Partitioning variance in reproductive success, within years and across lifetimes

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Abstract

Variance in reproductive success (σ_k^2, with k = number of offspring)—is the stuff of evolution. Evolutionary change by natural selection requires variation in offspring number, and the ratio $\phi = \sigma_k^2/u_k$ is the most important factor that reduces effective size (N_e) compared to census size (N). Various frameworks have been proposed to parse factors that contribute to σ_k^2, but none has focused on age-specific values of ϕ, which indicate the degree to which reproductive skew is overdispersed among individuals of the same age and sex. Here I show how an ANOVA framework can be used to partition σ_k^2 into between-age and within-age components. For seasonal reproduction, the between-age effect depends on mean age-specific fecundity (b_x, available in many published life tables), but few empirical data are available on the within-age effect, which depends on ϕ_x. Analysis of variance in lifetime reproductive success ($\sigma_{k\bullet}^2$) is more complicated; however, by using age at death rather than age as the treatment, the same ANOVA framework can be used to partition overall $\sigma_{k\bullet}^2$ into three components: between-treatment, within-treatment, and longevity. For both seasonal and lifetime reproduction, I also show how to quantify the expected contribution of random demographic stochasticity to these variance components. Analyses of empirical and simulated data illustrate the new methods and show that the largely-neglected within-age effect a) typically represents a substantial component of the overall variance in offspring number (even under a null model of random reproductive success), and b) can dominate the overall variance when ϕ_x>1.

Introduction

Variance in reproductive success—number of offspring, *k*, contributed to the next generation—is the stuff of evolution. Evolution that results from natural selection acting on heritable genetic variation requires variation in offspring number among individuals. Crow (1958) defined what has come to be known as the Opportunity for Selection as $I=\sigma_k^2/(u_k)^2$, where u_k and σ_k^2 are the mean and variance in offspring number: for a given mean fitness, selection has more scope within which to operate when σ_k^2 is large. In all finite populations (which is to say, all real populations in nature), genetic drift also contributes a random component to evolution that is inversely proportional to the effective population size, N_e. N_e is generally less (sometimes a great deal less) than the census size, *N*, and the most important factor that reduces N_e compared to *N* is the ratio of variance to mean offspring number, $\phi = \sigma_k^2/u_k$. This term appears in the denominator of demographic formulas for calculating N_e (see next section), so N_e is reduced when σ_k^2 is large compared to u_k (i.e., when variance is overdispersed compared to the random Poisson expectation).

Although discrete-generation models are the simplest and most tractable, most real species are age or stage structured, so it is important to consider two different frameworks for measuring reproductive success: within time periods, and across lifetimes (quantified as lifetime reproductive success, or *LRS;* aka lifetime reproductive output, van Daalen and Caswell 2017). Many species have strongly seasonal (birth-pulse) reproduction, in which case all reproduction can be considered to occur at integer ages around individual birthdays (Felsenstein 1971; Caswell 2001), and that is the model considered here. Every time period (hereafter assumed to be years), all mature adults have an opportunity to reproduce. In this case, one can measure the mean and variance among all adults reproducing in one year and use those values to calculate annual *I* and annual effective size, which in this case would be the effective number of breeders, N_b. For seasonal reproduction, two systematic components contribute to the overall variance, σ_k^2: an among-age effect, and a within-age effect. The among-age effect depends on how expected reproductive success varies with age, which is reflected in the vector of age-specific expected fecundity (b_x) values from a standard life table. The within-age effect depends on $\phi_x = \sigma_{k,x}^2/u_{k,x}$ = the ratio of variance to mean offspring number for individuals of age *x*.

For lifetime reproduction, the relevant metric is variance in *LRS*, $\sigma_{k\bullet}^2$ (Hill 1972; Brown 1988; Tuljapurkar et al. 2020). Lifetime $\sigma_{k\bullet}^2$ is affected by these within- and among-age effects, as well as another factor: longevity. All else being equal, individuals that live longer have more opportunities to reproduce, and this increases disparity in lifetime offspring number among individuals and increases $\sigma_{k\bullet}^2$. Caswell (2011) and van Daalen and Caswell (2017) use the term "Markov chains with rewards" to describe the random aspects of this process of accumulating *LRS*, and variation in longevity can be the dominant factor contributing to variance in *LRS* (e.g., Newton 1989). Furthermore, in many species (especially ectotherms with indeterminate growth) fecundity increases with age, in which case individuals receive an additional bonus for surviving to older ages.

In the AgeNe model, Waples et al. (2011) showed how to calculate expected lifetime $\sigma_{k\bullet}^2$ and generational N_e under Hill's (1972) model, which assumes stable age structure and independence of survival and reproduction over time. AgeNe relies on age-specific survivals and fecundities from a life table, and the vector of ϕ_x values that capture the within-age component of variation in reproductive success. However, two obstacles currently limit the ability to fully utilize this approach. First, although published life tables are available for

numerous species from a wide range of taxa (Fung and Waples 2017 used data for 78 animal and plant species with birth-pulse reproduction), data for the key age-specific parameter ϕ_x are rarely published. As a consequence, researchers generally must either a) assume that $\phi_x = 1$ for each age and sex, which is equivalent to assuming random reproductive success among individuals of the same age and sex (e.g., Wang et al. 2010; Waples et al. 2013), or b) explore the consequences of assuming a range of hypothetical values for ϕ_x (e.g., Waples et al. 2018a). General patterns of how ϕ_x varies among species and among ages within species are largely unknown.

The second obstacle is that no method has been developed that would allow researchers to systematically explore the relative importance of the two factors (the within-age and among-age effects) that determine the seasonal variance in reproductive success or the three factors (these two, plus longevity) that determine lifetime variance in reproductive success. Over the past several decades, several frameworks have been proposed for partitioning *LRS* into different components (Arnold and Wade 1984; Brown 1988; Broekman et al. 2021), but none of these has focused on the component that derives from variance in offspring number among individuals of the same age and sex. This is an important limitation; as shown below, this component of reproductive variance is generally a substantial fraction of the overall variance even when it is caused entirely by random stochasticity, and it can dominate the overall variance when same-age individuals have different expectations of reproductive success.

This paper has two main objectives, designed to address these two major obstacles. First, I describe a simple ANOVA-like analytical framework within which researchers can partition variance in seasonal reproductive success into within-age and between age effects, and can partition variance in *LRS* into within-age, between-age, and longevity effects. In addition, analytical methods are developed that allow researchers to calculate what fraction of these variance components can be attributed to random stochasticity in reproduction and survival.

The second objective is to highlight the importance of the neglected within-age component to the overall variance. Modern molecular tools and improved methods for parentage analysis make it easier than ever to collect empirical data on variance in offspring number. Understanding the relative magnitude of between-age and within-age effects should lead to richer insights into mating systems and reproductive biology, as well as an increased ability to predict evolutionary responses to environmental changes that can affect fitness.

Methods

See Table 1 for notation and definitions of terms. The treatments here assume a single, closed population and, except as noted, deal with population parameters (u_k, σ_k^2) and reflect an exhaustive inventory of the population.

DEMOGRAPHIC MODEL

The focal population is assumed to be iteroparous, with separate sexes. Analogous methods apply to both males and females; here for simplicity I consider data for a single sex, nominally female. In the discrete-time, seasonal reproduction model, age is indexed by x. At age x, each individual produces on average b_x offspring and then survives to age x+1 with probability v_x. Age at maturity (defined as the first age with b_x>0) occurs at age α and maximum age is ω. Newborns (age 0) do not reproduce, so b_x is scaled to production of offspring that survive to age 1, at which point they can be enumerated. Cumulative survival from age 1 through age x is $l_x = \prod_{i=2}^{x} v_{i-1}$, with l_1=1. In a constant population with each birth cohort consisting of N_1 yearlings, the expected number of individuals of age x alive at any given time is

$E(N_x) = N_1 l_x$, and expected total census size is given by $E(N_T) = \sum E(N_x) = N_1 \Sigma\, l_x$. Because we are interested in reproductive success, the focus here is on the adult population size, $N_A = \sum_{x=\alpha}^{\omega} N_x$.

EFFECTIVE POPULATION SIZE

Mean and variance in offspring number are the major factors that determine effective size. For seasonal reproduction in an age-structured species, the most relevant effective-size metric is the effective number of breeders per year (N_b) because it relates directly to the annual number of adults (N_A). For each sex, N_b can be calculated using the standard discrete-generation formula for inbreeding effective size (Crow and Denniston 1988; Caballero 1994):

$$N_b = \frac{u_k N_A - 1}{u_k - 1 + \sigma_k^2 / u_k} \quad . \tag{1}$$

N_b can be calculated separately for males and females and an overall N_b obtained using Wright's (1938) sex-ratio adjustment. Examples below show how to separate the within-age and between-age contributions to reduction of the key ratio N_b/N_A.

N_b relates directly to all adults breeding in a single year, but most evolutionary theory depends on effective size per generation (N_e). Calculating N_e in iteroparous species is complicated by the necessity of integrating information across multiple episodes of reproduction. Hill (1972) provided the most general solution:

$$N_e \approx \frac{4N_1 T}{\sigma_{k\bullet}^2 + 2} \quad , \tag{2}$$

where $T = \Sigma x l_x b_x / \Sigma l_x b_x$ is generation length and $\sigma_{k\bullet}^2$ is the variance in lifetime number of offspring produced by the N_1 individuals in a cohort.

VARIANCE COMPONENTS ANALYSIS

Data for seasonal reproduction

The underlying model for a simple one-way analysis of variance with one treatment is the following:

$$k_{i,x} = \mu + \tau_x + \varepsilon_{i,x} \ ,$$

where u is the parametric mean, τ_x is the effect of treatment x ($x = 1,n$), $k_{i,x}$ is the value of the response variable for individual i in treatment x, and $\varepsilon_{i,x}$ is a random error term. In the ANOVA sums of squares table, the sources of variation are partitioned into three components (SST = total sum of squares of deviations, SSB = between-treatment sum of squares, and SSE = error or within-treatment sums of squares), as follows:

$$SST = \sum_{i=1}^{N_x} \sum_{x=1}^{n} (k_{i,x} - \mu_k)^2 \tag{3a}$$

$$SSB = \sum_{k=1}^{n} N_x \, (\mu_{k,x} - \mu_k)^2 \tag{3b}$$

$$SSE = \sum_{i=1}^{N_x} \sum_{x=1}^{n} (k_{i,x} - \mu_{k,x})^2 \ , \tag{3c}$$

where n is the number of treatments, N_x is the number of measurements for treatment x and $\mu_{k,x}$ and μ_k are treatment and overall means, respectively. In the ANOVA model, the vector of samples sizes (N_x) is considered fixed and the sums of squares are additive, such that $SST = SSB + SSE$.

In the version of the model used here, the treatments are ages of individuals, $k_{i,x}$ is the number of offspring produced by parent i of age x, and N_x is the number of potential parents of

age x. To allow for delayed age at maturity, we define a new adult-lifetime parameter, which represents the number of treatments (adult age classes) as $AL = \omega-\alpha+1$. Our focus is on partitioning the overall variance in offspring number ($\sigma_k^2 = SST/N_A$) into within-age and between-age components. This can be done by weighting the age-specific variance components by the relative number of parents in each age class (i.e., the weights are the vector N_x/N_A).

The weighted variance in offspring number among all individuals of age x is

$$\sigma_{k,x}^2 = (N_x/N_A)\sum_{i=1}^{N_x}(k_{i,x} - \mu_{k,x})^2/N_x = \sum_{i=1}^{N_x}(k_{i,x} - \mu_{k,x})^2/N_A = (N_x/N_A)\phi_x\mu_{k,x}\ ,$$

and summed across all ages, the within-age component of σ_k^2 is

$$\sigma_{k(Within)}^2 = \sum_{x=\alpha}^{\omega}\sigma_{k,x}^2 = \sum_{x=\alpha}^{\omega}\sum_{i=1}^{N_x}(k_{i,x} - \mu_{k,x})^2/N_A = SSE/N_A. \qquad (4)$$

Thus, the residual (within-age) variance component is the sum of the product of the age-specific vectors for ϕ and mean offspring number, and it can be computed as the within-treatment sum of squares divided by the total number of parents.

In an analogous fashion, each age-specific term in the between-age component of σ_k^2 is given by $(N_x/N_T)(\mu_{k,x} - \mu_k)^2$, so the overall between-age component is

$$\sigma_{k(Between)}^2 = \sum_{x=\alpha}^{\omega}(N_x/N_A)\,(\mu_{k,x} - \mu_k)^2 = SSB/N_A. \qquad (5)$$

As with the sums of squares, the components of overall σ_k^2 are additive, such that $\sigma_{k(Within)}^2 + \sigma_{k(Between)}^2 = \sigma_k^2 = SST/N_A$. The relative contributions of the two variance components to overall σ_k^2, which are identical to the relative contributions to SST, are:

Between ages: $\sigma_{k(Between)}^2/\sigma_k^2$

Within ages: $\sigma_{k(Within)}^2/\sigma_k^2 = 1 - \sigma_{k(Between)}^2$.

In the ANOVA framework, random variation among individual datapoints affects both *SSE* and *SSB*. In ecology and evolutionary biology, it is often of interest to determine whether variation in reproductive success is greater than the random expectation, because this determines a) the scope for the action of natural selection, and b) the degree to which effective size is less than census size. Tuljapurkar et al. (2020) called this random source of variation "dynamic heterogeneity," while Caswell (2009) and van Daalen and Caswell (2017) prefer the term "individual stochasticity." The Wright-Fisher model of random reproductive success is a cornerstone of theoretical and empirical population genetics, so it is an appropriate null model to use as a reference point for seasonal reproduction. Wright-Fisher reproduction involves a multinomial sampling process, with expected variance in offspring number across adults of all ages of $E(\sigma_{k(Random)}^2) = \mu_k(N_A-1)/N_A$. The expected relative contributions of the two variance components to this total are N_A-AL for the within-age random effect and AL-1 for the between-age random effect (see Supporting Information and Equations S7 for details). Note that these relative weights are the same as the degrees of freedom for *SSE* and *SSB* (respectively) from an ANOVA table. These equations accurately predicted the actual values of these random variance components in simulated populations (Table S1).

This variance-partitioning approach makes no assumptions about the distribution of the response variable (offspring number) and can be applied generally to widely-available data for age-specific vital rates from a life table. For consistency and to facilitate comparisons across species, the life table should be standardized to values of survival and fecundity that produce a stable population. For each age, the within-age and between-age variance components can be calculated as described above and summed to obtain components $\sigma^2_{k(Within)}$ and $\sigma^2_{k(Between)}$. The resulting estimates would apply to a hypothetical population whose realized data exactly agreed with expectations from the life table. A potential limitation of this approach is that it requires age-specific estimates of ϕ, which most standard life tables do not provide; in that event, the user could conduct a sensitivity analysis to examine how different plausible assumptions about ϕ affect the results.

The variance-partitioning method also can be applied to empirical age-specific vital rates. Because the variance-to-mean ratio (ϕ) depends on mean offspring number in a sample ($\bar{k}$), it is best to rescale ϕ to its expected value for a stable population, which can be done using a method proposed by Crow and Morton (1955):

$$\phi_2 = 1 + \frac{\bar{k}_2}{\bar{k}_1}\left(\phi_1 - 1\right) \ . \qquad (6)$$

In Equation 6, $\bar{k}_1$ is mean offspring number in the sample, $\bar{k}_2$ is the target mean offspring number (the respective b_x value from a life table scaled to constant N), ϕ_1 is computed from the sample, and ϕ_2 is the rescaled variance-to-mean ratio. After this rescaling is done for each age and sex, analysis can the proceed as described above for data from a life table.

Data for lifetime reproductive success

Whereas seasonal reproduction involves individuals of different ages reproducing at the same time, analysis of *LRS* requires longitudinal tracking of multiple episodes of reproduction over time by the same individuals. We are interested in partitioning the variance in *LRS*, each term of which involves a summation across an adult lifetime. Computing the expected variance of *LRS* thus involves computing the variance of the sums of multiple vectors, which requires one to consider all the pairwise covariance terms involving reproductive output of the same individuals at different ages. This makes an analytical solution challenging, especially for long-lived species, and in any case it would be rare to have the data to adequately parameterize this full model.

Fortunately, a simple modification provides traction in the analysis of *LRS*. The most widely-used models for N_e when generations overlap (Felsenstein 1971; Hill 1972) assume that 1) survival from age x to age x+1 is independent of an individual's reproductive output in previous years; and 2) an individual's reproductive output is uncorrelated over time. Given these assumptions, it is possible to calculate the expected value of lifetime $\sigma^2_{k\bullet}$ and hence N_e per generation, using the vital rates from a standard life table, plus the age-specific vector ϕ. The program AgeNe (Waples et al. 2011) does this by grouping individuals by age at death (*AgeDeath*). Each individual has a single *AgeDeath* and a single *LRS*, so by using age at death as the treatment, lifetime reproductive output can be analyzed with the same ANOVA framework used for seasonal reproduction. Individuals that die at the same age all had the same number of seasonal opportunities to reproduce and the same expectation for *LRS*. In the ANOVA formulation for *LRS*, therefore, age at death rather than age is the treatment.

Calculation of the variance components for *LRS* from a life table proceeds as follows. [For simplicity in notation, here I assume that age at maturity is 1, so that age at death (denoted by q) takes the range 1-ω, which is the same range as x = age]. The number of individuals in each treatment is $D_q = N_q - N_{q+1}$, with $D_\omega = N_\omega$ because it is assumed no individuals live beyond age ω. D_q thus is the number of individuals that were alive at age q and had an opportunity to reproduce but died before reaching age q+1. Calculation of *LRS* is done separately for each birth cohort. Whereas $\Sigma N_x = N_A$ is the total number of adults alive at any given time, $\Sigma D_q = N_1$ is the number of individuals in each cohort. As with the analysis of seasonal reproduction, we assume that the population parameters exactly follow the expectations from the life table. Because of the independence assumptions, the expected means and variances of *LRS* for each age at death q are additive and given by $E(LRS_q) = \sum_{x=1}^{q} b_x$ and $E[var(LRS_q)] = \sum_{x=1}^{q} \sigma_{k,x}^2 = \sum_{x=1}^{q} b_x\, \phi_x$. The within-treatment sums of squares are these treatment-specific variances multiplied by the number of individuals in each treatment, so the overall within-treatment sums of squares for *LRS* is

$$SSE\bullet = \sum_{q=1}^{\omega} D_q \sum_{x=1}^{q} b_x\, \phi_x. \qquad (7)$$

The between-treatment sums of squares ($SSB\bullet$) has ω terms, each of which is proportional to the squared difference between treatment-specific $\overline{LRS_q}$ and the overall mean $\overline{LRS}$:

$$SSB\bullet = \sum_{q=1}^{\omega} D_q (\overline{LRS_q} - \overline{LRS})^2.$$

Because we assume a stable population (and equal adult sex ratio), $\overline{LRS} = 2$, so this becomes

$$SSB\bullet = \sum_{q=1}^{\omega} D_q (\overline{LRS_q} - 2)^2, \qquad (8)$$

with $SST\bullet = SSE\bullet + SSB\bullet$.

Longitudinal studies integrate reproductive success across multiple time periods, and as a consequence they introduce two additional factors that contribute to *var*(*LRS*): differences in longevity, and (potentially) non-zero correlations in individual reproductive success over time. As shown below, in the two-part ANOVA framework, these additional factors get subsumed into the between- and within-treatment effects, respectively. Our simplified *LRS* model assumes temporally-spaced reproductive events are uncorrelated, so the second factor can be ignored (this assumption is later relaxed). The effect of differences in longevity can be quantified by removing any differences in age-specific fecundity (i.e., by assuming constant b_x with age). In that case, the between-treatment effect only reflects differences in age at death = longevity. In Results this partitioning of the between-treatment effect is illustrated with a worked example.

In an empirical dataset with longitudinal data for *LRS*, the raw data are in a matrix with N_1 rows (one for each member of the cohort) and *AL* columns (one for each age in the maximum adult lifespan) (see Table S2 for an example). In each cell, $k_{i,x}$ gives the number of offspring (that survive to age at enumeration) produced by individual i at age x. The value $k_{i,x} = 0$ is used if individual i is alive at age x but produces no offspring, but $k_{i,x}$ = NA is used for individuals that die before reaching age x. The total matrix has $AL*N_1$ cells, of which ΣN_x are not 'NA', so ΣN_x represents the total number of potential reproductive events (individuals alive at specific ages) for the cohort. LRS_i for each individual is the sum of its numbers of offspring across its lifetime, $\overline{LRS}$ is the mean *LRS* for the cohort (which might not exactly equal 2 in an empirical dataset),

and $\sigma^2_{k\bullet}$ is the variance of *LRS*. Parsing this overall variance into its components proceeds by sequentially eliminating one component from the data, as illustrated with a worked example in Results.

In the life-table analyses of *LRS*, it was assumed there were no temporal correlations in reproductive success. In real populations, positive or negative correlations are likely in many datasets, and to the extent that these correlations occur they will affect the within-treatment sums of squares. Methods to evaluate these effects are illustrated in Results.

We can also calculate the expected random contribution to $SST\bullet$ and $\sigma^2_{k\bullet}$ under a null model that randomly assigns each of the total *LRS* offspring to a member of the cohort. Under the null model, all reproductive events have the same expectation (denoted below by $E(k)$), so expected *LRS* for each individual is directly proportional to its age at death. For example, under the null model with constant fecundity, an individual with *AgeDeath* = 5 has an expected *LRS* 5 times as large as another member of the cohort with *AgeDeath* = 1. More generally, in the null model $E(LRS_q) = q * E(k)$. Furthermore, in the null model population size is constant so overall $\overline{LRS}$ = 2. Given these equalities, the random expectations for the within-treatment and between-treatment sums of squares are given by (see Supporting Information for details):

$$E(SSE_{\bullet random}) = E(k) \sum_{q=1}^{\omega} \left(D_q - 1\right) * q; \tag{9}$$

$$E(SSB_{\bullet random}) = E(k) * \sum_{q=1}^{\omega} q * \frac{(D_q - 1)}{D_q} + \sum_{q=1}^{\omega} D_q * (q * E(k) - 2)^2 . \tag{10}$$

The random between-treatment sum of squares has two components (Equation 10): The first term accounts for random differences in mean age-specific reproductive success, and the second term accounts for random differences in age at death (longevity). As with seasonal reproduction, simulations showed that Equations 9 and 10 accurately predict the random components of variance in lifetime reproductive success (Table S3).

SIMULATIONS

Simulations were run to confirm the accuracy of analytical results and to illustrate effects of random stochasticity on variance partitioning. All simulations were done in R (R Core Team 2021), using code provided in the SI. Numbers in each age group were fixed across replicates, as were total numbers of offspring produced in each time period. Numbers of offspring produced by each age group varied randomly in each replicate, with the constraint that the overall total was fixed. This allowed the realized, age-specific mean offspring number ($\mu_{k,x}$) to vary randomly. Overdispersion was determined by the age-specific parameter $\phi_x = \sigma^2_{k,x}/b_x$, with $\phi_x = 1$ indicating Poisson variance. To simulate the desired level of overdispersion, vectors of parental weights $\boldsymbol{w}$ were generated as described in Waples (2022), where w_i is the relative probability that individual *i* will be the parent of a given offspring. In modeling lifetime reproductive output, parental weights were either shuffled randomly each year (to model independence of relative reproductive success over time) or retained across individual lifetimes (to model persistent individual differences), again as described in Waples (2022).

Results

The variance components analysis is illustrated with worked examples using empirical, hypothetical, and simulated data.

DATA FOR SEASONAL REPRODUCTION

Empirical life table data

Application to empirical data is illustrated using age-specific vital rates (Table 2) for male black bears in Michigan. Male black bears have a maximum longevity of at least 20 years, but data for bears older than 10 are sparse so the last age class (11+) is a plus group that includes all older males. This example assumes annual production of 800 yearlings, of which half are males (primary sex ratio is equal in this population). The best fit for the empirical age-at-death data indicated a lower survival prior to age 3, after which it was constant at 0.67/year. The N_x column in Table 2 shows the expected numbers in each age class, rounded to the nearest integer for purposes of this example. Age-specific fecundity (b_x) and the variance-to-mean ratio (ϕ_x)—both based on genetic parentage analysis and ageing from teeth—have been scaled to values expected for a stable population (see Table S4A in Waples et al. 2018b for details). Age-specific $\sigma^2_{k,x}$ is the product of b_x and ϕ_x, the column B_x shows the total expected number of offspring produced by each age class, and these sum to the total cohort size of 800. Because yearling males do not reproduce, we focus our analyses on the 698 adults age 2 and above, and adult lifespan consists of AL = 10 age classes, from 2 to 11+. Each year these males produce a cohort of 800 offspring, so an average adult produces μ_k = 800/698 = 1.15 offspring that survive to age 1. Note that in this population, expected male fecundity rises sharply through age 10 before declining in older adults. Furthermore, the distribution of reproductive success is skewed, and strongly so in males older than 5, for which ϕ_x is >10.

The next sets of columns illustrate calculations for the variance components analyses. The "sums of squares" columns show age-specific values for the within-treatment (*SSE*) and between-treatment (*SSB*) components of an ANOVA table, with age as the treatment, calculated using Equations 3a-b. The "variance" columns show contributions of the within-age ($\sigma^2_{k(Within)}$) and between-age ($\sigma^2_{k(Between)}$) components to the overall variance in offspring number, using Equations 4 and 5.

For this life table, the between-treatment sums of squares (*SSB*, arising from systematic changes in fecundity with age) total 959, but the within-treatment sums of squares (*SSE*) are much larger (5473), so $SST = SSB + SSE$ = 6432. Thus, the within-age component is responsible for the fraction 5473/6432, or 85.1%, of the total sums of squares, with the remainder attributable to the treatment (changes in fecundity with age). Because the components of σ^2_k are all directly proportion to their respective sums of squares, proportional partitioning of σ^2_k into within-age and between-age effects leads to the same result.

It also is of interest to ask how much of this overall variation in offspring number can be attributed to chance. As shown in Table 2, under the null model of random reproductive success, the expected value of SST_{random} is 798.9, or 12.4% of the total *SST*. In the ANOVA framework, the vast majority (>98%) of this stochasticity shows up under SSE_{random}. If we subtract the expected magnitudes of random effects, we get an estimate of the net (non-random) within-age and between-age effects. These amount to 14.7% of the overall sums of squares for *SSB* and 72.8% for SSE, and these proportional results are the same for partitioning the random, within-

age, and between-age effects of σ_k^2. These results can be neatly illustrated with a pie chart (Figure 1), which also shows results for female black bears. In females, changes in fecundity with age are more modest and ϕ is also generally lower (3.21 for all ages; see Table S4 for details). As a consequence, the random component is relatively more important for females (29% overall compared to 12.4% for males), and within-age effects still dominate the non-random components (Figure 1).

The variance-partitioning results for black bears also can be used to assess the relative importance of within-age and between-age effects in determining the ratio of effective number of breeders (N_b) to number of mature individuals (N_A). For males, inserting values for μ_k (1.15), σ_k^2 (9.21), and N_A (698) into Equation 1 produces N_b = 98 and N_b/N_A = 0.14—an overall reduction of 86% compared the expected result if seasonal reproduction exactly followed the WF model. Although the variance components are additive, because of the inverse relationship between σ_k^2 and N_b their effects in reducing the N_b/N_A ratio are not additive. Nevertheless, we can partition the overall reduction in N_b/N_A into within-age and between-age components based on their relative contributions to σ_k^2 (from Table 2 and Figure 1). Because the Wright-Fisher result that $E(N_b/N_A) = 1$ already accounts for random demographic stochasticity in σ_k^2, we use the net, greater-than-random variance components, which for males are (from Table 2) total $\sigma_{k(net)}^2$ = 8.07, with the within- and between-age components being 6.71 and 1.36, respectively. Of the 86% total reduction in N_b/N_A in male black bears, therefore, we can attribute the fraction 6.71/8.07, or 71%, to within-age effects and the remaining 15% to between-age effects (Figure 2). For females, σ_k^2 is lower (3.51) so the reduction in effective size is not as strong (N_b/N_A = 0.29, a 71% reduction), but this reduction is also dominated by within-age effects (Figure 2).

Synthetic data

Computer simulations based on vital rates for hypothetical species were used to explore variance partitioning and sensitivity under a wider range of scenarios. Table 3 shows a life table for one sex (nominally females) for a hypothetical species with maximum lifespan of 5 years, age at maturity = 1 year, annual survival constant at v_x = 0.5, expected fecundity (b_x) that is proportional to age, and expected variance in reproductive success that is 5 times the mean (ϕ_x = 5 for all ages). For purposes of this example, we assume that the actual data perfectly reflect these expectations.

Each year the 775 females produce 800 offspring (both sexes combined), so overall μ_k is 800/775 = 1.032. From Methods, the between-age sum of squared deviations is $SSB = \sum N_x(\mu_{k,x} - \mu_k)^2$. The table shows these age-specific products, which sum to 285.2. The residual (within-treatment) sum of squares is $SSE = \sum(N_x * \phi_x * \mu_{k,x})$, whose terms are also shown in Table 3 and sum to 4,000, so the total sum of squares is $SST = SSB + SSE$ = 4,285.2. The among-ages relative variance component therefore is 285.2/4285.2 = 0.067, so even though fecundity increases in proportion to age, this accounts for only 6.7% of the overall variance in offspring number.

To further partition the overall *SST*, we first calculate the expected random contributions to the residual sum of squares, using Equations S2, S3, and S6 and using the overall μ_k = 1.032 as $E(k)$. These expected random components are [799, 4.1, 794.8] for SST_{random}, SSB_{random}, and SSE_{random}, respectively. Therefore, random (~Poisson) variance contributes 100*799/4285 = 18.6% to the overall *SST*, and the overdispersed (> Poisson) component of the within-age effect (3205 = 4000-795) accounts for almost ¾ of the total variance in offspring number.

DATA FOR LIFETIME REPRODUCTION

Life table data

Analysis of *LRS* data using a life table is illustrated in Table 4, which uses the same vital rates as Table 3, except that ϕ is 3 at each age instead of 5. Based on the numbers-alive-at-age values (N_x), the numbers that die at ages q=1-5 are D_q = [200,100,50,25,25], with ΣD_q = 400 being the annual cohort size of females. Under the independence assumptions of our simple model, expected LRS_q for each treatment (age at death) is simply the cumulative b_x through age at death, and with constant ϕ the expected variance among individuals that die at the same age is $E(LRS_q)*\phi$. The sums of squares are then computed for each treatment using Equations 7 and 8, with the overall result that $SSE\bullet$ = 2400, $SSB\bullet$ = 1874.8, and $SST\bullet$ = 4274.8. The overall variance in *LRS* is $\sigma^2_{k\bullet} = SST\bullet/N_1$ = 4274.8/400 = 10.69. A bit over half (56.1%) of the overall sums of squares is due to within-treatment effects and the remainder to between-treatment effects.

The between-treatment $SSB\bullet$ can be further partitioned into between-age and longevity effects as demonstrated in Table S5. In the second panel of Table S5, the analysis is repeated after removing any age-related differences in fecundity. This is accomplished by replacing all the b_x values in the life table by the single fixed value that produces a stable population (μ_k = 1.032). When this is done, $SSE\bullet$ remains unchanged but $SSB\bullet$ drops to 611, which represents the magnitude of the effect due to random differences in longevity. The difference between $SSB\bullet$ with and without age-related changes in fecundity (1874.8-611 = 1263.8) therefore represents the among-age component to $SSB\bullet$. Thus, age-related differences in fecundity account for about two thirds of $SSB\bullet$ and random variation in fecundity about one third.

For this life table, random effects account for almost one third (32.9%) of the $SST\bullet$, and within-treatment effects account for the majority of the remainder. In this partitioning, essentially all of the effects of longevity are absorbed into the random component, so the net (non-random) contribution to $SSB\bullet$ comes from changes in fecundity with age (see Figure 3).

This example assumed that reproduction and survival were independent across time. To evaluate consequences of violating this assumption, simulations were conducted using the vital rates in Table 4 but under a scenario that generated positive correlations in reproductive success for the same individuals over time. This was accomplished by allowing each surviving individual to retain the parental weight it had in year 1. An index of temporal correlation was calculated as $cor(k_{i,1}, k_{i,2\text{-}5})$, which is the correlation between an individual's reproductive output in year 1 and the total number of offspring it produced for the rest of its life. When parental weights were randomly shuffled each year, total $SST\bullet$ varied randomly around a value a bit over 4200 and $SSE\bullet$ was consistently about a third higher than $SSB\bullet$ (Figure 4, left side)—all as expected from Table 4—and $|cor(k_{i,1}, k_{i,2\text{-}5})|$ was close to zero (<0.001). When parental weights were retained across individual lifetimes, $SSB\bullet$ was not affected, but $SSE\bullet$ more than doubled so $SST\bullet$ increased as well (Figure 4, right), and mean $cor(k_{i,1}, k_{i,2\text{-}5})$ jumped to 0.36. This result demonstrates that 1) persistent differences in individual reproductive success can substantially increase the variance in *LRS*, and that 2) these correlations affect only the within-treatment component of $\sigma^2_{k\bullet}$.

Empirical longitudinal data

The steps in partitioning variance in *LRS* for empirical longitudinal data are best illustrated with a simple example, based on a population with vital rates as shown in Table 4. The left panel of Table S2 shows longitudinal data over the 5-year lifespan for a sample of 40 randomly-generated individuals. The right panel summarizes these data by treatment = age at death. Calculation of the within-treatment and between-treatment sums of squares follows Equations 7 and 8. Mean *LRS* = (total number of offspring)/(sample size of parents) is $\overline{LRS}$ = 78/40 = 1.95. Two ways of computing variance in *LRS* ($V_1 = SST\bullet/\Sigma D_x$ and $V_2 = var(LRS)$) produce the same result (11.9) when V_2 is computed as the population variance. In this example, the between-treatment $SSB\bullet$ (310.6) is almost twice as large as the within-treatment $SSE\bullet$ (165.3).

Discussion

OTHER WAYS TO PARTITION VARIATION IN REPRODUCTIVE SUCCESS

The number of components of reproductive success that potentially could be identified is essentially unlimited [e.g., van Noordwijk and van Balden (1988) list data for 25 *LRS* components for great tits (*Parus major*) from the Netherlands], but Brown (1988) focused on four that are commonly used: survival to breeding age; adult lifespan; age-specific fecundity; and offspring survival to age at maturity. In their analysis of empirical data for a water-strider, Ferguson and Fairbairn (2001) focused on a similar partitioning: pre-adult survival, adult lifespan, and daily fecundity. Arnold and Wade (1984) partitioned reproductive success and Crow's Opportunity for Selection into sequential episodes of selection and showed that the components are additive only if one includes a residual factor that accounts for all the covariance terms. More recently, several authors interested in distinguishing 'pluck' from 'luck' (Snyder and Elner 2018) have focused on parsing out the component of *LRS* that can be attributed to random demographic stochasticity in survival and reproduction (van Daalen and Caswell 2017; Tuljapurkar et al. 2020; Broekman et al. 2020; Lee et al. 2020). All of these approaches can provide useful insights, depending on one's objectives and the kinds of data that are available.

The methods outlined here differ from these previous efforts in two major ways. First, this paper focuses on the largely-neglected component of reproductive variance that arises from differences in realized reproductive success among individuals of the same age and sex. Second, whereas most previous approaches to partitioning focus primarily or entirely on *LRS*, here equal treatment is given to partitioning reproductive variance for individual years or seasons. Analysis of seasonal data is important because any long-term, longitudinal study begins with data collected for individual years or seasons, and many empirical studies never encompass entire lifespans for the focal species (Nishida 1989). Furthermore, the distribution of seasonal reproductive success provides key insights into mating systems, and the most direct way to study sexual selection is by collecting data on all mature individuals that co-occur at the same time and place. That is not the case when analyzing *LRS*.

THE NEGLECTED AGE-SPECIFIC PARAMETER ϕ

The variance partitioning analysis emphasizes why it is important to pay more attention to the within-age component of variance in offspring number. For example, even though mean fecundity varies substantially with age in both male and female black bears (Tables 2 and S1), the within-ages component of σ_k^2 is much larger than the between-ages component in both sexes

(Figure 1). Furthermore, just the random component of within-age variance in reproductive success is almost as large as the sum of the random and non-random between-age components in males, and much larger than the between-age components in females (Figure S1). This indicates that a full understanding of reproductive variance cannot be achieved without considering the within-age component, even when the within-age variance is not overdispersed ($\phi = 1$).

NULL MODELS

Accuracy of the analytical results for the random expectations for σ_k^2 and $\sigma_{k\bullet}^2$ were confirmed by simulations. These results apply to a null model where a) each year or season, all adults behave like a Wright-Fisher ideal population with equal expectations of reproductive success, and b) for each individual in a cohort, survival to year *i* and reproduction in year *i* do not depend on realized reproductive success in any previous year. For seasonal reproduction, it was shown (Equations S7) that the relative magnitudes of the within-age and between-age random variance components are directly proportional to the degrees of freedom from an ANOVA table. This explains why the proportion of overall random variance in σ_k^2 due to within-age effects $[(N_T - n)/(N_T - 1)]$ generally will be much larger than the proportion due to between-age effects $[(n - 1)/(N_T - 1)]$, where *n* is the number of treatments (ages in the adult lifespan).

For analysis of LRS, a third random component (longevity) is important to consider. In this case the treatments are formed by grouping individuals by age at death, and random variation in longevity appears in the between-treatment component of random $\sigma_{k\bullet}^2$ (Equation S9). The other between-treatment component results from age-related changes in expected fecundity. These two components can be isolated by setting all b_x to the single value that will produce a stable population. This removes the between-age effect, so the remainder can be attributed to random variation in longevity.

These are not the only possible null models, and other random factors can contribute to variation in offspring number—for example, chance variation in mating success can depend on the operational sex ratio (Jennions et al. 2012), and parental coordination in provisioning offspring can arise from shared environments (Ihle et al. 2019). It is tempting to attribute family-correlated mortality to viability selection, but this phenomenon also can simply reflect bad luck. For example, nest predation in birds can eliminate entire clutches and greatly increase variance in offspring number—but how much of that family-correlated mortality is due to poor parental genes (and hence indicative of natural selection), and how much simply reflects a chance event that affects entire families only because the juvenile offspring co-occur in space and time? In the latter case, although mortality can be considered random, fates of individuals are not independent with respect to family, and this causes random variation in offspring number to exceed the Poisson expectation. Researchers should keep these issues in mind when trying to parse stochastic and deterministic factors contributing to variance in reproductive success.

TEMPORAL AUTOCORRELATIONS AND LIFETIME REPRODUCTIVE SUCCESS

The effects on $\sigma_{k\bullet}^2$ of random variation in survival (and hence random variation in the number of opportunities to reproduce) can be assessed as described in the previous section. Variance in *LRS* can also be strongly affected by correlations in individual reproductive success over time, and these correlations (if any) contribute to the within-treatment component of $\sigma_{k\bullet}^2$. Consistent positive correlations (e.g., some individuals consistently above or below average at producing offspring; see Figure 4) increase $\sigma_{k\bullet}^2$ (Lee et al. 2011). In contrast, negative correlations (often caused by skip breeding) generally reduce $\sigma_{k\bullet}^2$ because this life history

reduces the opportunity for certain individuals to consistently dominate production of offspring (Waples and Antao 2014). This can be thought of as a type of variance-buffering 'portfolio' effect.

LIMITATIONS

Some potential limitations of the analytical framework used here are important to keep in mind. First, the demographic model is age-based and discrete-time and assumes birth-pulse reproduction, which applies to a wide range of (but certainly not all) species. Modification for continuous reproduction should be possible but is not attempted here. Many species' life histories are more easily analyzed using stage-based models. Several recent authors (e.g., van Daalen and Caswell 2017, Tuljapurkar et al. 2020, and colleagues) have used stage-based models to separate random and deterministic components to variance in *LRS*. None of these, however, has focused on the within-age component of $\sigma^2_{k\bullet}$.

Second, the current analyses follow the ANOVA model in treating the sample sizes—numbers alive at age (N_x) for seasonal reproduction and numbers that die at each age (D_q) for lifetime reproduction—as fixed. Which specific individuals survive is random, and the proportion of offspring contributed by adults of each age is a random variable, subject to the constraint that the total cohort size is constant, as is population size. Based on results of similar models that have allowed random variation in the numbers surviving to each age (Waples et al. 2011; 2014), I expect that incorporating this feature would not appreciably change the results. However, some species experience large swings in abundance in response to environmental fluctuations, and in some cases vital rates can change with population density (Myhre et al. 2017; Lee et al. 2020). Caution should be used in applying results obtained here to species experiencing these kinds of population dynamic processes.

Finally, the ANOVA framework used here makes it easy to calculate the *F* statistic as the ratio of two scaled sums of squares, in which case users might be tempted to use this statistic to test the significance of the treatment effect (age for seasonal reproduction, age-at-death for *LRS*). However, it should be clear from results presented here that the assumption of equal variances often will be violated. Options for evaluating significance of the variance components for empirical data include 1) using Monte-Carlo methods with an appropriate null model (as done here and by van Daalen and Caswell (2017) and Tuljapurkar et al. (2020)); and 2) using generalized least-squares approaches that allow one to model the within-treatment variance itself as a function of some covariate (e.g., Zuur et al. 2009).

Data availability statement

This study did not generate any new empirical data, except by simulation. Code to conduct the simulations and analyses described here is available in Supporting Information. The author declares no conflict of interest.

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Table 1. Notation

x	Age (in years)
α	Age at maturity
ω	Maximum age
q	Age at death
v_x	Probability of surviving from age x to age x+1
l_x	Cumulative probability of surviving to age x
N_1	Cohort size = number of offspring produced per time period that survive to age 1
N_x	Number of individuals of age x alive at any given time; $N_x = N_1 l_x$
D_q	Number of individuals that died after reaching age q; $D_q = N_q - N_{q+1}$
N_T	Total number of individuals of all ages alive at any given time; $N_T = \Sigma N_x$
N_A	Number of adults with age$\geq\alpha$ alive at any given time
N_e	Effective population size per generation
N_b	Effective number of breeders in one time period
b_x	Expected number of offspring for parents of age x in one time period
k_i	Actual number of offspring produced by parent i in one time period
μ_k	Parametric mean k_i for all parents in one time period
σ_k^2	Parametric variance of k_i for all parents in one time period
$\sigma_{k,x}^2$	Variance of k for adults of age x
ϕ_x	Ratio of variance to mean reproductive success in one time period for adults of age x; $\phi_x = \sigma_{k,x}^2/b_x$
LRS	Lifetime reproductive success = total number of offspring produced across an individual's lifetime
$\overline{LRS_q}$	Mean LRS for individuals that died at age q
$\sigma_{k\bullet}^2$	Variance in LRS among the N_1 individuals in a cohort
SST	Total sum of squared deviations across all treatments, as in an ANOVA table
SSB	The between-treatment sum of squares
SSE	The error or within-treatment sum of squares
w_i	Relative probability that adult i will be the parent of a given offspring

Table 2. Variance partitioning analysis for seasonal reproduction based on a life table for male black bears from Michigan. These vital rates produce a constant cohort size of 800 age-1 offspring, of which half are male, and an adult male population size of 698 age 2+ individuals. In the top panel, columns 1-8 show vital rates from Waples et al. (2018b). The next two columns show the age-specific within-age and between-age sums of squares, and the last two columns show the same components for σ_k^2. The bottom panel shows results combining data for all ages. See Table 1 for notation, Table S4 for comparable data for females, and text for explanation of the calculations.

								Sums of squares		Variance	
Age	v_x	l_x	N_x	b_x	B_x	ϕ_x	$\sigma^2_{k,x}$	SSE_x	SSB_x	$\sigma^2_{k,x(W)}$	$\sigma^2_{k,x(B)}$
1	0.612	1	400	0	0	1.00	0.00	-	-	-	-
2	0.612	0.612	245	0.577	141	1.1	0.63	155.2	79.4	0.22	0.11
3	0.670	0.375	150	0.577	87	1.93	1.12	167.3	48.6	0.24	0.07
4	0.670	0.251	100	0.577	58	2.77	1.60	159.8	32.4	0.23	0.05
5	0.670	0.168	67	1.180	79	3.61	4.26	285.2	0.1	0.41	0.00
6	0.670	0.113	45	2.321	104	10.81	25.08	1128.8	62.1	1.62	0.09
7	0.670	0.076	30	2.984	90	10.81	32.24	967.3	101.3	1.39	0.15
8	0.670	0.051	20	3.739	75	10.81	40.41	808.1	134.5	1.16	0.19
9	0.670	0.034	14	4.515	63	10.81	48.80	683.2	158.9	0.98	0.23
10	0.670	0.023	9	7.131	64	10.81	77.06	693.6	322.3	0.99	0.46
11	0.670	0.015	18	2.182	39	10.81	23.58	424.5	19.3	0.61	0.03
		11+	18								
		Adults	698		800			5473	959	7.84	1.37

		%	E_{random}	Net	%
μ_k	1.15				
SSE	5473	85.1	787	4686	83.2
SSB	959	14.9	12	947	16.8
SST	6432		799	5633	
$\sigma^2_{k(W)}$	7.84	85.1	1.13	6.71	83.2
$\sigma^2_{k(B)}$	1.37	14.9	0.02	1.35	16.8
σ^2_k	9.21		1.14	8.07	

Component		%
Random	799	12.4
Within	4686	72.8
Between	948	14.7
Total	6432	

Table 3. Variance components analysis for seasonal reproduction in a hypothetical species with a 5-year lifespan, fecundity that increases with age, and age-specific variance in reproductive success 5 times the mean. The top panel shows age-specific data and the bottom panel shows results combining data for all ages. See text for discussion.

Age	l_x	N_x	b_x	ϕ_x	$\sigma^2_{k,x}$	SSB_x	SSE_x
1	1	400	0.561	5	2.807	88.7	1122.8
2	0.5	200	1.123	5	5.614	1.6	1122.8
3	0.25	100	1.684	5	8.421	42.5	842.1
4	0.125	50	2.246	5	11.228	73.6	561.4
5	0.0625	25	2.807	5	14.035	78.7	350.9
	N_A	775				285.2	4000.0

μ_k	1.032
σ^2_k	5.529
ϕ	5.356

		Fraction	E_{Random}	Net	Component	%
SST	4285.2		799.0	3486.2	Random	18.6
SSB	285.2	0.067	4.1	281.1	Between	6.6
SSE	4000.0	0.933	794.8	3205.2	Within	74.8

Table 4. Variance components analysis for lifetime reproduction in a hypothetical species with vital rates as those in Table 3, but with $\phi = 3$ at each age. Long = longevity. The top panel shows age-specific data and the bottom panel shows results combining data for all ages. See text for discussion.

								Overall Sums of Squares				Random Expectations			
Age	N_x	b_x	ϕ_x	$\sigma^2_{k,x}$	D_x	*E(LRS$_x$)*	$\sigma^2_{k,x\bullet}$	*SSE•*	*SSD•*	*Age*	*Long*	*SSE•*	*SSD•*	*Age*	*Long*
1	400	0.561	3	1.68	200	0.56	1.68	336.8	413.9	226.6	187.3	111.7	188.4	1.0	187.4
2	200	1.123	3	3.37	100	1.68	5.05	505.3	10.0	9.6	0.4	166.7	2.5	2.0	0.4
3	100	1.684	3	5.05	50	3.37	10.11	505.3	93.6	33.5	60.1	165.1	63.1	3.0	60.1
4	50	2.246	3	6.74	25	5.61	16.84	421.1	326.5	213.2	113.3	134.7	117.2	4.0	113.2
5	25	2.807	3	8.42	25	8.42	25.26	631.6	1030.7	780.9	249.8	202.1	254.6	5.0	249.6
	775				400			2400.0	1874.8	1263.8	611.0	780.4	625.7	15.0	610.7

E(LRS)	2.0			%	E_{Random}	Net	Component	%
$\sigma^2_{k\bullet}$	10.69							
		SST•	4274.8		1406.1	2868.7	Random	32.9
		SSE•	2400.0	56.1	780.4	1619.6	Within	37.9
		SSB•	1874.8	43.9	625.7	1249.0	Between	29.2
		Age	1263.8	29.6	15.0	1248.8	Age	29.2
		Longevity	611.0	14.3	610.7	0.3	Longevity	<0.1

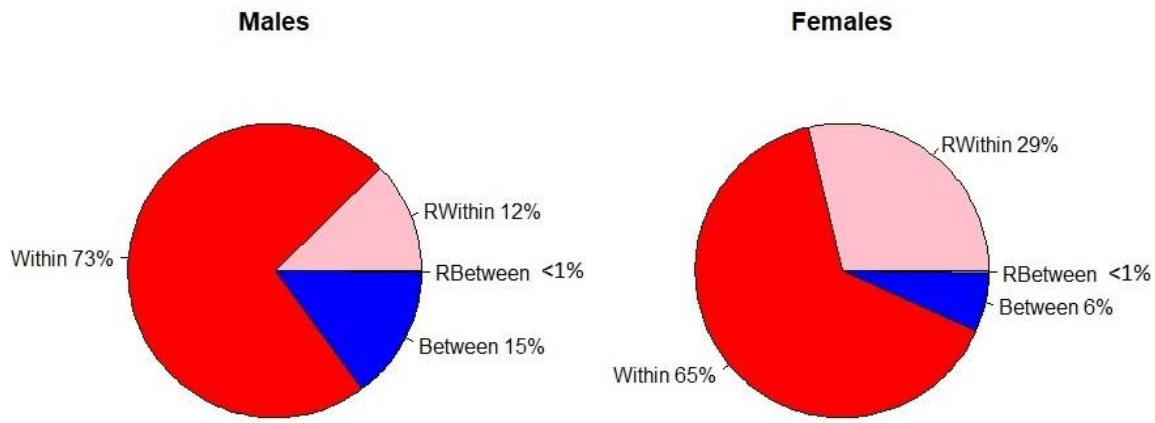

Figure 1. Relative contributions of random (denoted by initial 'R'), net within-age, and net between-age effects to seasonal variance in offspring number (σ_k^2) in black bears from Michigan. Results for males are from Table 2 and those for females are from Table S4.

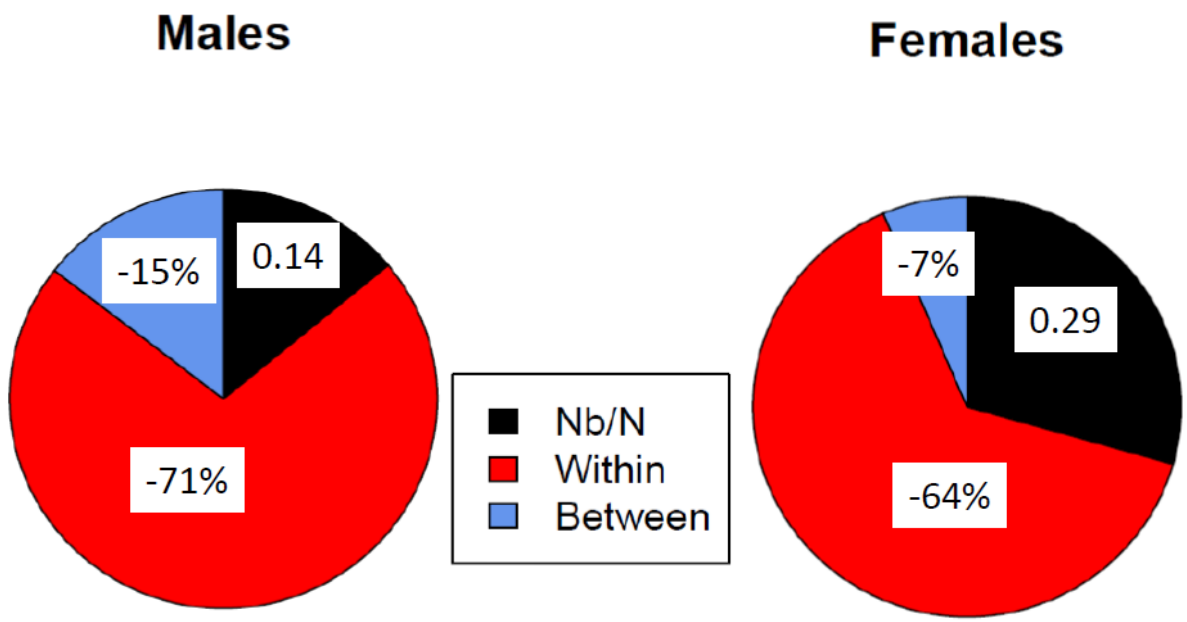

Figure 2. Relative contributions of within-age and between-age components of seasonal variance in offspring number (σ_k^2) to the N_b/N ratio for black bears from Michigan. Random variation in reproductive success already is accounted for in reducing the N_b/N ratio to 1.0, so results depicted apply to the net (>random) variance components. Across all adults breeding in a given year, σ_k^2 is higher in males, so N_b/N is lower (0.14) than in females (0.29). Based on the variance partitioning results in Figure 1, for both sexes most of the total reduction in N_b/N (86% for males and 71% for females) can be attributed to variance in offspring number among individuals of the same age.

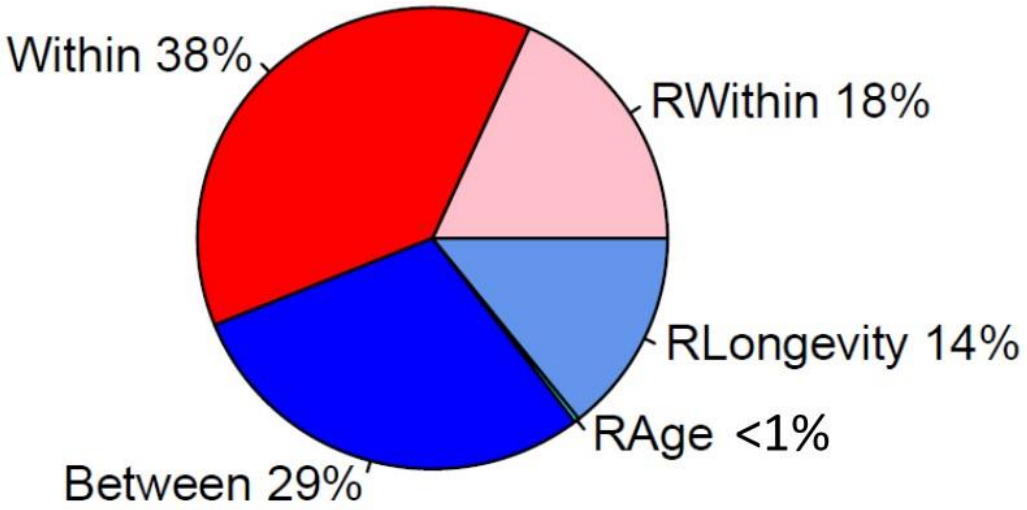

Figure 3. Results of partitioning lifetime variance in offspring number, using data from Table 4. Of the overall $\sigma^2_{k\bullet}$, 56% (reddish slices) can be attributed to within-treatment effects and 44% (bluish slices) to between-treatment effects. Of the total, 32% (paler slices) can be attributed to random stochasticity, leaving 38% and 29% (bolder colors) for the net (non-random) within-treatment and between-treatment effects, respectively. Most of the stochastic contributions are attributable to random variation in reproductive success among individuals that die at the same age (RWithin) and random variation in longevity (RLongevity); random between-age effects (RAge) account for <1% of the total $\sigma^2_{k\bullet}$.

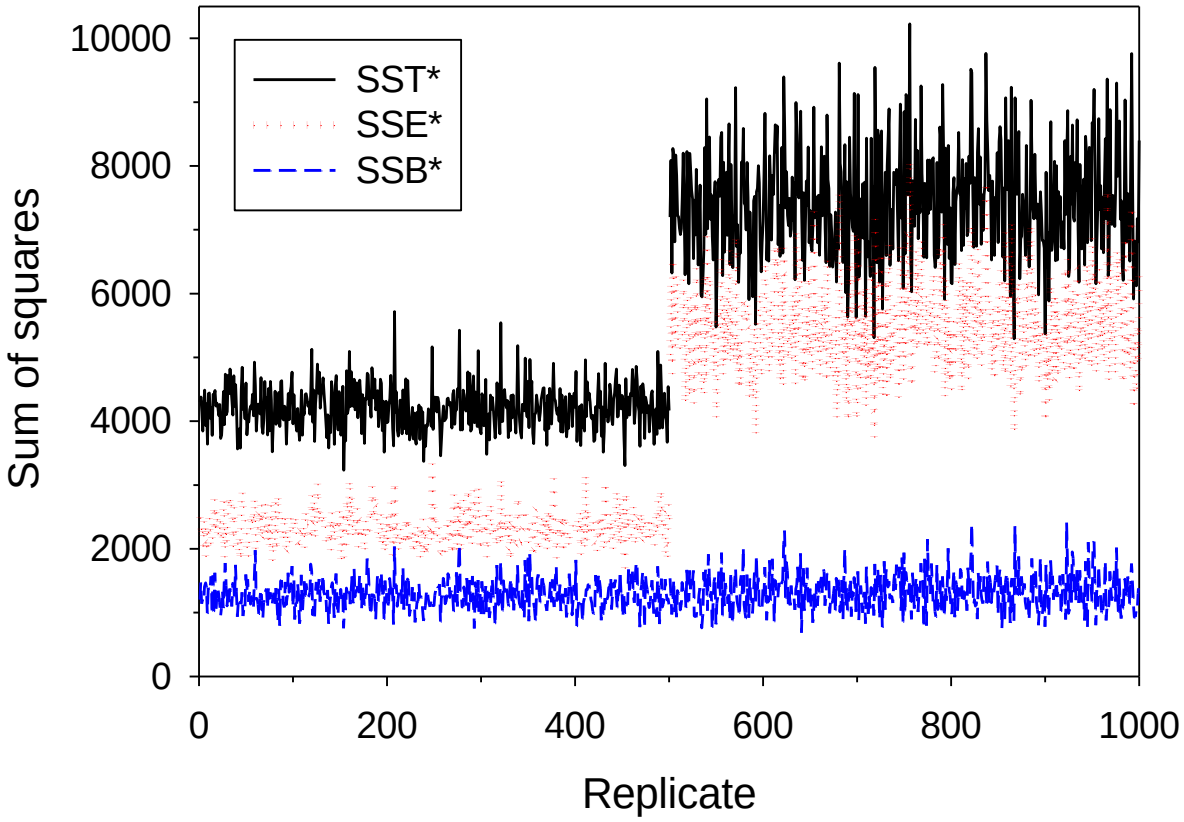

Figure 4. Results of simulations of *LRS* using the vital rates shown in Table 4. The *Y* axis shows the sum of squares for the three variance components, with age at death being the treatment. On the *X* axis, in replicates 1-500 parental weights were shuffled each year, so there were no persistent individual differences in reproductive success. In replicates 501-1000, the same parental weights were retained across individual lifetimes, which introduced positive correlations in realized reproductive success across time; this had no effect on *SSB* but sharply increased *SSE* and hence *SST*.