lead to a biased overestimate of  $N_e$ .

We show that it is possible to generate reliable estimates of the ratio of effective to census population size, even in the absence of information on recruitment rates, by combining the means and variances of breeding life expectancy and some measure of annual reproductive success. Of course, certain assumptions must be made, but we discuss both how violations of the assumptions can be detected and the effect of such violations on the estimate. We present an alternative, computer-model approach to estimating this ratio when those assumptions are not likely met and more data are available. Using this individual-based model, we discuss several additional limitations that must be considered when estimating  $N_e/N_c$  with any method.

## Estimation of $N_e/N_c$ When Only Means and Variances Are Known

### Constant and Independent Survival of Offspring

Let  $X_L$  and  $V_L$  be the mean and variance of breeding life expectancy. Let  $X_M$  and  $V_M$  be the mean and variance of some easily measured component of fecundity (such as clutch size in birds). Finally, let  $p$  and  $V_p$  be the probability and variance that one unit of that observed measure of fecundity (such as an egg) reaches breeding age. Barrowclough and Rockwell (1993) showed that, when they are independent, these estimates can be combined to form both the expectation and the variance of lifetime reproductive success:

$$E_{LRS} = p \cdot X_L \cdot X_M \quad (3)$$

$$V_{LRS} = p^2 \cdot X_M^2 \cdot V_L + p^2 \cdot X_L \cdot V_M + X_L \cdot X_M \cdot V_p. \quad (4)$$

These estimates can be entered into equation 2, as  $\bar{k}$  and  $V_k$  respectively, to obtain the ratio  $N_e/N_c$ . For simplicity, we have assumed that the parameters in equations 3 and 4 are the same for males and females. When they are not, and especially when the differences result from the mating system, more-complex equations must be used (Nunney 1991, 1993).

The mean and variance of  $p$ , offspring survival to adulthood, are often the least well-known estimates available in studies of natural populations (Newton 1989). In part, this is due to difficulties in monitoring young (and often small) stages of the life cycle and to the failure of new recruits to return to natal areas for breeding (dispersal). As a first approximation, we assume that the survival of one unit of fecundity to breeding age is a Bernoulli process in which an "offspring" ei-

ther lives with probability  $p$  or dies with probability  $1 - p$ . Further, we assume that offspring survival is independent both within and between families and can thus be viewed as a set of Bernoulli trials with constant  $p$ . (Tossing a coin is a Bernoulli process; independently tossing several identical ones would be a set of Bernoulli trials with constant  $p$ .) Under these assumptions variance in offspring survival to adulthood is  $V_p = p \cdot (1 - p)$ , and equation 2 can be rewritten as

$$\frac{N_e}{N_c} \cong \frac{p \cdot X_L \cdot X_M}{(p \cdot X_L \cdot X_M)^{-1} + \frac{p^2 \cdot X_M^2 \cdot V_L + p^2 \cdot X_L \cdot V_M + p \cdot (1 - p) \cdot X_L \cdot X_M}{p \cdot X_L \cdot X_M}}, \tag{5}$$

which can be rearranged to

$$\frac{N_e}{N_c} \cong \frac{X_L \cdot X_M}{(X_L \cdot X_M)^{-1} + \frac{X_M^2 \cdot V_L + X_L \cdot V_M}{X_L \cdot X_M}}. \tag{6}$$

By letting  $k^* = X_L \cdot X_M$  and  $V_{k^*} = X_M^2 \cdot V_L + X_L \cdot V_M$  be, respectively, the mean and variance of reproductive success based on easily measured variables (Barrowclough & Rockwell 1993, equations 1 and 2), equation 6 can be recast in a form similar to that of equation 2:

$$\frac{N_e}{N_c} \cong \frac{k^*}{k^* - 1 + (V_{k^*}/k^*)}. \tag{7}$$

Conveniently, the survival probability of the unit of fecundity ( $p$ ) has canceled from the equations. Under these conditions of independent offspring survival, then, the most difficult to obtain and least accurate variable involved in many studies of lifetime reproductive success is not required to calculate the ratio of effective to census population size.

Nolan's (1978) data on Prairie Warblers (*Dendroica discolor*) constitute an example, in which the mean and variance of reproductive lifespan are  $X_L = 2.80$  and  $V_L = 4.30$ , and those for reproductive success, measured as

number of hatchlings, are  $X_M = 2.47$  and  $V_M = 3.59$ . Assuming that survival of the hatchlings until they are recruited into the breeding population can be viewed as a set of Bernoulli trials with  $p = 0.29$ , the ratio of effective to census population size from equation 6 is  $N_e/N_c \cong 0.62$ . The accuracy of this estimates depends, of course, on whether the survival of one offspring is independent of that of other offspring, both within and between families.

**Non-Independent Survival of Offspring**

How can it be determined if among-offspring survival is completely independent? Moreover, how do departures from this ideal situation affect the estimates of  $N_e/N_c$ ? Finally, are there alternatives when offspring survival is not independent?

When offspring survival is independent both within and between families, the distribution of numbers of surviving offspring among families, each of which were initially the same size  $k$ , takes the familiar form of a binomial distribution (Fig. 1a). The variance of this distribution is  $V_{pfam} = p \cdot (1 - p) \cdot k$ , where  $k$  is the initial size of the family before any offspring mortality (Feller 1950). A separate binomial distribution and  $V_{pfam}$  can be calculated for each family size class in the population (for example,  $k = 4$  hatchlings, 5 hatchlings, etc.) It is important to note that the variance of the binomial distribution is not  $V_p$  from above; rather, it is the often more easily measured variance in the number of surviving offspring among families that began with the same initial size.

In many species, parents and offspring remain together until the young reach an age of demographic independence (Findlay et al. 1982). While together, and especially while under parental care, siblings may suffer a common fate. For example, some parents may lose all of their offspring while others lose few if any. In such

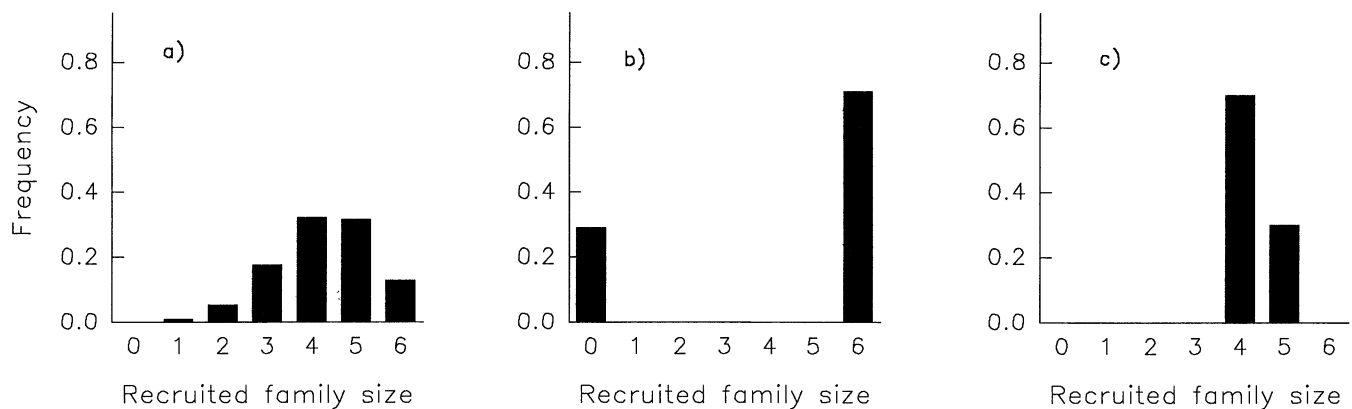


Figure 1. The distribution of recruited offspring from families of an arbitrary species with six egg clutches and an average survival of 0.29 per egg under binomial (a), bimodal (b), and clumped (c) family survival patterns.

cases, offspring survival would not be independent within families (it would be positively correlated), and the distribution of the number of surviving offspring among families with the same initial size would tend toward bimodality (Fig. 1b). Although mean individual offspring survival could retain, for example, a prairie warbler value of  $p = 0.29$ , the variance among families beginning with the same number of hatchlings would be greater than the binomial expectation ( $V_{\text{pfam}} > p \cdot (1 - p) \cdot k$ ).

Alternatively, families could all suffer similar mortality. Consider a scenario wherein all families lose the same proportion of their offspring. In effect, offspring survival within families would be negatively correlated. This would result in a more narrow and peaked distribution (clumped) of the number of surviving offspring per family (Fig. 1c). Again, mean offspring survival could remain  $p = 0.29$ , but the variance among families beginning with the same number of hatchlings would be less than the binomial expectation ( $V_{\text{pfam}} < p \cdot (1 - p) \cdot k$ ).

If data are available on the distribution of surviving offspring from families beginning at the same size, then they can be compared to expectations under the binomial distribution for each initial family size  $k$ , given an estimate of  $p$ . The comparison could be based on either the distributions or the variance. As in all cases of testing a null prediction with finite sample sizes, failure to reject the hypothesis that an observed distribution is binomial is not sufficient proof that the distribution is binomial nor that the underlying survival process is strictly independent. As long as sample sizes are reasonable, however, such a result would provide support for using equation 6 to estimate  $N_e/N_c$ .

If the data do not fit a binomial distribution, then use of equation 6 will lead to a biased estimation of  $N_e/N_c$  because the estimate of variance in lifetime reproductive success in equation 4 requires that offspring survival is strictly independent within and between families (Barrowclough & Rockwell 1993). If it is not, then a covariance term must be included when the variance of a random sums process is estimated (Papoulis 1965). When within-family offspring survival is positively correlated, as in the bimodal distribution example above, equation 4 underestimates  $V_{\text{LRS}}$  and equation 6 overestimates  $N_e/N_c$ . Conversely, when within-family offspring survival is negatively correlated, as in the example depicted in Fig. 1c, equation 4 overestimates  $V_{\text{LRS}}$  and equation 6 underestimates  $N_e/N_c$ . The direction and extent of the bias in  $N_e/N_c$  resulting from the inappropriate application of equation 6 depends on the precise nature of the nonindependence of offspring survival.

When the distribution of surviving offspring does not fit the binomial expectation, it may still be possible to use equation 6 by redefining (and reestimating) adult fecundity and offspring survival with respect to a different point of reference in the reproductive cycle. In our prai-

rie warbler example, our "easily measured" unit of fecundity was the number of hatchlings in a brood. Because entire life cycles must be considered when  $E_{\text{LRS}}$  and  $V_{\text{LRS}}$  and ultimately  $N_e/N_c$  are estimated (Barrowclough & Rockwell 1993), the survival probability  $p$  was the rate at which hatchlings became recruited breeding adults. Our concern thus far has been whether the survival process was strictly independent over this entire period. Because hatchling sibs share a single nest and are equally dependent on the same parents, it is not hard to imagine them suffering a common and non-independent fate.

If, on the other hand, we had used fledging as the point of reference for measuring fecundity, then  $p$  would refer to the rate at which fledglings became breeding adults, and we would concern ourselves with whether the survival process was independent over that shorter and later portion of the reproductive cycle. There is no necessary reason to suppose that just because survival is non-independent during an early portion of the period that it will also be non-independent during a later portion. Indeed, once the family unit dissolves, there is every reason to expect the fate of siblings to become independent. In this sense, the assumption of independent offspring survival may be more likely to be met if adult fecundity is defined with respect to the stage in the life cycle when offspring achieve demographic independence. At the very least, it is advisable when estimating  $N_e/N_c$  with equations like equation 6 to pick as late a stage in the reproductive cycle as possible as the point of reference for estimating adult fecundity and offspring survival.

### Estimation of $N_e/N_c$ with Known Distributions or Violated Assumptions

When the distributions of adult survival, adult fecundity, and offspring survival to recruitment are available (as opposed to just the means and variances of these variables), it is usually more efficient and informative to estimate  $N_e/N_c$  using individual-based models and computer simulation (Huston et al. 1988; DeAngelis & Gross 1992). Any distributional pattern is acceptable in these models, and no particular underlying survival process need be assumed. For example, if a bimodal distribution of offspring recruitment per family is known or suspected (Fig. 1b), all the offspring of  $p$  individual females can be tallied as surviving, while all those of  $1 - p$  females can be considered lost.

Individual-based models allow other problematic details of lifetime reproductive success to be considered realistically when  $N_e/N_c$  is estimated. For example, use of equation 4 to estimate variance in lifetime reproductive success requires that all individuals begin breeding

at the same age (Barrowclough & Rockwell 1993). It also requires that adult survival, adult fecundity, and offspring recruitment do not change over time and are independent of each other. Departures from each of these life-history ideals can be incorporated directly into the structure of an individual-based model so that estimates of  $N_e/N_c$  are based on our best understanding of a species' biology rather than on heroic assumptions. In all cases, the models can be simulated as a set of Monte Carlo trials that allow generation of the 95% confidence limits of  $N_e/N_c$  (Barrowclough & Rockwell 1993). Such limits greatly enhance the utility of the estimates.

We illustrate the use of an individual-based model in estimating  $N_e/N_c$  for the Lesser Snow Goose (*Anser caerulescens*). Such a model is particularly well suited to

this species because Snow Geese have a bimodal pattern of offspring survival across families during the interval from egg laying to hatching and also have a variable age of first breeding (Cooke et al. 1995). We use the model to examine three problems that may often be encountered when estimating or using  $N_e/N_c$  with data from real populations.

The model (Fig. 2) traces the lifetime reproductive performance of a cohort of fledgling female Snow Geese in a closed population. Performance at each of five age-specific stages of reproduction and survival (breeding propensity, clutch production, clutch survival, egg-to-fledgling survival, and adult survival) is assessed stochastically with reference to empirical distributions of success. We model the probability that an egg becomes a

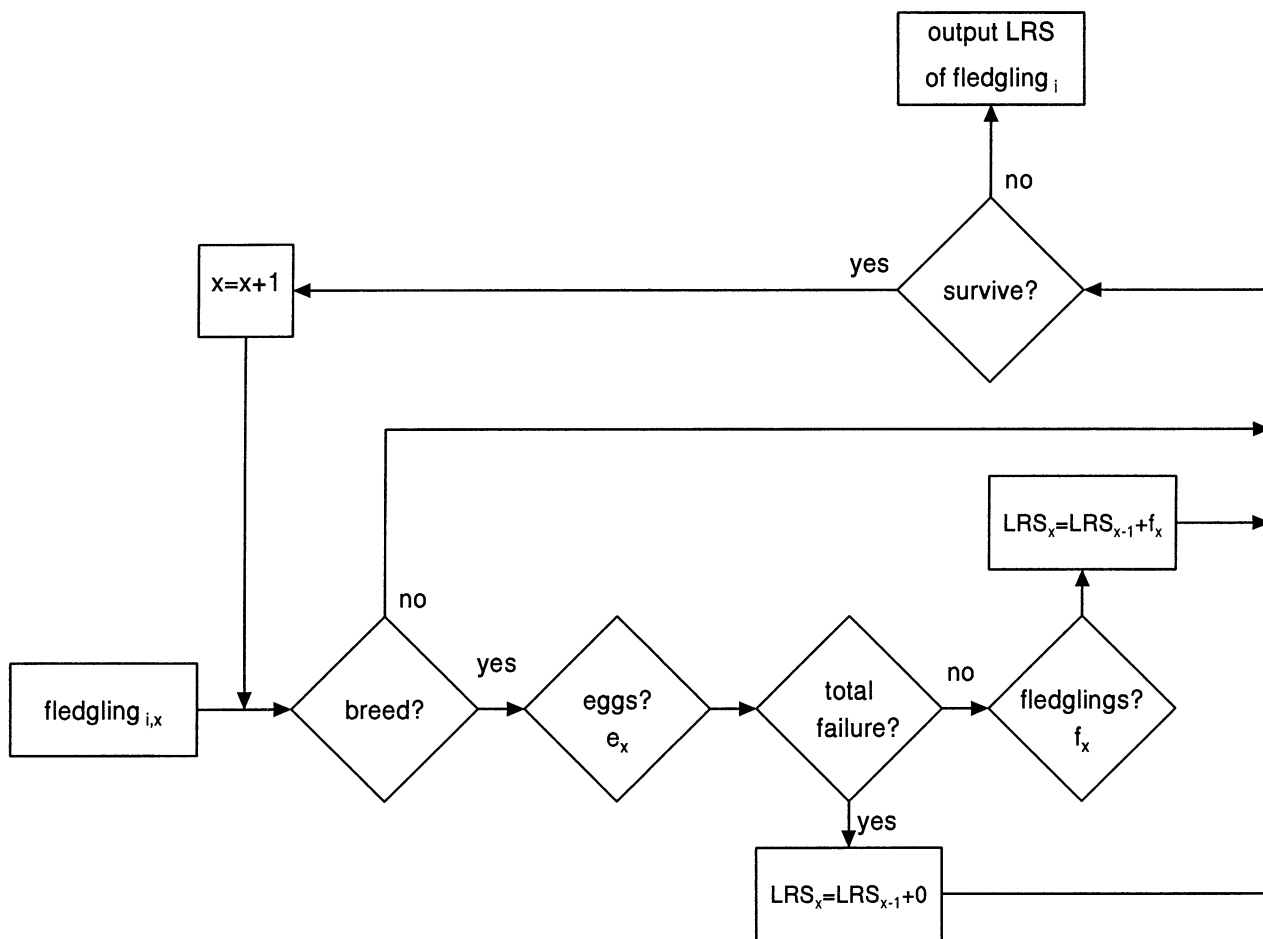


Figure 2. An individual-based model of lifetime reproductive success (LRS) for Lesser Snow Geese. The number of fledglings produced by each member of a cohort of fledglings is simulated using empirical distributions of age-specific breeding propensity (breed?), fecundity (eggs?), clutch survival (total failure?), fledgling production for successful nests (fledglings?) and survival by members of the original cohort (survive?). Two transitions are required between the production of eggs and the tallying of fledglings to account for the bimodal pattern of loss during incubation by this species. "Total failure?" operates on entire clutches and, therefore, individual eggs are not treated independently. "Fledglings?" acts independently on each egg both within and between clutches and reflects a true Bernoulli survival process.

fledgling with two separate variables to account for the bimodal pattern of loss of eggs during the portion of the reproductive cycles from nest initiation and hatch (Cooke et al. 1995). It is important to note that "clutch survival" affects all the eggs in a nest jointly (non-independently) and "egg-to-fledgling survival" affects each egg from successful nests independently (Rockwell et al. 1993).

Annual production of each of the original fledglings is defined as the number of fledglings she produces in a year and is summed over the years she survives. The mean and variance of these sums define the mean and variance of lifetime reproductive success for the sample cohort. One hundred thousand Monte Carlo trials of the simulation are used to estimate the parametric values and confidence limits of  $E_{LRS}$  and  $V_{LRS}$  for the cohort. It should be noted that, by tracking each member of the cohort throughout her life, the model directly incorporates age structure into the estimation of  $E_{LRS}$  and  $V_{LRS}$  and does so without assuming a stable age distribution. An alternative approach to age structure corrections in such estimates can be found in Emigh and Pollak (1979).

The distribution of lifetime reproductive success for a typical trial is depicted in Figure 3a. Clearly, a large portion of the cohort has zero reproductive success. This group includes both breeding-age adults that were unsuccessful and those members of the original fledgling cohort that died before reaching the minimum breeding age of two. Such individuals account for approximately 71% of the nonproductive members of the cohort. Substituting  $E_{LRS}$  and  $V_{LRS}$  as  $\bar{k}$  and  $V_k$  in equation 2, under the assumption, again, that female and male estimates are equivalent, we find that in *Anser caerulescens*  $N_e/N_c \cong 0.13$  for the complete life cycle measured from fledgling to fledgling.

#### Left-Censored Cohorts Overestimate $N_e/N_c$

The distribution of lifetime reproductive success for only those members of the original cohort that at least reached the minimum breeding age is depicted in Figure 3b. This figure is similar in form to those summarized for several species in Newton (1989); such distributions are often used to estimate  $E_{LRS}$  and  $V_{LRS}$ . But, the mean and variance of such left-censored distributions do not estimate  $E_{LRS}$  and  $V_{LRS}$  for the cohort because the lifetime reproductive success of all members of the cohort must be included (Barrowclough & Rockwell 1993). The effect of using means and variances of left-censored distributions of lifetime reproductive success to estimate the ratio  $N_e/N_c$  is profound. In this case, substituting the mean and variance from Fig. 3b into equation 2 generates  $N_e/N_c = 0.44$ . Because this is based on the partial life cycle from two-year-old to fledgling, it overestimates the true value of 0.13 by 239%.

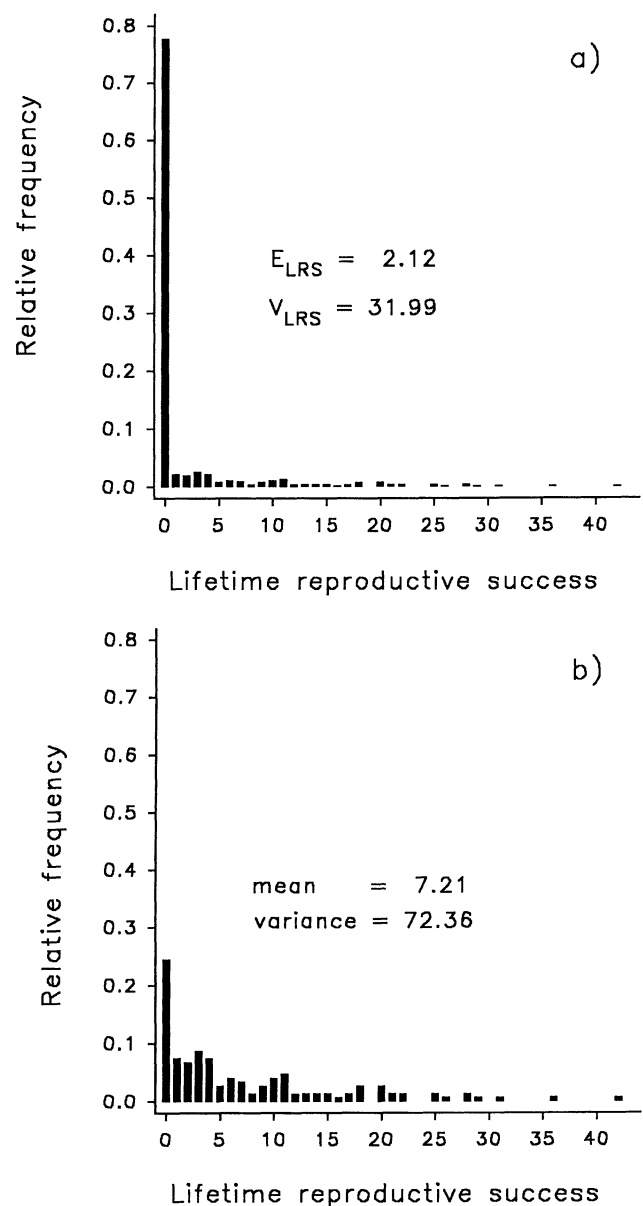


Figure 3. Distribution of lifetime reproductive success for Lesser Snow Geese: an entire cohort of 500 fledglings (a) and the subset of the cohort that survived to two years of age (b). Reproductive success is measured in terms of fledglings produced by individual fledglings. The mean and variance of (b) do not estimate expectation ( $E_{LRS}$ ) and variance ( $V_{LRS}$ ) of lifetime reproductive success for this species.

#### Unknown Age Samples Overestimate $N_e/N_c$

In an ideal situation, a field study of either lifetime or annual reproductive success would monitor the productivity of a true cohort (or several of them). If we were interested in the production of two-year-olds, for example, then all the members of the cohort should be two years old when monitoring begins (Barrowclough & Rockwell 1993). Owing either to inability to determine precise

ages of individuals or to time constraints (we should study the population before it goes extinct), a sample could contain breeding adults of unknown and mixed age. In such a circumstance, estimates of  $E_{LRS}$  and  $V_{LRS}$  from both long-term empirical monitoring and analytical combinations of annual demographic measures may be biased.

To examine the extent and pattern of such bias, we simulated the lifetime reproductive success of a cohort of adult Snow Geese whose initial age distribution was randomly drawn from the stable age distribution expected for this species. Lifetime reproductive success was measured as the number of two-year-olds produced by each individual. Figure 4 summarizes the results and compares them to estimates for a true cohort of two-year-old counterparts. The changes in  $E_{LRS}$  and  $V_{LRS}$  translate into a 13% increase in the estimate of  $N_e/N_c$  from equation 2.

Most species of birds and mammals display an initial increase in reproductive success with age. Studies of these taxa using unknown-aged samples will typically overestimate population growth rate (which is a function of  $E_{LRS}$ ) and underestimate the potential for inbreeding (which varies inversely with  $N_e/N_c$ ). The extent of these biases will depend on the precise form of the increase in age-specific breeding propensity and fecundity curves. In general, bias will increase directly with the initial steepness of those curves and will be greater in longer-lived species with stable or declining populations

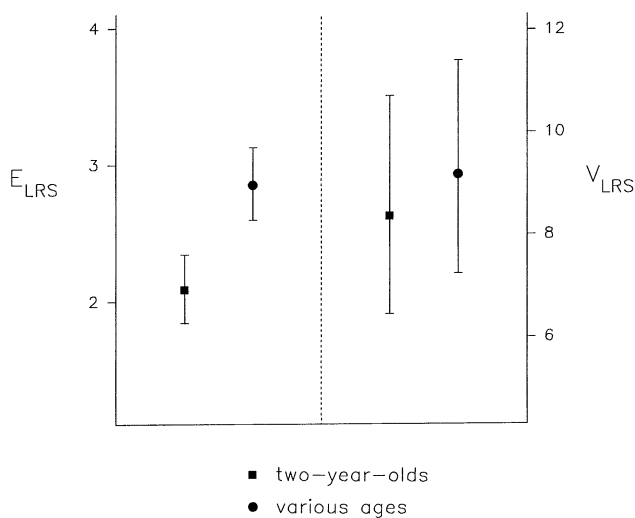


Figure 4. The effect of the age composition of a "cohort" of 500 individuals on the expectation ( $E_{LRS}$ ) and variance ( $V_{LRS}$ ) of the lifetime reproductive success of Lesser Snow Geese. The 500 individuals of various ages were drawn randomly from the stable age distribution of breeding-age adults. Means and 95% confidence limits are based on 100,000 Monte Carlo simulation trials.

because they will have lower proportions of young individuals.

### Estimates of $N_e/N_c$ Depend on the Point of Reference of the Life Cycle

We have estimated the lifetime reproductive success of a cohort of fledglings by using the total number of fledglings each member of the cohort produced. We also assessed the total number of two-year-olds produced by a cohort of two-year-olds. In principle, we could even enumerate the lifetime number of eggs produced by a cohort of eggs. Barrowclough and Rockwell (1993) showed that, under conditions of no selection, the  $E_{LRS}$  of a species does not depend on which stage of the life cycle is taken as the initial point of reference. On the other hand, they showed that  $V_{LRS}$  depends strongly on it.

This effect is illustrated for Snow Geese in Figures 5a and 5b, where  $E_{LRS}$  and  $V_{LRS}$  are given with respect to four different stages of the Snow Goose life cycle. In each case, the entire life cycle has been modeled with only the initial point of reference being changed. Clearly,  $V_{LRS}$  is higher when lifetime reproductive success is measured in terms of eggs produced by a cohort of eggs than when measured as goslings (hatchlings) produced by goslings, fledglings produced by fledglings, or two-year-olds produced by two-year-olds. When these estimates of  $E_{LRS}$  and  $V_{LRS}$  are substituted into equation 2 as  $\bar{k}$  and  $V_k$ , four different estimates of  $N_e/N_c$  are obtained (Fig. 5c).

Knowing that the census population size of Snow Geese is 20,000, for example, one might wonder which of the four ratios should be used to estimate the effective size of the population. On the surface, it might seem that each would yield a different estimate of  $N_e$ . But effective population size is a genetic parameter (Crow & Kimura 1970), and because our model assumes no genetic change between stages of the reproductive cycle,  $N_e$  should be independent of the point of reference in the life cycle. That is, there should be only one  $N_e$  for this closed population.

The resolution here is that, like the  $N_e/N_c$  ratio,  $N_e$  also changes with the point of reference. The census population size of Snow Geese based on eggs is not the same as that based on goslings, fledglings, or two-year-olds. Each  $N_e$  must be used with its appropriate  $N_e/N_c$  ratio. Given the life history characters of this species, 35,000 eggs are demographically equivalent to 28,875 goslings, 18,682 fledglings and 5380 two-year-olds.  $N_e$  for a population of that many Snow Geese is approximately 2394 (Fig. 5d).

### Conclusions

The mean and variance of lifetime reproductive success influence the ratio of effective to census population size

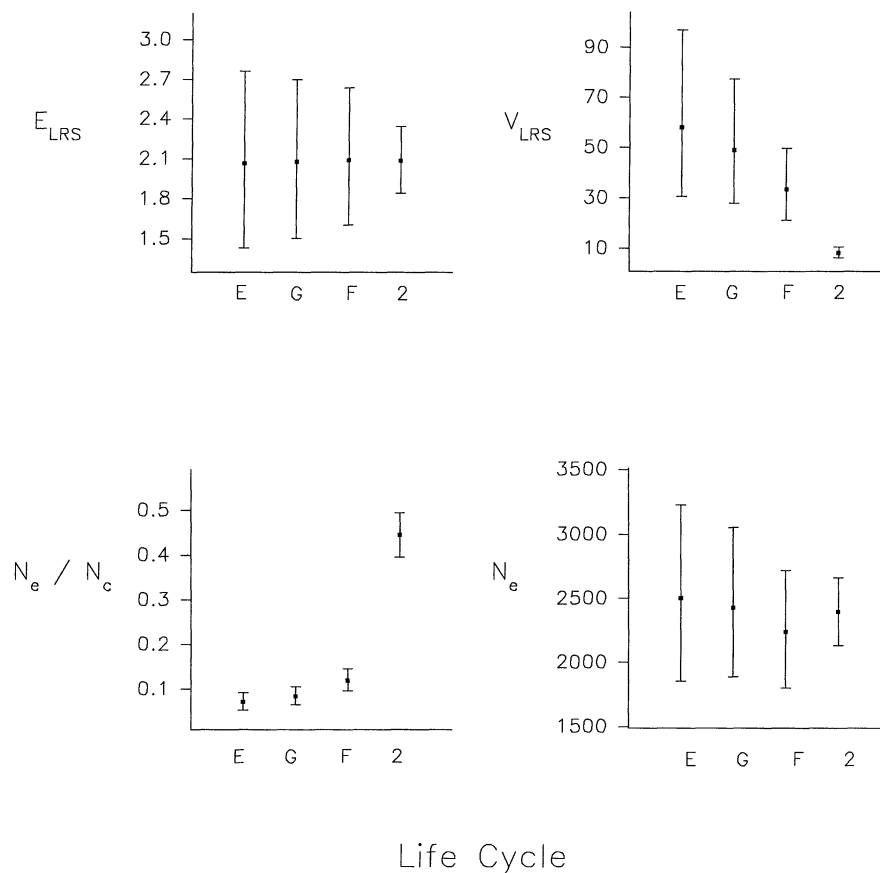


Figure 5. The effect of the life-cycle stage (E = egg, G = gosling, F = fledgling, 2 = two-year-old) used as a point of reference on the estimation of expectation of lifetime reproductive success ( $E_{LRS}$ ), variance of lifetime reproductive success ( $V_{LRS}$ ), ratio of effective to census population size ( $N_e/N_c$ ) and effective population size ( $N_e$ ) for cohorts of 500 Snow Geese. Means and 95% confidence limits are based on 100,000 Monte Carlo simulation trials.

( $N_e/N_c$ ). When  $V_{LRS}$  exceeds  $E_{LRS}$ , as it does for many organisms, estimates of  $N_e$  are biased overestimates if corrections are not made. Unfortunately, the complete data on lifetime reproductive success needed for such corrections are rare, and even data on annual performance are seldom complete. Often, for example, the survival or recruitment probability of some easily tallied unit of reproductive success (such as an egg) is missing. If we can assume that survival of those units is independent both within and between families, however, then we can estimate  $N_e/N_c$  using only estimates of the mean and variance of reproductive lifespan and annual measures of that easily tallied unit. Thus, unbiased estimates of  $N_e/N_c$  can be obtained without any knowledge of the mean or variance of this often difficult to obtain demographic parameter, as long as survival is strictly independent.

It is possible to test the validity of the independent survival assumption using data on the distribution of loss of reproductive potential among families. Depending on the pattern of such loss among families, it is even possible to determine the direction and possibly the extent of bias in the estimate. Biases will be less if the unit of reproductive success is chosen to correspond to a stage of the life cycle that is nearer the point of demographic independence, where continued survival depends more on the individual than its parents or sibs (on a fledgling, for example, rather than an egg).

When the distributions (rather than the means and variances) of adult survival, fecundity, and at least the offspring loss rates among families are known, it is possible to use individual-based models and Monte Carlo simulation to estimate  $N_e/N_c$  and its confidence limits. We illustrate this approach using data from a long-term study of Lesser Snow Geese.

We also use the model and the Snow Goose data to examine three general problems that must be considered when  $N_e/N_c$  is estimated by any method. First, entire cohorts must be used when estimating  $N_e/N_c$  or even the mean and variance by lifetime reproductive success. Left-censored data that excludes individuals not surviving to breeding age or surviving but not breeding overestimates  $N_e/N_c$ . Second, use of samples of unknown age results in overestimation of  $N_e/N_c$ . This effect should be greater in taxa that display an initial increase in age-specific reproductive success, that are long lived, and that have stable or declining populations. Third,  $N_e/N_c$  depends on the stage of the reproductive cycle chosen as a point of reference. Care must be taken to select the appropriate census size ( $N_c$ ) when using the ratio to estimate the effective population size ( $N_e$ ).

The effective population size can be estimated even in the absence of complete data. Although that estimate may be biased, it is our view that biased estimates are better than no estimates as long as the pattern and ex-



tent of potential bias is examined and conclusions or management recommendations are appropriately tempered.

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