An estimator of the Opportunity for Selection that is independent of mean fitness

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Abstract

In the 1950s, James Crow introduced two indices of reproductive success that depend on mean ($\bar{k}$) and variance (V_k) in offspring per parent. The Index of Variability ($\varphi = V_k/\bar{k}$) is the primary factor determining effective population size (N_e). The Index of Total Selection ($I = V_k/\bar{k}^2 = \varphi/\bar{k}$; aka Opportunity for Selection) is the variance in relative fitness and sets an upper limit to the rate of change of fitness through selection, given population demographics. Because both φ and I depend on sample $\bar{k}$, some authors have concluded that I is not suitable for drawing inferences about selection. However, a simple method Crow introduced to rescale φ to remove dependence on $\bar{k}$ has not been routinely applied to I. A new index is introduced, $\Delta_I = I - E(I_{drift})$, which removes the dependence of I on sample $\bar{k}$ without the need for rescaling φ. Δ_I has a straightforward interpretation as the component of variance in relative fitness that exceeds the value expected under a null model of random variation in reproductive success. Δ_I could be used to directly compare empirical estimates of the Opportunity for Selection from different studies; different samples; samples from different life stages; or males and females when sex ratio is uneven.

Introduction

Over a half century ago, James Crow introduced two indices that quantify variation in reproductive success (RS) among individuals, based on the mean ($\bar{k}$) and variance (V_k) in the number of offspring per individual. Crow and Morton (1955) defined the ratio $V_k/\bar{k}$ as the Index of Variability, denoted here by φ. With random RS of N parents, the expect variance in offspring number due to drift [E($V_{k(\text{drift})}$)] takes the binomial variance $\bar{k}(N\text{-}1)/N$, which is often approximated by the Poisson variance $V_k = \bar{k}$, leading to E(φ_{drift}) ≈ 1. Therefore, the Index of Variability is a useful indicator of the degree to which variance in offspring number is overdispersed ($V_k/\bar{k} > 1$), which in turn has a strong influence on the effective population size (N_e) and the key ratio N_e/N. Shortly thereafter, Crow (1958) defined the parameter $I = V_k/\bar{k}^2 = \varphi/\bar{k}$, which he called the Index of Total Selection, but subsequent authors generally refer to this as the Opportunity for Selection (Arnold and Wade 1984a,b; Clutton-Brock 1988; Brodie et al. 1995). Crow's I measures "the total amount of selection possible, given the demographics of a population. It answers the question, By what fraction would the mean population fitness increase in one generation of selection if its heritability were perfect (i.e., $h^2 = 1$)?" (Crow 1989, p 776). The Opportunity for Selection thus sets an upper limit to the evolutionary response to selection; mathematically, I also represents the variance in relative fitness (Walsh and Lynch 2018).

Crow and Morton (1955) showed that the Index of Variability is very sensitive to sample $\bar{k}$, and it is well known that Crow's I also depends on mean offspring number (= mean fitness) in the sample. In a stable population of diploids, each parent contributes on average half the genes to two adult offspring; therefore, assuming exhaustive sampling of offspring, $\bar{k} = 2$. However, $\bar{k} > 2$ is possible for increasing populations, or when sampling juvenile offspring of a highly fecund species (e.g., a marine fish); conversely, $\bar{k}$ can be <2 for declining populations or when only a portion of the offspring are sampled. Therefore, sampling from real populations in nature can produce a wide range of estimated $\bar{k}$ values, even when the population is stable. Dependence of φ and I on $\bar{k}$ means that, based on experimental design and sampling effort, the same underlying biological process could lead to very different conclusions about the distribution of RS and the Opportunity for Selection. For this reason, a number of authors have questioned the practical utility of Crow's I for drawing inferences about natural selection (Trail 1985; Downhower et al. 1987; Fairbairn and Wilby 2001).

This topic merits a new look, for two reasons. First, Crow and Morton (1955) proposed a simple solution to the problem caused by dependence of the Index of Variability on $\bar{k}$: one can rescale φ to its expected value at a different mean offspring number using the following equation:

$$E(\varphi_2) = 1 + \frac{\bar{k}_2}{\bar{k}_1}(\varphi_1 - 1) \quad , \qquad (1)$$

where $\bar{k}_1$ is mean offspring number in the initial sample, $\bar{k}_2$ is the target mean offspring number, φ_1 is the initial Index of Variability, and φ_2 is the rescaled index. Equation 1 solves for the

expected value of φ, assuming random mortality of offspring until the target $\bar{k}$ is reached. Statistically, this is equivalent to randomly sampling fewer offspring in the first place. Setting $\bar{k}_2$ = 2 yields the expected value of φ for a constant population that is exhaustively sampled. Waples (2002) showed that Equation 1 also can be used for the common situation where $\bar{k}_1$ < 2; in this case, the result is the value of φ one would expect to find if the same offspring distribution were sampled more intensively, until $\bar{k}_2$ = 2. There is nothing magical about scaling to $\bar{k}_2$ = 2, but it is a useful reference point because most populations that persist for any period of time must have a long-term mean offspring number close to 2. Because of the simple relationship between *I* and φ, Crow and Morton's method for rescaling φ can also be applied to *I* to remove the dependence on the sample mean. However, few published papers cite both Crow (1958) and Crow and Morton (1955). Crow himself did not mention the 1955 variance-rescaling method in either his original 1958 paper introducing the Index of Total Selection or his 1989 retrospective. Wade and Arnold (1980) noted that the Crow and Morton method could be used to scale *I* to a constant $\bar{k}$ = 2, but subsequent papers of theirs (e.g., Arnold and Wade 1984a,b) did not follow up on this idea. In their meta-analysis of published data for the Opportunity for Selection, Cabana and Kramer (1991) showed that empirical estimates of *I* were in general agreement with predictions of Equation 1, but they did not report rescaled *I* values. Therefore, it is important to evaluate the degree to which rescaling raw *I* values can resolve ongoing controversies regarding the Opportunity for Selection.

The second interesting issue is that, under random RS, the Opportunity for Selection has a simple expectation: $E(I_{\text{drift}}) = E(\varphi)/\bar{k} \approx 1/\bar{k}$. Downhower et al. (1987) suggested, but did not recommend, that the difference between empirical *I* and $1/\bar{k}$ might be used to compare *I* values from different studies. Their logic was that the result would still be a ratio, and ratios have some undesirable statistical properties. As demonstrated below, Downhower et al.'s idea has some real merit: Although both empirical *I* and $E(I_{\text{drift}})$ depend on sample $\bar{k}$, their difference does not and hence is independent of mean fitness in the sample.

Here, analytical and numerical methods are used to explore the relationship between Crow's Index of Variability and the Opportunity for Selection. Objectives are to: (1) Illustrate the effects of rescaling φ and *I* to a constant $\bar{k}$ = 2, under three different reproductive systems: random reproductive success, and moderate and strong reproductive skew. (2) Introduce a new index $\Delta_I = I - E(I_{drift})$ and show that this removes the dependence of *I* on mean offspring number, without any need for rescaling to constant population size. Δ_I adjusts the raw *I* for the expected contribution under random RS and hence represents the component of variance in relative fitness that exceeds that due to random demographic stochasticity. (3) Examine an index of relative resource monopolization (*Q*) proposed by Ruzzante et al. (1997) for evaluating the Opportunity for Selection, but recast the index in terms of *I* rather than the variance in offspring number. (4) Use raw and scaled RS data to calculate inbreeding and variance effective sizes and show that, unlike variance N_e, inbreeding N_e is not sensitive to the scaling issues that affect φ. This makes inbreeding N_e much more generally useful for analysis of empirical data for natural populations, which produce a wide range of mean offspring numbers in samples.

Methods

Analytical model

The model used here assumes a diploid species with separate sexes. Initially it is also assumes discrete generations, but later that assumption will be relaxed to account for age structure. The simplest way to analyze Crow's indices is to treat each sex separately. Consider a population of N adults (N_m males and N_f females) that produces N_{Off} offspring that can be assigned to parents. For illustration, reproductive success is tracked only for females, but exactly equivalent results apply to males. The fraction of adults that are female is $f = N_f/N$, so $N_f = f*N$. The mean number of offspring per female is $\bar{k} = N_{Off}/N_f = N_{Off}/(f*N)$. If the population is stable and offspring are exhaustively sampled as adults, $N_{Off} = N$ and $\bar{k} = 1/f$. If in addition the adult sex ratio is equal ($f = 0.5$), $\bar{k} = 2$ for each sex.

Both of the 1s in Crow and Morton's Equation 1 are a consequence of using the Poisson approximation that $E(\varphi_{drift}) \approx 1$. As shown below, although the difference between the exact $E(\varphi_{drift}) = (N-1)/N$ and the Poisson approximation is generally small, this difference can become important when mean offspring number also is small. Therefore, I also considered the following adjustment to Crow and Morton's formula for rescaling the Index of Variability:

$$E(\varphi_2) = (N-1)/N + \frac{\bar{k}_2}{\bar{k}_1}(\varphi_1 - (N-1)/N) \quad . \tag{1A}$$

For the Opportunity for Selection, random reproductive success produces the following expectation:

$$E(I_{drift}) \approx E(\varphi)/\bar{k} = \frac{(N_f-1)/N_f}{\bar{k}} \approx \frac{1}{S/N_f} = N_f/S = 1/\bar{k}. \tag{2}$$

That is, under a pure drift model, the expected value of the Opportunity for Selection is essentially the inverse of the mean offspring number per parent (Downhower et al. 1987).

It is useful to define new metrics Δ_φ and Δ_I, which are obtained by subtracting the random expectation from the raw value of the index. Letting subscript 1 represent raw data and subscript 2 rescaled data, we have:

$$\Delta_{\varphi 1} = \varphi_1 - E(\varphi_{drift}) = \varphi_1 - (N_f-1)/N_f \approx \varphi_1 - 1;$$

$$\varphi_2 = 1 + \frac{\bar{k}_2}{\bar{k}_1}(\varphi_1 - 1);$$

$$\Delta_{\varphi 2} = \varphi_2 - E(\varphi_{drift}) \approx \frac{\bar{k}_2}{\bar{k}_1}(\varphi_1 - 1).$$

Thus, $\Delta_{\varphi 1}$ and $\Delta_{\varphi 2}$ differ by the factor $\bar{k}_2/\bar{k}_1$. Δ_φ quantifies the degree of overdispersion in V_k, but since the adjustment only involves subtracting a constant, Δ_φ still depends on $\bar{k}_1$, regardless whether raw or scaled values are used.

Results are different for the Opportunity for Selection:

$$I_1 = \frac{\varphi_1}{\bar{k}_1};$$

$$\Delta_{I1} = I_1 - \frac{(N_f - 1)/N_f}{\bar{k}_1} \approx I_1 - \frac{1}{\bar{k}_1} = \frac{1}{\bar{k}_1}(\varphi_1 - 1);$$

$$I_2 = \frac{\varphi_2}{\bar{k}_2} \approx \frac{1}{\bar{k}_2} + \frac{1}{\bar{k}_1}(\varphi_1 - 1);$$

$$\Delta_{I2} \approx I_2 - \frac{1}{\bar{k}_2} = \frac{1}{\bar{k}_1}(\varphi_1 - 1).$$

Therefore,

$$\Delta_{I1} = \Delta_{I2} = \Delta_I = \frac{1}{\bar{k}_1}(\varphi_1 - (N_f - 1)/N_f) \text{ (exact);} \tag{3A}$$

$$\Delta_I \approx \frac{1}{\bar{k}_1}(\varphi_1 - 1) \text{ (Poisson approximation).} \tag{3B}$$

Notably, the Opportunity for Selection, adjusted to account for the contribution from random RS, is the same whether it is calculated for raw or rescaled values of I (hence independent of $\bar{k}_2$). Furthermore, it can be shown that Δ_I is also independent of $\bar{k}_1$. Rearranging Equation 1 produces

$$(\varphi_1 - 1) = (\varphi_2 - 1)\frac{\bar{k}_1}{\bar{k}_2}, \text{ so}$$

$$\Delta_I \approx \frac{1}{\bar{k}_1}(\varphi_2 - 1)\frac{\bar{k}_1}{\bar{k}_2} = \frac{1}{\bar{k}_2}(\varphi_2 - 1).$$

When scaling to $\bar{k}_2 = 2$, this reduces to

$$\Delta_I \approx \frac{\varphi_2 - 1}{2}. \tag{4}$$

It also can be useful to identify upper limits to possible values for V_k, φ, and I. For this purpose, we use the relationship that the unbiased sample variance is $n/(n-1)$ times the mean of the squares minus the square of the mean: $V_k = [N_f/(N_f - 1)]\,[\sum(k_i^2)/N_f - \bar{k}^2]$. The maximum possible V_k occurs when one parent produces all S offspring, in which case (using the relationship that $S = N_f * \bar{k}$):

$$V_{k(MAX)} = [N_f/(N_f - 1)][S^2/N_f - \bar{k}^2] = [N_f/(N_f - 1)][N_f\,\bar{k}^2 - \bar{k}^2] = N_f\,\bar{k}^2; \tag{5}$$

$$\varphi_{(MAX)} = N_f\,\bar{k}^2/\bar{k} = N_f\,\bar{k} = S; \tag{6}$$

$$I_{(MAX)} = N_f\,\bar{k}/\bar{k} = N_f. \tag{7}$$

Using a different approach, Ruzzante et al. (1996) also derived Equation 5 and used $V_{k(MAX)}$ to define an index of relative resource monopolization as

$$Q = \frac{V_k - \bar{k}}{V_{k(MAX)} - \bar{k}}\ .$$

Q is the ratio of the empirical variance in offspring number to the maximum possible variance, after both have been adjusted by subtracting the expected value under Poisson variance in RS ($\bar{k}$). In the current notation, $Q = \Delta_{Vk}/\Delta_{Vk(MAX)}$. As a result of this standardization, Q is independent of mean RS. However, as noted by Fairbairn and Wilby (2001), because Q is calculated using the variance in RS rather than I, it is not readily interpretable in terms of the Opportunity for Selection. A more useful index for this purpose is

$$Q_I = \frac{\Delta_I}{I_{MAX} - E(I_{drift})} \approx \frac{\Delta_I}{N_f - 1/\bar{k}}\ , \tag{8}$$

which uses I directly.

In many species, fecundity (in terms of clutch size or little size) is limited to a relatively small number, which constrains how large these maximum values can be. If X is the maximum number of offspring one female can produce, then constrained $V_{k(MAX)\$}$ occurs when S/X females each produce X offspring and the rest produce none. In that case, $\sum(k_i^2) = (S/X)X^2 = SX$ and

$$V_{k(MAX)\$} = [N_f/(N_f-1)][SX/N_f - S^2/N_f^2] = [N_f\,\bar{k}/(N_f-1)][X-\bar{k}]; \tag{9}$$

$$\varphi_{(MAX)\$} = [N_f/(N_f-1)][X-\bar{k}]; \tag{10}$$

$$I_{(MAX)\$} = [N_f/(N_f-1)][X/\bar{k} - 1]. \tag{11}$$

For the special case where $X = S$ (no effective constraints on litter size), $V_{k(MAX)\$}$ reduces to $S^2/N = S\bar{k} = N_f\,\bar{k}^2 = V_{k(MAX)}$, and $\varphi_{(MAX)\$}$ and $I_{(MAX)\$}$ also reduce to the unconstrained values $\varphi_{(MAX)}$ and $I_{(MAX)}$ shown above.

Simulations

To this point all variables have been defined as population parameters, but in most real populations researchers have to estimate these parameters from samples. Offspring can be sampled at a variety of life stages and with variable sampling intensity, so mean offspring number and other parameters estimated from a sample can vary widely. In what follows, estimates of population parameters are denoted by a "hat" (^).

To generate empirical RS data with a range of mean offspring numbers, female parents were randomly chosen for each of N_{Off} offspring, with $N_{Off} >> N_f$. Next, random subsamples of different numbers of offspring (S) were taken to produce a series of raw $\hat{\bar{k}}_1$ values, with $\hat{\bar{k}}_1 = S/N_f$. Three reproductive scenarios were considered. (1) Each female was equally likely to be the parent of every offspring (equal parental weights; $W_1 = 1, 1, \ldots 1$). This modeled Wright-Fisher dynamics with random and independent reproductive success among females. (2) Moderate reproductive skew created by unequal weighting of parents ($W_2 = 1, 2, 3, \ldots N_f$). (3) Stronger reproductive skew created by more unequal parental weights ($W_3 = W_2^2$). Both for the raw data and after scaling to constant N, $\hat{\bar{k}}$, $\hat{V}_k$, $\hat{\varphi}$, and $\hat{I}$ were calculated for each sample size for each of 1,000 replicates, with 10-fold additional replication for $\bar{k} < 1$. Because the ratios $\hat{\varphi}$ and $\hat{I}$ are upwardly skewed, geometric means across replicates were used as measures of central tendency.

The Index of Variability can also be used to calculate effective population size (Crow and Denniston 1988):

$$\text{Inbreeding } N_e = \frac{\bar{k}N_f - 1}{\bar{k} - 1 + {V_k}/{\bar{k}}}; \tag{12}$$

$$\text{Variance } N_e = \frac{\bar{k}(2N_f - 1)}{2(1 + {V_k}/{\bar{k}})}. \tag{13}$$

These equations give effective size for a single sex, and Eq. 13 ignores the (generally minor) adjustment for departure from Hardy-Weinberg genotypic proportions. Both effective sizes were estimated using geometric means of $\hat{\bar{k}}$, $\hat{V}_k$, and raw and scaled $\hat{\varphi}$ from the simulated RS data. If effective size is calculated separately for males and females (N_{em}, N_{ef}), overall N_e can be obtained using Wright's (1938) sex ratio adjustment: $N_e = 4N_{em}N_{ef} / (N_{em} + N_{ef})$.

Results

Equations 1A, 3-4, and 6-11 in Methods are new and their practical implications are illustrated using the simulated data. Figures 1-3 show results for a representative scenario with $N_f = 100$ adult females and $N_{Off} = 10^4$ total offspring. Taking a series of random subsamples of offspring ($S = 10 \ldots 5000$) produced results for sample $\hat{\bar{k}}_1$ spanning three orders of magnitude (0.1 – 100).

Crow's indices

Sensitivity of both raw $\hat{\varphi}_1$ and raw $\hat{I}_1$ to sampling intensity is apparent; the one exception is for φ under random RS, in which case $\hat{\varphi}_1 \approx 1$ regardless what $\hat{\bar{k}}_1$ is (Figure 1A). But with overdispersed variance in RS, $\hat{\varphi}_1$ increases strongly with $\hat{\bar{k}}_1$ (raw $\hat{\varphi}_1 > 80$ for $\hat{\bar{k}}_1 = 100$ under

strong reproductive skew). Underdispersed variance in RS produces the mirror-image pattern: raw $\hat{\varphi}_1$ is very low (<<1) when $\hat{\bar{k}}_1$ >> 2 and converges on 1 as $\hat{\bar{k}}_1$ approaches 0 (Appendix A and Figure S1). It is apparent from Figure S1 that sparse sampling of offspring will generally have a poor chance of detecting underdispersed variance in reproductive success, even when underdispersion is pronounced.

For the scenarios depicted in Figure 1, both $\hat{I}_1$ and $\hat{\bar{k}}_1$ span 3 orders of magnitude, and stronger reproductive skew produces larger values of $\hat{I}_1$. However, whereas $\hat{\varphi}_1$increases with $\hat{\bar{k}}_1$ when RS is overdispersed, $\hat{I}_1$ shows the opposite pattern: the Opportunity for Selection is negatively correlated with mean offspring number (Downhower et al. 1987; Cabana and Kramer 1991).

Scaling raw $\hat{\varphi}_1$ and $\hat{I}_1$ values to a fixed $\bar{k}_2$ = 2 removes the dependence on mean offspring number for both indices (Figure 1B). This figure used the modified Equation 1A to rescale φ; use of the Poisson approximation in Crow and Morton's formula (Equation 1) produces a slight bias when $\hat{\bar{k}}_1 < \bar{k}_2$ (Figure S2). The scaled values in Figure 1B, obtained from the raw values in Figure 1A using Equation 1A, are the same values identified in Figure 1A by the intersection of the vertical line for $\bar{k}_2$ = 2 and the curves for the empirical data. That is, subsampling from the original data to reach $\bar{k}_2$ = 2 produces the same result as scaling the raw data using the modified Crow and Morton's method. This demonstrates that Equation 1A is also useful for removing the dependence of the Opportunity for Selection on $\hat{\bar{k}}_1$. Note, however, that for both $\hat{\varphi}_2$ and $\hat{I}_2$, the magnitude of the rescaled values depends on choice of $\bar{k}_2$.

Independence of $\hat{\Delta}_I$ from both raw and scaled $\bar{k}$ is illustrated in Figure 1. Although it is not visually apparent with the log scaling of the Y axis, for strong reproductive skew the two $\hat{\Delta}_{I1}$ values for different $\hat{\bar{k}}_1$in Figure 1A are the same ($\hat{\Delta}_{I1}$ = 0.8), and both are equal to rescaled $\hat{\Delta}_{I2}$ from Figure 1B ($\hat{\Delta}_{I2} = \frac{\hat{\varphi}_2 - 1}{2} = \frac{2.6-1}{2} = 0.8$ using Equation 4).

In the simulations, the estimator $\hat{Q}_I = \hat{\Delta}_I/(\hat{I}_{MAX}\text{-}1/\hat{\bar{k}}_1)$ (modified from Ruzzante et al. 1996 according to Eq. 8) was independent of sample $\hat{\bar{k}}_1$, under both random and overdispersed variance in RS (Figure 2). Equations 6 and 7 show that maximum possible $\hat{\varphi}$ is just the number of offspring sampled (*S*), whereas the maximum possible $\hat{I}$ is the number of parents. These results show that $\hat{Q}_I$ could be useful in quantifying the effects of resource monopolization in the context of the Opportunity for Selection (Ruzzante et al. 1996; Fairbairn and Wilby (2001). As outlined in Methods and shown in Equations 9-11, for some species it also can be important to account for constraints on litter or clutch size when estimating the maximum possible variance ($V_{k(MAX)}$) and related indices. Waples et al. (2018) used a litter-constrained estimate of $V_{k(MAX)\$}$ to estimate $\varphi_{(MAX)\$}$ and female effective size in black bears (*Ursus americanus*), based on empirical data indicating that a female could not successfully raise more than 3-4 cubs in one year.

Effective population size

The central importance of $\varphi = V_k/\bar{k}$ to N_e is apparent, as the term appears in the denominator of both Equations 12 and 13. With random RS, $E(\hat{\varphi}_1) \approx 1$ and inbreeding $\hat{N}_e \approx \hat{\bar{k}}_1 N_f/\hat{\bar{k}}_1 = N_f$, regardless what $\hat{\bar{k}}_1$ is because inbreeding N_e depends on the number of parents (Crow 1954). In contrast, in Equation 13 for variance N_e, the $\bar{k}$ term in the numerator is not balanced by a separate $\bar{k}$ term in the denominator, and as a consequence variance $\hat{N}_e$ depends heavily on mean offspring number in a sample. This effect is apparent in Figure 3A, which uses the RS data from Figure 1 to estimate inbreeding and variance N_e as a function of mean offspring number. Inbreeding $\hat{N}_e$ is invariant with $\hat{\bar{k}}_1$ for all reproductive scenarios, whereas variance $\hat{N}_e$ is directly proportional to $\hat{\bar{k}}_1$ for random RS and has a more complex but positive correlation with $\hat{\bar{k}}_1$ when variance in RS is overdispersed. The two effective sizes are the same only when $\hat{\bar{k}}_1 = 2$, indicative of a stable population (Crow 1954). Rescaling $\hat{\varphi}_1$ to its expectation for a population of constant size removes the dependence of variance $\hat{N}_e$ on mean offspring number (Figure 3B). Rescaling to $\bar{k} = 2$ actually produces identical values for variance and inbreeding $\hat{N}_e$; in Figure 3B, the rescaled variance $\hat{N}_e$ is plotted against the raw inbreeding $\hat{N}_e$ to illustrate why it is not necessary to rescale sample $\hat{\varphi}_1$ when estimating inbreeding N_e.

Age structure

All of the above analyses have implicitly assumed that generations are discrete. Because most species are age structured (Hughes 2017), this is an important limitation. In age-structured species having birth-pulse reproduction (Caswell 2001), there are two major ways to calculate the mean and variance in reproductive success: 1) seasonal RS among all mature individuals during a single year or reproductive season; 2) lifetime RS among all individuals born into the same cohort. In this section I consider some of the consequences of age structure for Crow's indices of RS and related analyses.

Index of Variability

Analysis of seasonal RS conforms to the discrete-generation model, with one exception: RS for all adults in a single season can be partitioned by parental age. Seasonal reproduction within an age-structured population can be described by vectors of age-specific mean RS and age-specific variance in RS: $\hat{\bar{k}}_{1x}$ and $\hat{V}_{k1x}$, where x indicates age. $\hat{\bar{k}}_{1x}$ is an estimate of the familiar b_x (or m_x) from a standard life table, published data for which are available for many species. $\hat{V}_{k1x}$ is the analogous age-specific variance, but empirical estimates of this key parameter are seldom published. The ratio of the age-specific variance and mean is $\hat{\varphi}_{1x}$ (Waples et al. 2011; Waples 2016), which also is rarely reported in the literature.

As is the case with discrete generations, $\hat{V}_{k1x}$ and $\hat{\varphi}_{1x}$ are sensitive to $\hat{\bar{k}}_{1x}$. These indices can be rescaled to a different mean offspring number using Equation 1, but there is a complication: it is not generally the case that scaling to $\bar{k}_x = 2$ will produce results expected for

a stable population. Instead, $\hat{V}_{k1x}$ and $\hat{\varphi}_{1x}$ can be rescaled to the vector of b_x values that produce a stable population. This requires that measures of relative, age-specific RS be converted to measures of absolute RS by ensuring that $\Sigma l_x b_x = 2$, where l_x is cumulative survival through age x. This in turn requires knowing or being able to estimate age-specific survival rates. Table 2 in Waples et al. (2018) shows how $\hat{V}_{k1x}$ and $\hat{\varphi}_{1x}$ can be rescaled to constant size in a species with overlapping generations.

Effective size

For seasonal reproduction Equations 12 and 13 can be used to estimate effective size, but in this case the estimate applies to the effective number of breeders per year or season (N_b) (Waples 1990; 2016) rather than N_e per generation. For this purpose, the vectors of $\hat{\bar{k}}_{1x}$ and $\hat{V}_{k1x}$ values are converted into scalars ($\hat{\bar{k}}_1$, $\hat{V}_{k1}$) that reflect seasonal RS for adults of all ages. Because of its insensitivity to mean offspring number, inbreeding effective size is much more generally useful for analysis of data for age-structured species. Regardless what sample $\hat{\bar{k}}_1$ is, Equation 12 can be used to estimate seasonal inbreeding N_b, without the need to rescale RS indices.

Lifetime reproductive success is generally measured for all members of a single cohort. Hill (1972) provided the most general formula for N_e when generations overlap:

$$N_e \approx \frac{4N_1T}{V_{k\bullet}+2} \quad , \tag{14}$$

where T = generation length and $V_{k\bullet}$ is the lifetime variance in reproductive success among the N_1 members of a cohort. In a stable population with overlapping generations, lifetime mean offspring number ($\bar{k}\bullet$) must be 2, which appears in the denominator of Equation 14. When dealing with empirical data based on samples, therefore, rescaling the empirical $\hat{V}_{k\bullet}$ to its expected value at $\bar{k}\bullet = 2$ is appropriate when estimating generational N_e using Hill's equation. Accumulating enough longitudinal demographic data to estimate lifetime RS parameters is very challenging (e.g., see Clutton-Brock 1988). However, if one adopts the assumptions of Hill's model (stable age structure and population size; independence of survival and reproduction across time), lifetime $V_{k\bullet}$ and hence N_e can be estimated from the program *AGENE* (Waples et al. 2011), which uses data from a standard life table (age-specific survival and fecundity), plus the age-specific parameter $\hat{\varphi}_x$.

Opportunity for Selection

The previous section showed that it can be important to partition the overall variance in RS among adults in one year or season ($\hat{V}_k$) into components that account for systematic difference in mean RS by age (b_x) and differences among individuals of the same age and sex ($\hat{V}_{k1x}$). In contrast, the concept of age-specific Opportunity for Selection isn't particularly meaningful. Nevertheless, Crow's I can be (and often is) calculated in two fundamentally different ways: (1) among all individuals reproducing in a single year or season, and (2) among all individuals in a single cohort. When applied to seasonal RS data, $\hat{I}_1 = \hat{V}_{k1}/(\hat{\bar{k}}_1)^2$ and $\hat{\Delta}_{I1} = \hat{I}_1 -$

$E(\hat{I}_{drift}) \approx \hat{I}_1 - 1/\bar{k}$. As is the case with discrete-generation data, $\hat{\Delta}_I$ for seasonal reproduction is independent of mean offspring number in the sample, whether raw or scaled data are used.

When applied to lifetime RS data for members of a cohort, $\hat{I}_\bullet = \hat{V}_{k1}\bullet/(\hat{\bar{k}}_1\bullet)^2$ is appropriate when estimating the Opportunity for Selection across a generation. Calculation of $E(\hat{I}_{\bullet\mathrm{drift}})$ for lifetime RS is complicated by the necessity of considering random stochasticity in both survival and reproduction over the lifetimes of individuals. In general, even under a null model that assumes all individuals in a cohort experience the same age-specific probabilities of survival and reproduction, $E(\hat{V}_{k1}\bullet)$ will exceed $E(\hat{\bar{k}}_1\bullet)$ because some individuals, by chance, survive longer than others and have more opportunities to reproduce. It does not appear that an analytical approximation is currently available for lifetime $E(\hat{I}_{\bullet\mathrm{drift}})$. However, under the null model, a stochastic, absorbing Markov chain model with rewards developed by Caswell and colleagues (Caswell 2011; van Daalen and Caswell 2017) can be used to calculate lifetime $E(\hat{I}_{\bullet\mathrm{drift}})$ and hence lifetime $\hat{\Delta}_{I\bullet}$, given information on age-specific vital rates from a standard life table. A limitation of the Caswell model is that it implicitly assumes that $\varphi_x \approx 1$ for each age and sex. The *AGENE* model is more general, as it allows for age-specific and sex-specific values of φ_x, but has the limitation that it is deterministic. Age-structured simulations have shown, however, that *AGENE* accurately predicts lifetime $\hat{V}_k\bullet$ and N_e under conditions of random demographic stochasticity, as envisioned by Caswell and colleagues (Waples et al. 2014). Therefore, lifetime $\hat{V}_k\bullet$, calculated in *AGENE* after setting $\varphi_x = 1$ and assuming lifetime $\bar{k}\bullet = 2$, could be used to estimate $E(\hat{I}_{\bullet\mathrm{drift}})$ as $= \hat{V}_{k1}\bullet/(\hat{\bar{k}}_1\bullet)^2 = \hat{V}_{k1}\bullet/4$. From this one can estimate lifetime Δ_I as $\hat{\Delta}_{I\bullet} = \hat{I}_\bullet - \hat{V}_{k1}\bullet/4$.

Discussion

Crow's indices

Natural selection involves differential survival and reproduction of individuals with different phenotypes; if phenotypes are correlated with genotypes, selection can lead to an evolutionary response in the population. Because the number of offspring produced by an individual integrates information about both survival and reproduction, the distribution of offspring number is central to the quantitative analysis of natural selection. For this reason, Crow's two indices, and especially the Opportunity for Selection, have generated a great deal of discussion in the literature.

However, as is the case for Crow's Index of Variability, the Opportunity for Selection is sensitive to the mean offspring number in a sample ($\hat{\bar{k}}_1$), which means that one could reach different conclusions about the same underlying biological process, depending on experimental design and sampling effort. Unlike the situation with $\hat{\varphi}_1$, $\hat{I}_1$ depends on the sample $\hat{\bar{k}}_1$ even under random RS. Like $\hat{\varphi}_1$, $\hat{I}_1$ based on a sample can be scaled to a new mean offspring number

($\bar{k}_2$), which removes the dependence on sample $\hat{\bar{k}}_1$. However, for both indices the result still depends on choice of $\bar{k}_2$. Although an argument can be made that $\bar{k}_2$ = 2 is a logical reference point for standardizing offspring number, that is not the only plausible target for variance rescaling. Furthermore, this transformation raises the question whether rescaled $\hat{I}_2$ can still be interpreted as the variance in relative fitness.

The new index $\hat{\Delta}_I$ introduced here solves this problem by simultaneously (1) removing the dependence of $\hat{I}$ on mean fitness in the sample, without the need for rescaling variance in RS; and (2) quantifying the degree to which empirical $\hat{I}$ exceeds the value expected under a null model of random variation in RS. This means that Δ_I can be used to compare empirical estimates of the Opportunity for Selection from:

- different studies;
- different samples within the same study;
- samples taken from different life stages;
- samples of males and females when the sex ratio is uneven.

The $\hat{\Delta}_I$ index also directly addresses the need for an appropriate null model for the Opportunity for Selection, which has been pointed out by numerous authors (e.g., McClain 1986; Downhower et al. 1987; Ruzzante et al. 1996). Although the analytical and numerical methods used here modeled diploids with separate sexes, the approach could easily be extended to monoecious or haploid populations.

A case can be made that Crow's *I* can be meaningfully applied to either seasonal or lifetime RS data, and examples of both are common in the literature. Quantifying variance in lifetime RS is clearly important, as this parameter strongly influences N_e per generation and long-term evolutionary behavior of the population. Calculation of $\hat{\Delta}_{I\bullet}$ based on lifetime RS is complicated by having to account for stochastisity in both survival and reproduction propagated across the lifespan (Brommer et al. 2002), but the stochastic "Markov chain with rewards" model of Caswell and colleagues should be useful here. On the other hand, reproduction only occurs among individuals that co-occur in space and time. Furthermore, sexual selection in terms of competition for mates only occurs among individuals reproducing in the same season. Seasonal/annual data on variance in RS and the estimators $\hat{\varphi}$ and $\hat{I}$ therefore can provide valuable insights into mating systems and behavioral dynamics associated with reproduction.

Although Δ_I provides a simple way to standardize empirical estimates of Crow's *I*, interpretation of the Opportunity for Selection remains complicated. Even if $\hat{\Delta}_I$ is positive, it does not prove that natural selection is operating–it only shows that the distribution of RS is more skewed than expected under random mating dynamics. For example, family-correlated mortality following random mating leads to overdispersed variance in RS. Crow and Morton (1955) considered an extreme case of family correlated mortality, in which entire families either survive or do not as a unit. This type of result could occur in two general ways. First, survival might reflect individual survival phenotypes of the offspring or nurturing phenotypes of the parents. In this scenario, high mortality within a clutch of offspring could be due to failure of the offspring to grow quickly and avoid predators, or failure of the parent to provide food or ward

off predators. To the extent that these phenotypes have a genetic basis, this would reflect the operation of natural selection. This can be called the "bad genes" explanation for family correlated mortality.

Under an alternative scenario, most or all offspring from a family might fail to survive merely because, for a short period of time, they share a common environment. This could occur, for example, if the tree supporting a bird nest blows over in a storm, or if all the eggs a female salmon lays in the gravel get washed away during a flood. In these scenarios, survival or mortality might have nothing to do with offspring phenotypes or genotypes; instead, it could simply be a case of being in the wrong place at the wrong time, together with your siblings. This can be called the "bad luck" explanation. Parsing family-correlated survival into "bad genes" vs "bad luck" hypotheses can be complicated and is likely to be species and population specific (e.g., see Snyder and Ellner 2018). One needs to consider questions such as, "When choosing nest sites, would some birds (those with better genes) have avoided trees likely to suffer storm damage?" and "Would a bigger, stronger female salmon have dug a nest deep enough to withstand high flows, or located the nest in an area less prone to scouring?" This and related issues are why most authors refer to Crow's I as the Opportunity for Selection; his original term Index of Total Selection seems to imply a more direct link to actual natural selection.

The modified index Q_I is cast in terms of the Opportunity for Selection and might have some practical utility. However, conditions that lead to I_{MAX}, where one or a few parents produce all the offspring and all the rest none, are quite extreme for any stable population. This is the type of scenario proposed by Hedgecock (1994) in his Sweepstakes Reproductive Success hypothesis, which might apply to some marine fishes with high fecundity and Type III survivorship (Hauser and Carvalho 2008; Hedgecock and Pudovkin 2011). For species with more modest maximum offspring numbers, scaling Q using I_{MAX} will generally produce very low $\hat{Q}_I$ values even when overdispersion is relatively strong (Figure 2).

Effective size

With modern genomics technology and access to methods that can non-invasively sample DNA from individuals in the wild, parentage analyses are now routinely conducted for natural populations of many plants and animals. Such data are typically collected annually and later integrated across years. Each set of annual RS data can be used to estimate the annual effective number of breeders, N_b, and the ratio N_b/N. These demographic estimates can also be compared with single-sample genetic estimates of N_b, which are now widely applied to natural populations (Palstra and Fraser 2012; Wang 2016). Because of its sensitivity to sample $\hat{\bar{k}}_1$, variance effective size is not well-suited for these applications. Inbreeding effective size (Equation 12) is much more versatile, as the result is independent of mean offspring number in the sample.

The Hill, Caswell, and *AGENE* models for iteroparous species all assume that survival and reproduction are independent across time. Negative correlations between an individual's reproduction at ages x and $x+i$ are common in species that practice intermittent or skip breeding (Shaw and Levin 2013), and some of the consequences for estimating effective size are discussed

by Waples and Antao (2014) and in the next section. The converse scenario, in which individuals with positive (negative) residuals for RS at age x also tend to produce more (less) offspring than average at age $x+i$, implies persistent individual differences in RS, which increase lifetime $V_{k\bullet}$ and reduce N_e per generation (Lee et al. 2011, 2020). Long-term empirical datasets should capture this effect, but null models that assume independence across time would underestimate lifetime variance in RS and related indices, if persistent individual differences are important.

Sampling considerations

The above analyses have assumed random subsampling of all offspring. Family-correlated sampling, in which siblings are collected together more often than would occur by chance, can affect the estimate of mean fitness and can have complex, cascading effects on $\hat{V}_k$, $\hat{\varphi}$, and $\hat{I}$. These sampling effects can be difficult to avoid for highly fecund species when offspring are sampled at an early life stage.

For adults, a key consideration is whether sampling probability is independent of (a) an individual's reproductive success, and (b) whether its offspring also have been sampled. If both criteria are met, then randomly sampling just a portion of the adults should not lead to bias, although it would increase uncertainty in extrapolating from the sample to the population as a whole. Also, performance of some genetic parentage programs can degrade if the fraction of unsampled parents becomes too large (Jones et al. 2010), so incomplete sampling of potential parents could indirectly affect performance of indices that estimate variance of RS.

Probably the most pervasive source of potential bias in sampling adults involves those that produce no offspring. Under random RS, it is expected that some fraction of mature adults will produce no offspring in a given year/season, or even across their entire lifetime; with overdispersed variance in RS, the fraction of null parents will be higher. In practical applications, it is essential to know whether these null parents and those that actually produce offspring are equally likely to be sampled. This equiprobable-sampling criterion would be violated, for example, if potential parents are only sampled on the breeding grounds, but each year some fraction of adults skip breeding. Failing to account for these null parents would overestimate mean fitness and underestimate variance in RS and related quantities (Hadfield 2007; Klug et al. 2010; Waples and Antao 2014; van Daalen and Caswell 2019). Interestingly, failing to sample non-reproducers has no effect on inbreeding $\widehat{N}_e$; this type of sampling would affect all the parameters in Equation 12, but they change in such a way that $\widehat{N}_e$ and $\widehat{N}_b$ remain constant (Waples and Waples 2011). However, this scenario would affect the estimated N_e/N or N_b/N ratios, if some fraction of mature adults are not accounted for in the denominator.

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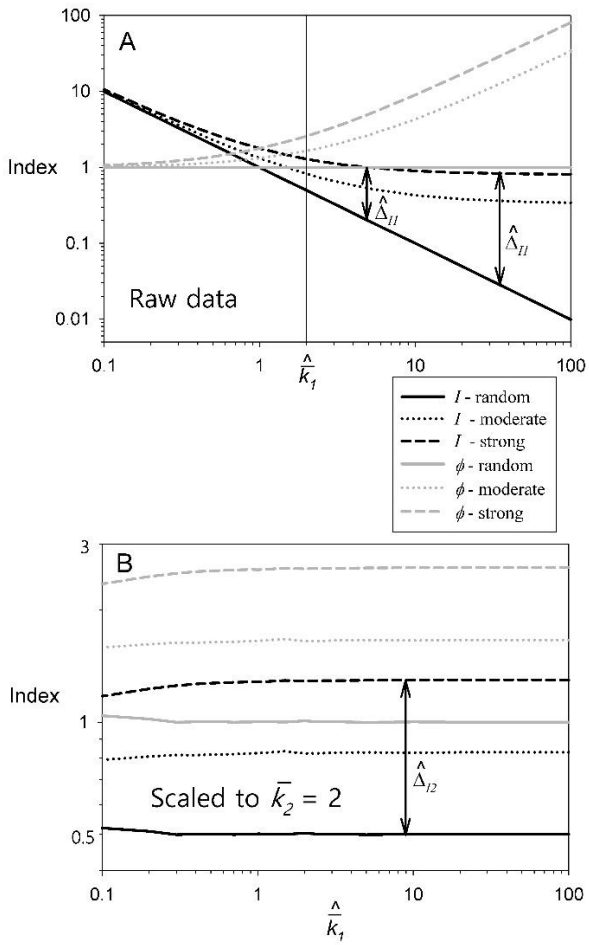

Figure 1. Dependence of Crow's Index of Variability (φ) and Opportunity for Selection (*I*) on mean number of offspring per parent ($\bar{k}$). With N_f female parents and *S* offspring in the sample, $\hat{\bar{k}} = S/N_f$. A stable population occurs when N_f female parents each contribute on average half the genes to two offspring, so $S = 2N_f$ and $\bar{k} = 2$. Sample $\hat{\bar{k}} > 2$ can occur in an increasing population or when sampling early life stages; $\hat{\bar{k}} < 2$ implies a declining population or incomplete sampling of offspring. Shown are geometric mean values of $\hat{\varphi}$, $\hat{I}$, and $\hat{\Delta}_I$ for 10,000 simulated reproductive events, using either a Wright-Fisher, random reproductive success model (each parent equally likely to produce offspring), or moderate or strong overdispersion (unequal parental weights). A: raw data, plotted as a function of mean offspring number in the original sample ($\hat{\bar{k}}_1$). B: raw data scaled to expected values at $\bar{k}_2 = 2$, using Eq. 1A. Rescaled values in panel B are essentially the same values obtained by random subsampling the original data to reach $\bar{k} = 2$ (indicated by vertical line in panel A). $\hat{\Delta}_I$ is the difference between the sample $\hat{I}$ and the expected value of $\hat{I}$ under random reproductive success. The three $\hat{\Delta}_I$ values for strong reproductive skew in the two panels (plotted at arbitrary values of $\hat{\bar{k}}_1$) are all of the same magnitude ($\hat{\Delta}_I = 0.8$).

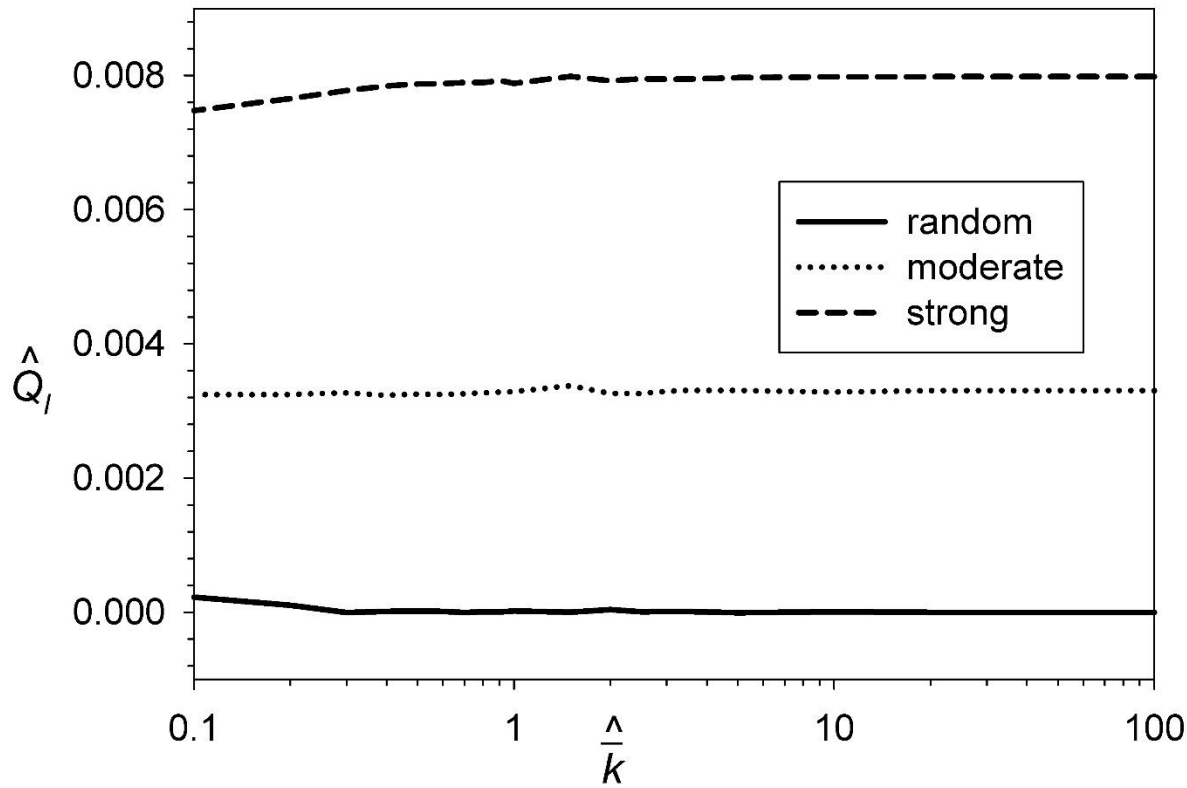

Figure 2. The Q index of relative resource monopolization, modified from Ruzzante et al. (1996) as shown in Equation 8. $\hat{Q}_I$ is the ratio of the empirical $\hat{I}$ to the maximum possible $\hat{I}$, after both have been adjusted by subtracting the expected value under random reproductive success ($E(\hat{I}_{drift})$) = $[(N_f\text{-}1)/N_f]/\ \hat{\bar{k}}$. Results are based on the same simulated data analyzed in Figure 1.

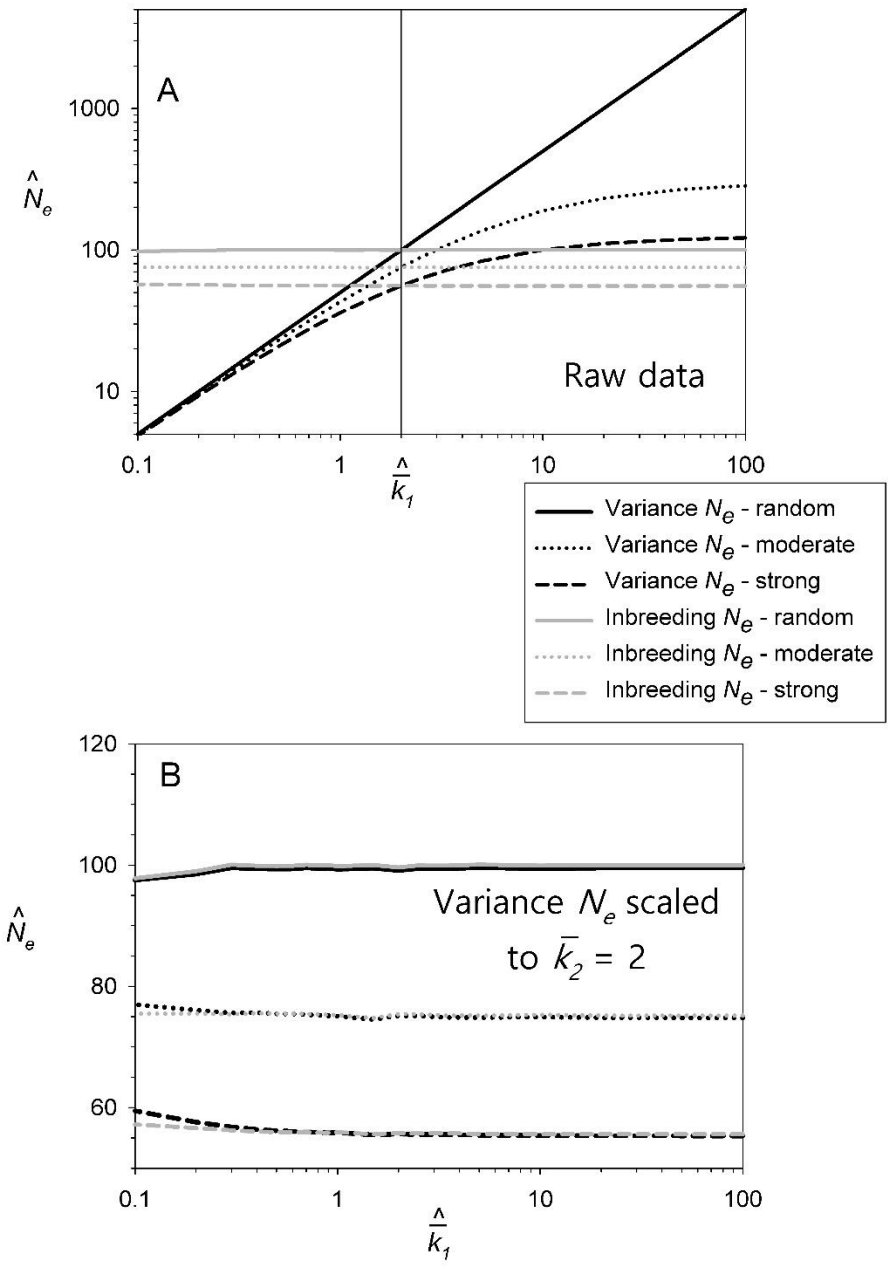

Figure 3. Dependence of variance $\widehat{N}_e$ (but not inbreeding $\widehat{N}_e$) on mean offspring number in a sample ($\hat{\bar{k}}$), for the three reproduction scenarios considered in Figure 1 with N = 100 female parents. A: raw data; variance $\widehat{N}_e$ is positively correlated with $\hat{\bar{k}}_1$ for all reproductive scenarios, whereas inbreeding $\widehat{N}_e$ is independent of $\hat{\bar{k}}_1$. B: after scaling raw $\hat{\varphi}_1$ to constant population size ($\bar{k}$ = 2) using Equation 1A, variance $\widehat{N}_e$ produces essentially the same result as raw (unscaled) inbreeding $\widehat{N}_e$ ($\widehat{N}_e \approx 100$ for random reproductive success, $\widehat{N}_e \approx 75$ for moderate reproductive skew, and $\widehat{N}_e \approx 56$ for strong reproductive skew).

Appendix A. Underdispersed variance in reproductive success.

This paper has focused on overdispered variance in reproductive success ($\hat{V}_{k1} > \hat{\bar{k}}_1$, using the Poisson approximation), which reduces effective size and provides opportunities for natural selection to operate. Underdispersion ($\hat{V}_{k1} < \hat{\bar{k}}_1$) is less common but nevertheless occurs in many taxa, at least with respect to seasonal reproduction. For example, the number of eggs or early-juvenile offspring can be constrained to a relatively small range of values, and this limits how large $\hat{V}_{k1}$ can be. At the extreme, females of many large animal species, and some birds, can only produce 0 or 1 offspring per season, in which case it is impossible for the variance in offspring number to be as large as the mean. This can be shown as follows. Of the *N* females, assume that *XN* produce exactly 1 offspring that appears in a sample, and the rest produce none. Mean offspring number in the sample is $\hat{\bar{k}}_1 = X$ and $\hat{V}_{k1}$= mean of the squares minus the square of the mean = $SS/N - (\hat{\bar{k}}_1)^2 = XN/N - X^2 = X - X^2$, which leads to $\hat{\varphi}_1 = 1 - X$.

The original Wright-Fisher model of reproduction incorporated an extreme version of this underdispersion scenario: each of *N* potential parents were imagined to contribute equally to an infinitely large pool of gametes, which then united at random to form the next generation of *N* individuals. Under this scenario, using the current notation, $\hat{V}_{k1}$ and $\hat{\varphi}_1$ were both 0 while $\hat{\bar{k}}_1$was infinitely large, and substituting these values into Eq. 1A produces

$$\mathrm{E}(\hat{\varphi}_2) = \frac{N-1}{N} + \frac{\bar{k}_2}{\infty}\left(0 - \frac{N-1}{N}\right) = \frac{N-1}{N} \ , \qquad \text{(A1)}$$

which is simply $\mathrm{E}(\hat{\varphi}_{drift})$ (i.e., RS is neither overdispersed nor underdispersed). Note that because the initial gamete pool (and hence $\hat{\bar{k}}_1$) is assumed to be infinitely large, this result holds regardless what $\bar{k}_2$ is.

All real populations of are of course finite in size. Also, we can generalize the idea of an initial gamete pool to production of diploid offspring ranging from zygotes to adults. If we still assume equal contributions to the initial pool of offspring ($\hat{V}_{k1}$= 0), but in finite amounts by each parent, we have

$$\mathrm{E}(\hat{\varphi}_2) = \frac{N-1}{N} + \frac{\bar{k}_2}{X}\left(0 - \frac{N-1}{N}\right) = \frac{N-1}{N}\left(1 - \frac{\bar{k}_2}{X}\right) , \qquad \text{(A2)}$$

where $X = \hat{\bar{k}}_1$ could be relatively large but is finite. Equation A2 shows that $\mathrm{E}(\hat{\varphi}_2)$ is always less than the random expectation, so variance in RS is underdispersed, and the degree of underdispersion depends on the ratio $\bar{k}_2/X$.

This model is still not very realistic, as it assumes 0 variance among parents in contributions to the initial gamete pool. Overdispersion can be generated by having unequal parental contributions to the initial gamete pool. Waples et al. (2018) used a variation of this approach to provide a minimum estimate of $\hat{\varphi}_2$ in southern bluefin tuna (*Thunnus maccoyii*), based on empirical data for variation in female size at specific ages (and hence assumed variance in age-specific egg production). For the current project, in modeling underdispersion I relaxed that restrictive assumption that $\hat{V}_{k1}$= 0 by having two separate processes for producing offspring: 1) a

directed process, whereby each parent contributes equally to the fraction *Y* of all offspring; and 2) a random process, whereby parents for the remaining fraction (1-*Y*) of all offspring are chosen randomly from the *N* candidates. As in the main text, in the simulations 100 parents produced a total of 10,000 initial offspring (so $\hat{\bar{k}}_1$ = 100), and random subsampling produced $\bar{k}_2$ values as small as 0.1. I considered two values of *Y*: 0.5 (moderate underdispersion) and 0.9 (strong underdispersion).

Results (Figure S1) show that initial Index of Variability for the two scenarios is simply the fraction of offspring that were randomly assigned to parents (i.e., $\hat{\varphi}_1$ = 1-*Y*). As the sample size of offspring declines, $\hat{\varphi}_1$ for both scenarios rapidly approach 1, in agreement with predictions from Equation 1A. It is apparent that sparse sampling of offspring will generally have a poor chance of detecting underdispersed variance in reproductive success, even when underdispersion is pronounced.

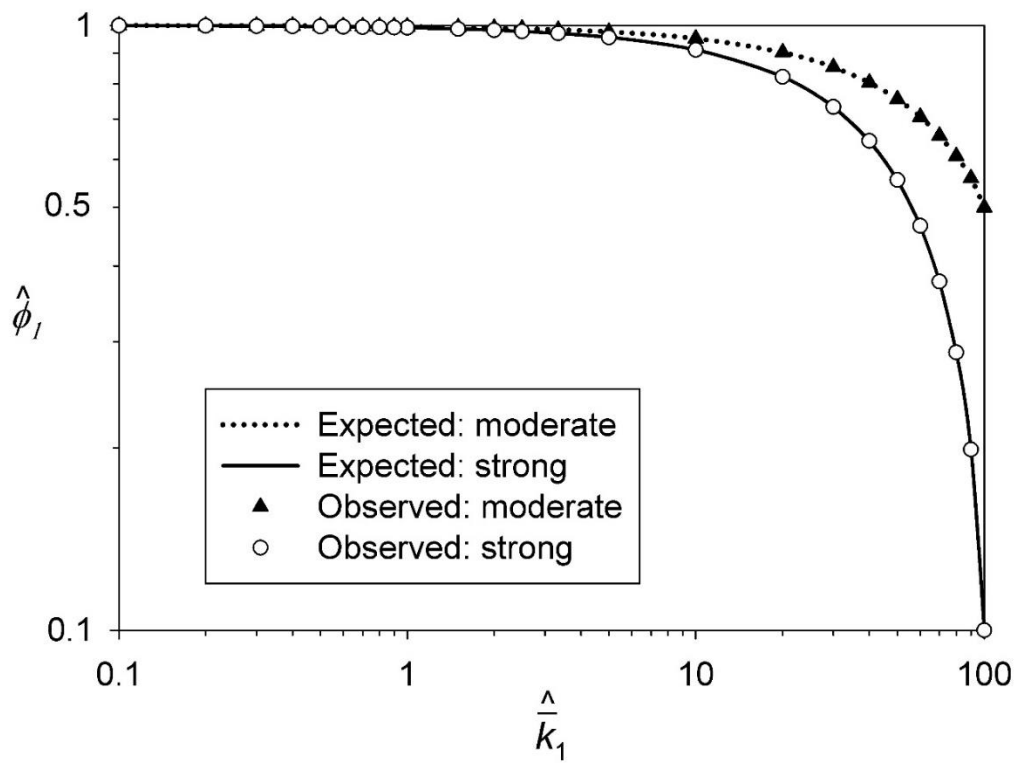

Figure S1. Relationship between the estimated Index of Variability ($\hat{\varphi}_1$) and sample $\hat{\bar{k}}_1$ when variance in reproductive success is underdispersed. Observed values (symbols) are from simulations that initially generated 10,000 offspring from 100 parents and then randomly subsampled offspring to produce smaller sample $\hat{\bar{k}}_1$ values. Expected values (lines) were obtained from Equation 1A using the empirical value of raw $\hat{\varphi}_1$ for maximum $\hat{\bar{k}}_1$ = 100. Moderate and strong underdispersion scenarios are described in the Appendix text.

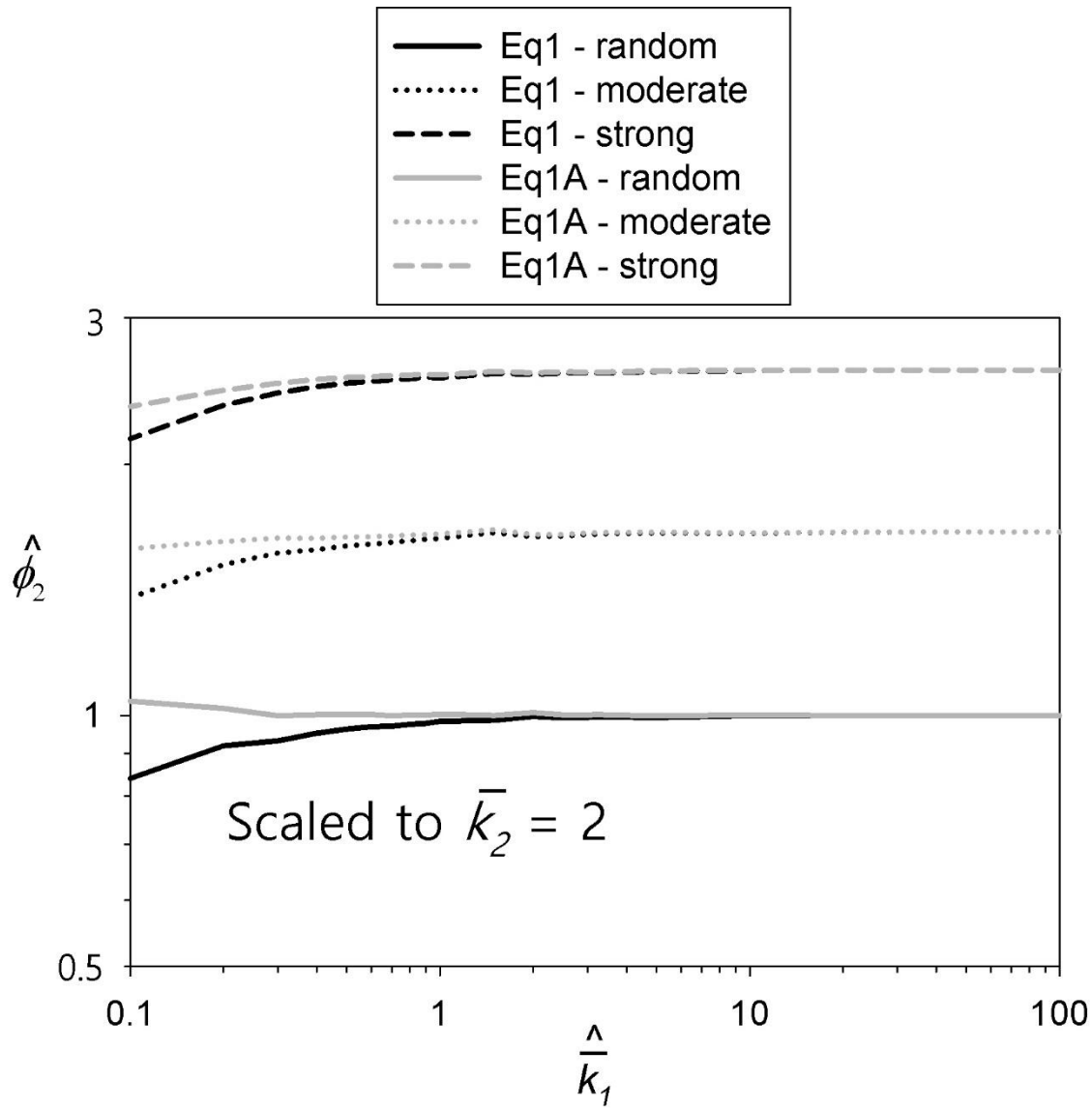

Figure S2. Comparison of results for rescaling empirical data for $\hat{\varphi}_1$ from Figure 1A to $\bar{k}_2$ = 2, using Equation 1 (black) and Equation 1A (gray). The two equations differ in that 1 uses the Poisson approximation that E($\hat{\varphi}_{drift}$) ≈ 1, whereas 1A uses the exact value E($\hat{\varphi}_{drift}$) = (N-1)/N, with N being the number of parents. The difference between (N-1)/N and 1 is small (0.99 vs 1 for the N = 100 parents used in simulating the data), but that difference becomes magnified when $\hat{\bar{k}}_1$ is small, in which case the term $\bar{k}_2/\hat{\bar{k}}_1$ = 2/$\hat{\bar{k}}_1$ becomes large.