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Selection Gradients, the Opportunity for Selection, and the Coefficient of Determination

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Abstract

We derive the relationship between R^2 (the coefficient of determination), selection gradients, and the opportunity for selection for univariate and multivariate cases. Our main result is to show that the portion of the opportunity for selection that is caused by variation for any trait is equal to the product of its selection gradient and its selection differential. This relationship is a corollary of the first and second fundamental theorems of natural selection, and it permits one to investigate the portions of the total opportunity for selection that are involved in directional selection, stabilizing (and diversifying) selection, and correlational selection, which is important to morphological integration. It also allows one to determine the fraction of fitness variation not explained by variation in measured phenotypes and therefore attributable to random (or, at least, unknown) influences. We apply our methods to a human data set to show how sex-specific mating success as a component of fitness variance can be decoupled from that owing to prereproductive mortality. By quantifying linear sources of sexual selection and quadratic sources of sexual selection, we illustrate that the former is stronger in males, while the latter is stronger in females.

Keywords

sexual selection; Bateman gradients; fitness; directional selection; stabilizing selection

When a trait is considered “adaptive,” it implies that a causal relationship exists between the value of that trait and individual fitness, such that variations among individuals in the trait values lead to predictable variations among the same individuals in fitness. Variation in relative fitness is necessary for adaptation by natural selection (Fisher 1958). Its description is essential to depicting the effect of natural selection on the distribution of trait values, since the multivariate relationship between trait values and relative fitness is natural selection (Robertson 1966; Price 1970, 1972; Lande 1980; Arnold and Wade 1984*b*; Phillips and Arnold 1989; Brodie et al. 1995). The second fundamental theorem of natural selection states that, for comparably variable and heritable traits, the greater the covariance between trait value and relative fitness, the greater is the change in trait mean from one generation to the next (Robertson 1968). When the trait in question is fitness itself, this covariance reduces to the variance in relative fitness. As a result, the mean fitness of a population increases whenever there is heritable variation in fitness, which is Fisher’s fundamental theorem (Fisher 1958), or the first fundamental theorem of natural selection.

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Given its central role in adaptation by natural selection and in the evolution of fitness itself, the variance in relative fitness, I, has been called both the “intensity of selection” and the “opportunity for selection” (Crow 1958; O’Donald 1970; Wade 1979; Wade and Arnold 1980). It is defined as $I=\sigma_w^2=\sigma_w^2/\overline{W}^2$, where w is relative fitness, W is absolute fitness, and the bar indicates the population mean. Here, we extend the recommendation of Hersch and Phillips (2004) that “the total opportunity of selection [should] be considered along with the pattern of selection on individual traits, and nonsignificant results be actively reported combined with an estimate of power.” In this article, we use standard concepts from statistics and phenotypic selection theory to determine how much of the variance in fitness can be accounted for in terms of individual variations in trait values. Our goal is different from that of standard phenotypic selection theory, which tries to determine how selection acting within (or among) populations is shaping trait values. Here, we are asking the reciprocal: How do trait values determine fitness? If we view the total variance in fitness as a population’s resource for adaptation, our approach quantifies how much of this generation’s resource is being used to alter trait means, trait variances, or the integration between traits. With data from several generations, one can investigate the consistency in the apportionment of the adaptive resource across phenotypes over time. With data from several populations, one can study whether local variation in an environmental factor accounts for differences in the apportionment of the adaptive resource across the phenotypes.

Our approach illustrates the relationship between selection gradients, the opportunity for selection, and R^2, the coefficient of determination. The familiar parameter R^2 measures the “goodness of fit” of a linear regression model to data. In our case, R^2 measures the degree to which individual fitness can be predicted or accounted for with the values of some phenotypic traits. The remaining variation in fitness, the proportion$(1 - R_2)$, is presumably the “random,” “chance,” or, more accurately, the “unaccounted for” variation in fitness, which has invited skepticism on the part of some toward the utility of I.

We derive the relationship between R^2, the selection gradient, and the opportunity for selection for the univariate case. After this, we turn to the multivariate case. Our approach can be considered as a first step in empirically distinguishing the contributions of chance and cause to the variance in relative fitness among individuals in a population (Wade and Kalisz 1990).

One Trait That Affects Fitness

For each individual i in a population, we assign a trait value, z_i, and a relative fitness, w_i. We employ the standard definition of a product-moment correlation to define the correlation between trait value and fitness, ρ_{wz}. When we move to matrix notation to handle more traits, it will be helpful to recognize that ρ_{wz} is equivalent to ρ_{zw}. The slope of the regression of w on trait value is β_{wz}; this is the selection gradient. We recognize that, when this selection gradient is multiplied by the standard deviation of trait value divided by that of relative fitness, it is equal to ρ_{wz}:

$$\rho_{wz}=\beta_{wz}\frac{\sigma_z}{\sigma_w}. \quad (1)$$

By the definition of a correlation, the total relative fitness variance “explained by” the trait, z, is the product of the opportunity for selection and the coefficient of determination, ρ_{wz}^2. In terms of the selection gradient, this follows directly from equation (1),

$$\rho_{wz}^{2}I=\beta_{wz}^{2}\sigma_{z}^{2}, \quad (2)$$

or the product of the trait variance and the square of the selection gradient. Equation (2) tells us, in absolute terms, how much of the variance in relative fitness in a population is explained by variation in the trait of interest. We use “explain” in its statistical meaning, namely, the proportion of the variance in relative fitness that is predictable from knowledge of the trait value z. That is, if ρ_{wz}^{2} equaled 0.60, then 60% of the variance in relative fitness is described (or “explained”) by its covariance with z.

Equation (2) is a well-defined component of the opportunity for selection and can be considered the upper limit for the evolutionary change in the mean of fitness that can be brought about by selection on z. In a single generation, selection on trait z will cause the mean of fitness to change by an amount equal to the product of $h_{w}^{2}\rho_{wz}^{2}I$, where h_{w}^{2} is the narrow-sense heritability of fitness. In the next section, we generalize the relationship given in equation (2) to many traits. This will allow us to decompose I into multiple, additive components, even when traits are correlated with each other. In addition, we will decompose I into components accounted for by quadratic (e.g., stabilizing or disruptive) or correlational selection (see below).

Multiple Traits Affect Fitness

Let us allow many traits to affect fitness. We will define a collection of traits with the vector $\mathbf{z}$, such that individual relative fitness equals

$$w_{i}=\mu+\beta\mathbf{z}+\varepsilon_{i}, \quad (3)$$

where $\boldsymbol{\beta}$ is a vector of selection gradients (a vector of partial regression coefficients) and ε_{i} is the ith individual’s deviation from the expectation of the linear model. This deviation could be caused by factors that are not included in the model, or it could be owing to chance; it is unaccounted for in the statistical sense. Traditionally, phenotypic selection studies find the selection gradients by applying the Lande-Arnold (1983) regression $\boldsymbol{\beta} = \mathbf{P}^{-1}\mathbf{s}$, where $\mathbf{P}$ is the intertrait variance-covariance matrix, $\mathbf{s}$ is a vector of selection differentials, and s_{i} = Cov (w, z_{i}). We will use a slightly different but equivalent formulation of the Lande-Arnold regression to highlight the relationship between the opportunity for selection, the multivariate selection gradients, and the coefficient of multiple determination.

We define the block matrix $\mathbf{R}$ as

$$\mathbf{R}=\begin{matrix}\mathbf{R}_{\mathbf{zz}} & \mathbf{R}_{\mathbf{z}w}\\ \mathbf{R}_{w\mathbf{z}} & 1\end{matrix}, \quad (4)$$

where $\mathbf{R}_{\mathbf{zz}}$ is the intertrait correlation matrix (this is the Lande-Arnolds $\mathbf{P}$ matrix standardized by the standard deviations of all traits), $\mathbf{R}_{\mathbf{z}w}$ is a column vector of correlations between relative fitness and trait values ($\mathbf{s}$ that has been standardized by the variance in traits and relative fitness), and $\mathbf{R}_{w\mathbf{z}}$ is the row-vector transpose of $\mathbf{R}_{\mathbf{z}w}$. The 1 is the correlation between relative fitness and itself. The selection gradient, standardized by trait variances and relative fitness variance, is

$$\beta_{w\mathbf{z}}^{\prime}=(\mathbf{R}_{\mathbf{zz}})^{-1}\mathbf{R}_{\mathbf{z}w}, \quad (5)$$

whose individual elements are $\beta'_{wz}=\beta_{wz}\sigma_z/\sigma_w$. The standardized selection gradient in this relationship is a partial correlation coefficient, analogous to the correlation co-efficient in equation (1) for the univariate case.

From the fundamental equation of multiple regression analysis (Allison 1998), and using the transpose of $\mathbf{R}_{\mathbf{z}w}$, we find R^2, the coefficient of multiple determination for the vector of traits **z**,

$$R^2=\mathbf{R}_{w\mathbf{z}}\beta'_{w\mathbf{z}}. \quad (6)$$

Equation (6) returns a scalar, which tells us proportionally how much of the variance in relative fitness is determined by all of the traits in the vector, **z**, acting together. However, we would like to apportion I to each trait separately, in order to say exactly which traits account for more or less of the variance in relative fitness. To this end, we substitute $\mathbf{R}_{\mathbf{z}w}$ for its transpose to obtain a column vector. Multiplying both sides of equation (6) by the variance in relative fitness or the opportunity for selection yields

$$\mathbf{i}_\mathbf{z}=\mathbf{R}_{\mathbf{z}w}\beta_{w\mathbf{z}}\sigma_\mathbf{z}\sigma_w, \quad (7a)$$

where $R^2 I = \Sigma_\mathbf{z}\mathbf{i}_\mathbf{z}$. This formula can be rearranged to give the multivariate generalization of equation (2), where each component z to be summed is equal to

$$\mathbf{i}_\mathbf{z}=\beta_{w\mathbf{z}}\mathbf{b}_{w\mathbf{z}}\sigma^2_\mathbf{z}, \quad (7b)$$

and where b_{wz} is the slope of the simple regression of relative fitness on the values of each trait. Equations (7a) and (7b) decompose the total opportunity for selection I into additive components, i_z, one for each trait in the vector. These show that the relative influence of each trait on the variance in relative fitness is equal to the product of its selection gradient and its selection differential. Equations (7a) and (7b) are tautological and follow directly from the definitions of means, variances, slopes (regressions), and correlations; we make no assumptions at all about the distribution of individual traits or of fitness itself. We provided a script for R, available online as a PDF (R Development Core Team 2011), that estimates $\mathbf{i}_\mathbf{z}$ for multivariate data. It is possible to test specific hypotheses regarding the components of I. For example, equation (7b) implies that a conservative test for significance of i_z is met when values for b_{wz} and β_{wz} both differ significantly from zero. When traits are multivariate normal, then t statistics can be used to assess significance. Otherwise, nonparametric approaches should be considered, such as resampling (e.g., Mitchell-Olds and Shaw 1987). The provided R script applies a bootstrapping approach (Efron 1987; DiCiccio and Efron 1996; Davison and Hinkley 1997) to estimate confidence intervals.

Stabilizing and Correlational Selection

Sometimes selection favors intermediate trait values rather than larger or smaller values; this is called stabilizing selection. Its converse is disruptive selection. Selection can also favor coadapted trait complexes when it favors some trait combinations over others. Lande and Arnold (1983; see also Arnold 1986) defined stabilizing selection as the covariance between relative fitness and the squared deviations of trait values from the mean, Cov $[w, (z-\bar{z})^2]$, and correlational selection as the covariance between relative fitness and the product of trait deviations, Cov $[w, (z_1-\bar{z}_1)(z_2-\bar{z}_2)]$. The relationship between either of these kinds of selection and the variance in relative fitness is not straightforward. For trait z, with stabilizing selection, a portion of the relative fitness variance goes toward changing the mean of z^2, while another portion is allotted to changing the mean of z. These two proportions are then combined to describe the change in the variance of z resulting from selection, which is important to iterating $\mathbf{P}$ over time.

Similarly, for two traits, z_1 and z_2, some of the relative fitness variance is used to change the product, $z_1 z_2$, as individuals with particular combinations of trait values have higher or lower relative fitness than others. Another portion of the relative fitness variance is allotted to changing the means of z_1 and z_2. These two changes are then combined to describe the change in the covariance, which is also important to iterating $\mathbf{P}$ over time.

In order to relate stabilizing and correlational selection values to the opportunity for selection, Arnold (1986) had to assume multivariate normality. We use a somewhat different approach that frees us from this assumption, with the caveat that when multivariate normality is violated, estimates of linear and quadratic selection are not necessarily interpretable as directional and stabilizing selection (Walsh and Lynch 2010). Our approach allows us to apportion the variance in relative fitness to linear, quadratic, and interaction traits. Any trait can be assessed for its contribution toward the opportunity for selection through directional selection, stabilizing/disruptive selection, or correlational selection by including it in any or all of three vectors: $\mathbf{z}_1$ (traits under directional selection), $\mathbf{z}_2$ (traits under stabilizing or disruptive selection), or $\mathbf{z}_{1\times1}$ (traits under correlation selection). The trait value is included in $\mathbf{z}_1$ with no change, its squared deviation from the trait mean is included in $\mathbf{z}_2$, and for each potentially interacting trait, the cross products of the deviations from the respective trait means are included in $\mathbf{z}_{1\times1}$.

Consider the case of three traits, for example. The three vectors may include

$$\mathbf{z}_1=\begin{pmatrix} z_{1,1}-\bar{z}_{1,1} \\ z_{1,2}-\bar{z}_{1,2} \\ z_{1,3}-\bar{z}_{1,3} \end{pmatrix},$$

$$\mathbf{z}_2=\begin{bmatrix} (z_{2,1}-\bar{z}_{2,1})^2 \\ (z_{2,2}-\bar{z}_{2,2})^2 \\ (z_{2,3}-\bar{z}_{2,3})^2 \end{bmatrix},$$

$$\mathbf{z}_{1\times1}=\begin{bmatrix} (z_{1\times1,1}-\bar{z}_{1\times1,1})(z_{1\times1,2}-\bar{z}_{1\times1,2}) \\ (z_{1\times1,1}-\bar{z}_{1\times1,1})(z_{1\times1,3}-\bar{z}_{1\times1,3}) \\ (z_{1\times1,2}-\bar{z}_{1\times1,2})(z_{1\times1,3}-\bar{z}_{1\times1,3}) \end{bmatrix},$$

although it should be noted that there is no requirement that all these elements must be included. If one’s causal model of fitness precludes certain interactions, for example, then $\mathbf{z}_2$ or $\mathbf{z}_{1\times1}$ may include fewer quadratic or interaction traits. We concatenate these three vectors to make a new vector of traits $\mathbf{z} = \{\mathbf{z}_1, \mathbf{z}_2, \mathbf{z}_{1\times1}\}$.

We can apply this new vector $\mathbf{z}$ to equation (7) and treat it as before to identify additive components of the opportunity for selection

$$\mathbf{i}_{\mathbf{z}}=\begin{matrix} \mathbf{i}_1 \\ \mathbf{i}_2 \\ i_{1\times1} \end{matrix}=\beta_{w\mathbf{z}}\mathbf{b}_{w\mathbf{z}}\sigma^2_{\mathbf{z}}. \quad (8)$$

The vector $\mathbf{i}_{\mathbf{z}}$ is a concatenated list of three subvectors, each made up of trait-specific contributions to the opportunity for selection. The vector $\mathbf{i}_1$ defines contributions arising from directional selection; the vector $\mathbf{i}_2$ defines contributions generated by stabilizing and disruptive selection; and $\mathbf{i}_{1\times1}$ defines contributions that follow from correlational selection. As these contributions are additive within and among these subvectors, the portion of the total opportunity for selection that is attributable to directional selection, stabilizing and diversifying selection, and correlational selection is $\Sigma_i\,\mathbf{i}_{1,i}$, $\Sigma_i\,\mathbf{i}_{2,i}$, and $\Sigma_i\,\mathbf{i}_{1\times1,\,i}$, respectively. When it is of interest to know how much of selection for fitness comes from stabilizing selection as opposed to directional selection, we can compare the fractions $\mathit{\Gamma}^{-1}\Sigma_i\,\mathbf{i}_{2,i}$ and $\mathit{\Gamma}^{-1}\Sigma_i\,\mathbf{i}_{1,i}$. Similarly, we can measure the contribution from selection directed toward adjusting trait values to one another, $\mathit{\Gamma}^{-1}\Sigma_i\,\mathbf{i}_{1\times1,i}$, and compare it to the fraction arising from selection that acts to change trait means, $\mathit{\Gamma}^{-1}\Sigma_i\,\mathbf{i}_{1,i}$.

As we see in equation (8), directional, stabilizing, and correlational selection gradients follow from this quadratic model of relative fitness and partially determine the opportunity for selection. These can be measured directly from the partial regression coefficients of relative fitness on the vector **z** or by inverting the intratrait correlation matrix and solving

$$\begin{aligned}\beta_{w\mathbf{z}} = & \begin{matrix}\beta_{w\mathbf{z}_1}\\ \beta_{w\mathbf{z}_2}\\ \beta_{w\mathbf{z}_{1\times1}}\end{matrix}\\ = & (\mathbf{R}_{\mathbf{zz}})^{-1}\mathbf{R}_{\mathbf{z}w}\frac{\sigma_w}{\sigma_{\mathbf{z}}}.\end{aligned} \qquad (9)$$

These vectors $\boldsymbol{\beta}_{w\mathbf{z}_1}$, $\boldsymbol{\beta}_{w\mathbf{z}_2}$, and $\boldsymbol{\beta}_{w\mathbf{z}_{1\times1}}$ are the directional, quadratic, and interaction selection gradients. In the special case where all trait combinations are included in the analysis, these gradients will be the same as those calculated using the method from Lande and Arnold (1983), with the added caveat that quadratic selection gradients estimated by multiple regression, or by equation (9), must be doubled to ensure equivalency with selection gradients obtained by the Lande-Arnold method (Stinchcombe et al. 2008).

When Data Are Nonexistent for Some Individuals

Values may not exist for some traits in some individuals. For example, male mating success has no sensible value for females. Furthermore, one could argue that because mating is precluded in some cases by juvenile mortality, male mating success may not exist for males who die before reaching an age of reproductive ability. These “nonexistent data” are fundamentally different from “missing data,” because the latter exist but are unobserved (Haitovsky 1968; Allison 2001). In both cases, individual values must be included in the multiple regressions used to estimate multivariate selection, and values must be such that the phenotypic variance-covariance matrix is invertible. These two different situations call for different imputation strategies, however. For nonexisting data, we impute nonexisting trait values using the moments of the distribution generated by the fraction of the population that expresses the trait (or traits) of interest. Specifically, existing trait means are imputed into the traits in $\mathbf{z}_1$, the existing trait variances are imputed into traits in $\mathbf{z}_2$, and the existing trait covariances are imputed into traits in $\mathbf{z}_{1\times1}$. There are three desirable consequences of this imputation strategy: (1) the phenotypic variance-covariance matrix is assured to be invertible, (2) the fraction of nonexisting data $(1 - p)$ has no effect on selection gradients, and (3) the phenotypic variance for any trait is equal to the existing trait variance discounted by the fraction $1 - p$. This approach is further justified and explained in more detail in the appendix. Note that for purposes of hypothesis testing, the sample size is the product of the total number of individuals and p.

Example from a Human Population

Here we apply these principles to a human data set in order to quantify sources of sexual selection, including directional and quadratic sources, while decoupling mating success from prereproductive mortality. Here, we de-fine relative fitness as

$$w_i=1+L_i+S_i+M_{\mathrm{m}i}+M_{\mathrm{f}i}+(M_{\mathrm{m}i}-\overline{M}_{\mathrm{m}})^2+(M_{\mathrm{f}i}-\overline{M}_{\mathrm{f}})^2+\varepsilon_i, \quad (10)$$

where L is the indicator of survival to age 15 (1 is alive and 0 is dead), S is the indicator for sex (1 is male and 0 is female), M_{m} is the number of mates taken by a male, M_{f} is the number of mates taken by a female, and ε is the error term associated with causal factors that are not included in the linear model of relative fitness. Individual fitness and other trait values are taken from a cohort of 895 human males and 1,029 human females born in 1840 that was provided by the Utah Population Database. For this birth-year cohort, approximately 10% of men who married were polygamists. Fitness is measured as the number of children born, and existing sex-specific numbers of reproductive partners (M_{m} and M_{f}, for male and female, respectively) are estimated using the methods detailed in Moorad et al. (2011) applied to both sexes, with the added assumption that sex ratio at birth remained constant across generations. Nonexistent traits are imputed from the existing class means. For example, we have defined M_{m} measurements to exist only for those males that survive to 15 years of age (no father in this population dies before this age). The mean of these measurements is used as the measure for all females and males that die before reaching this age. Applying the multivariate regression methods described previously, we find the selection gradients and the components of the opportunity for selection that correspond to each factor in equation (10). These are shown in table 1.

In aggregate, these traits explain 65% of the total opportunity for selection. The strength of selection (as measured by selection gradients) was greatest and roughly equivalent for survival and male mating success. Together, these two sources of selection accounted for 89% of the relative fitness variation explained by the entire model. Linear selection for male mating success explains 48% of the opportunity for selection, despite the fact that M_{m} varied in less than half of the population (i.e., the trait existed only in males that survived to 15 years of age). Very weak quadratic selection acted on male mate number, but strong quadratic selection was observed to act on female mating success (the quadratic selection gradients were −0.067 and −0.460, respectively). These are consistent with the recent observation made by Moorad et al. (2011) of linear relationships between mating success and reproductive success in males and pronounced concave relationships between mating success and reproductive success in females from this population. Linear selection on female mating success explained only 7% of the total opportunity for selection, and quadratic selection explained about 4%.

Discussion

In standard phenotypic selection theory and its application to data, the focus is on how associations with fitness change the distribution of trait means, variances, and covariances. Here, we have investigated the inverse, that is, how changes in relative fitness variance can be accounted for in terms of linear and quadratic measurements of traits. Our method allows a portion, R^2, of the total variance in fitness among individuals to be statistically accounted for in terms of measured trait values. A common interpretation of R^2 is causal; namely, this suite of traits causes a proportion of the fitness variation among individuals. The complementary proportion, the “random” or unaccounted-for variance in relative fitness, is given by $(1 - R^2)$. Like the Lande-Arnold vector of selection gradients, our approach is built on correlation, which is not a synonym for causation. In interpreting R^2, we prefer the more cautious approach, similar to that advocated by Wade and Kalisz (1990), for identifying the causal agents of selection. Associations between relative fitness and trait values should be considered hypotheses, and these should be tested for their causal import using manipulative experiments. Wade and Kalisz (1990) recommended manipulations directed toward identifying the agents of selection, such as excluding a predator and observing whether selection gradients acting on prey traits changed as predicted. Similarly, we recommend manipulating the phenotypic traits that contribute to R^2 and observing whether fitness changes as predicted by the causal hypothesis. A notable case where the issue of causality versus correlation may not be a concern is when selection for vital rates (age-specific survival and fertility) is measured. When vital rates for all ages up to the last age of reproduction are included in a linear model of fitness, then there are no missing fitness traits, and $R_2 = 1$ (Moorad 2013*a*).

Earlier theoretical investigations (e.g., Arnold and Wade 1984*b*; Wade 1995; Shuster and Wade 2003) have also partitioned total I into components. The relationship between our derivation above and those earlier methods varies with the study. Arnold and Wade (1984*b*) modeled total selection when lifetime fitness equals a multiplicative product of a series of episodes of selection, each with its own fitness. They then decomposed I into a sum of additive components, ΣI_i, one for each episode of selection, with the addition of a series of "co-intensities" of selection for those cases where components of fitness were correlated across episodes. Here, we do not synthesize fitness from a series of fitness measures; instead, we measure it directly. In principle, however, one could use our methods in combination with Arnold and Wade (1984*b*) to ask how much of the variance in relative fitness among individuals at a given episode of selection can be accounted for by the differences among individuals in trait values at that episode.

Wade (1995) partitioned the variance in plant fitness by considering plant reproductive fitness to have three parts, with covariances between pairs of them. One part was seed numbers resulting from selfing, a second part was one-half the seeds resulting from ovule fitness, and the third was one-half the seeds resulting from pollination of seeds on other plants. The derivation in Wade (1995) can be reframed using the methods introduced in this article.

Shuster and Wade (2003) advocated the use of the opportunity for sexual selection (I_S) to measure the fraction of the variance in relative fitness that is attributable to sexual selection. For either sex, I_S is the sum of the components of I that involve linear as well as nonlinear components of selection resulting from variation in mating success or its covariates. We recommend the regression-based method described in this article when a finer-scaled perspective of sexual selection is desired. The regression-based approach advocated here defines a lower bound on I_S,

$$\sum_{z\in\mathbf{MS}} \mathbf{i}_{\mathbf{z}} \le I_s \le \sum_{z\in\mathbf{MS}} \mathbf{i}_{\mathbf{z}} + (1-R^2)I, \qquad (11)$$

where **MS** is the set of traits included in the linear model of fitness that involve mating success and its correlates.

As we showed in our example, nonlinear relationships between relative fitness and mate number exist. The standard Bateman gradient measures the strength of linear selection acting on mating success (Arnold and Duval 1994; Jones 2009). New, formal Bateman gradients based on the quadratic components of mating success can be defined with our approach. We suggest that these quadratic Bateman gradients capture the idea that multiple mating by females tends to have both positive and negative effects on relative fitness, and these might come into balance at an intermediate number of mates or at least show pronounced diminishing fitness returns with additional matings. On the negative side, multiple mating by females can reduce relative fitness owing to damage from males (Muller et al. 2007), sexually transmitted diseases (Hurst et al. 1995), or a combination of these and other effects (Post and Greenlaw 1982). On the positive side, multiple mating by females may be a means of avoiding inbreeding in some species (e.g., Tregenza and Wedell 2002), although here the genetic benefit to a female of adding additional mates diminishes rather quickly. We believe that our extension of the concept of the Bateman gradient to these quadratic terms and its relationship to I is a significant step forward in addressing some of the shortcomings identified with the opportunity for selection (Jennions et al. 2012). For those interested only in the fraction of the variance in relative fitness that can be accounted for or explained by measured phenotypes, our formulation illustrates the relationship between Fisher's fundamental theorem, Robertson's secondary theorem, and the coefficient of determination on a trait-by-trait basis.

Survival to reproductive age correlates with mating success (Clutton-Brock 2007). In a simple three-trait analysis (fitness, male mating success, and female mating success), juvenile mortality will contribute to the opportunity for sexual selection. To control for the effects of juvenile mortality, we can add binary sex-specific values (alive or dead at some threshold age) to the model and recalculate equation (1) and equation (2), imputing different-sex trait values using the population mean (as we do in our example). We now have two new selection intensities that correspond to selection on sex-specific survival to maturity, holding sex-specific mating success constant. Importantly, the Bateman gradients are now partial correlations of relative fitness on mating success that hold survival constant. Using these partial correlations in equation (3) yields opportunities for sexual selection that do not reflect the variance in adult mating fitness caused by juvenile mortality. This approach is developed more fully in Moorad (2013*b*). At the very least, using these methods will allow one to test the hypothesis that juvenile mortality is a component of reproductive competition in some species. Conversely, in the sense of Arnold and Wade (1984*b*), it can also be of interest to examine the causes of relative fitness variance at one episode of selection, independent of prior episodes.

We have presented a method of fitness analysis that treats a population's total variance in relative fitness as a resource for adaptation constructed from multivariate phenotypic variation. All phenotypic change by natural selection, whether directional, quadratic, or correlational, draws on the variance in relative fitness as though it were a common resource. If a large fraction of the adaptive resource is devoted to altering one aspect of the phenotype, the fraction available for other alterations is necessarily a smaller fraction. Our analysis permits the investigation of how this adaptive resource is allocated in one generation of a population, and it permits these allocations to be compared across generations, populations, and environments. Where previous phenotypic selection theory asks how selection shapes the multivariate distribution of trait values, our method asks how much a demand on the pool of adaptive resource is made by one trait's fit or lack thereof to the environment.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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APPENDIX

A Comment on Imputing Trait Values for Individuals with Nonexistent Characters Using the Population Mean

Traits may be defined in such a way as to preclude expression by some individuals in a population. With separate sexes, for example, the number of female reproductive partners is a trait that exists only for males (and, conversely, number of male reproductive partners is a trait that is conditioned on individuals being female). Other familiar examples with nonexisting data include phenotypic plasticity, where individuals vary because of their exposure to different environments and do not have trait values for the environments they do not experience, and with mortality, where late-life traits exist only in those individuals that live long enough to express them. Grafen (1988) argued that the last example represents a major weakness in the multivariate approach that the Chicago School used to understand phenotypic selection (Lande and Arnold 1983; Arnold and Wade 1984*a*, 1984*b*) because the “invisible fraction” of dead individuals does not appear in the linear model of relative fitness. To account for this perceived problem, Lynch and Arnold (1988) recommended measuring age-specific correlation matrices and selection gradients and then using these to work backward to synthesize a phenotypic correlation matrix that represents the entire (e.g., premortality) population (e.g., Bennington and McGraw 1995). Alternatively, Hadfield (2008) advocated modeling the “missing data” to impute reasonable values for use in the regressions, allowing for measurements of selection in these cases.

We argue here that, from the perspective of understanding selection acting on phenotypes, these compensatory approaches are not necessary because phenotypic selection (the function that maps relative fitness to phenotypes) is insensitive to hypothetical trait values that are not expressed. Consequentially, selection gradients are insensitive to the fraction of individuals with nonexisting trait values. Note that by nonexistent values, we mean those data that cannot be collected because they are logically precluded; this is a fundamentally different situation from “missing data” caused by incomplete sampling (Haitovsky 1968). Breeding values and allelic content associated with specific traits exist for all individuals and do not qualify as nonexistent.

Phenotypic variances are affected by the fraction of individuals with nonexisting data, however. Thus, the sole effect of the “invisible fraction” on the strength of selection is to discount the covariance between relative fitness and traits by the fraction of the population that dies before selection is applied. Evolutionary models of aging (Hamilton 1966; Lande 1982; Charlesworth 1994, 2000; Caswell 2001) make this relationship explicit when they describe the strength of selection acting on age-specific survival and fertility in age-structured populations with mortality. These models weight the selection gradient specific to any age x by the cumulative survival rate to that age, l_x, but the effect on the covariance between relative fitness and trait values is the same as if they discounted the variance by that same factor.

We show here that the appropriate method for dealing with the nonexisting data, including those that arise from the “invisible fraction,” is to impute values using the trait mean of the subset of the population that is capable of exhibiting the trait (or the variance or covariance for quadratic terms). Imputing by the mean is not recommended for accounting for missing data, but it is appropriate for dealing with nonexistent data (Allison 2001). When the nonexistent data correspond to second-order, or higher, terms, then the appropriate moment of the population with existing data is substituted instead. For example, if one were interested in quadratic selection in a male-only trait, then the variance among males is imputed for the nonexistent data in females. The “trait” in this case is the squared deviation from the mean; nonexistent data are imputed from the variance because, by definition, this is the mean squared deviation. Likewise, nonexistent interaction traits are imputed from the covariance derived from the portion of the population with existing data.

We assert that, given two requirements, any invariant data can be substituted for nonexistent traits with no effect on measurements of phenotypic selection, provided that information is included in the multiple regression that identifies whether data are imputed (an indicator, or dummy, variable), but using the mean has certain advantages. Here we prove this assertion. These requirements are (1) fitness is known for all individuals in the population and (2) all individuals can be identified as belonging to either the class with nonexistent data or the class with existent data.

Essentially, we wish to know how much selection acts on an index trait defined for some individual i,

$$z_i^* = z_{ai}, \quad \text{(A1)}$$

where a is a dummy variable and z_i is the focal trait. It is measured directly in those individuals that have a demonstrable trait. These individuals belong to class $a = 1$. Trait z_0 can be any constant value for individuals that are logically incapable of expressing the trait (e.g., they die before an age-specific trait is realized, they are the wrong sex, or they develop in a different environment). These individuals belong to class $a = 0$. Selection on this trait is its covariance with relative fitness (Robertson 1966; Li 1967; Price 1970, 1972). This covariance can be decomposed into within- and among-class covariances:

$$\begin{array}{c} \mathrm{Cov}\,(w, z^*) = \mathrm{Cov}\,(w, z_a) \\ = p(1-p)(\overline{w}_1 - \overline{w}_0)(\overline{z}_1 - \overline{z}_0) + p\,\mathrm{Cov}\,(w, z_1), \end{array} \quad \text{(A2)}$$

where w is relative fitness, p is the proportion of the population belonging to class $a = 1$, subscripts indicate the class of individuals, and bars indicate averages. Selection on the index trait depends on the frequency of class $a = 1$ and the within-class covariance between existing phenotypes and relative fitness. Selection measured this way is also sensitive to differences between mean class fitness and the mean phenotype of individuals with existing traits. As we show below, the latter component disappears if class is treated as a covariate in our linear model of relative fitness.

Consider a bivariate model of relative fitness that includes the dummy variable a as another component,

$$w_i = \mu + b_{w,a} a_i + b_{w,z^*} z_i^* + e_i. \quad \text{(A3)}$$

Selection on the index trait is now the partial covariance that holds the dummy variable constant. This can be expressed as total covariances, correlations, and standard deviations,

$$\mathrm{Cov}\,(w, z^* \cdot a) = \mathrm{Cov}\,(w, z^*) - \sigma_w \sigma_{z^*} r_{w,a} r_{z^*,a} \bullet \quad \text{(A4)}$$

The following relationships hold:

$$\sigma_w^2 = p(1-p)(\overline{w}_1 - \overline{w}_0)^2 + p\sigma_{w_1}^2 + (1-p)\sigma_{w_0}^2, \quad \text{(A5a)}$$

$$\sigma_{z^*}^2 = p(1-p)(\overline{z}_1 - \overline{z}_0)^2 + p\sigma_{z_1}^2, \quad \text{(A5b)}$$

$$\sigma_a^2 = p(1-p), \quad \text{(A5c)}$$

$$\mathrm{Cov}\,(w, a) = p(1-p)(\overline{w}_1 - \overline{w}_0), \quad \text{(A5d)}$$

$$\mathrm{Cov}\,(z^*, a) = p(1-p)(\overline{z}_1 - \overline{z}_0). \quad \text{(A5e)}$$

We express equations (A5d) and (A5e) in terms of correlations and substitute these and equations (A5a) and (A5b) into the last term in equation (A4) and find that

$\sigma_w \sigma_{z^*} r_{w,a} r_{z^*,a} = p(1-p)(\bar{w}_1 - \bar{w}_0)(\bar{z}_1 - \bar{z}_0)$. From equation (A4) and equation (A2) and the definition of a slope,

$$\mathrm{Cov}\,(w, z^* \cdot a) = p\,\mathrm{Cov}\,(w, z_1) = b_{w,z_1} p \sigma_{z_1}^2. \quad \text{(A6)}$$

In the relative fitness model that includes class, selection on the trait of interest is independent of both the distribution of both class means and the mean relative fitness of z_0. As we may intuit, selection on phenotypes is entirely dependent on the joint distribution of relative fitness and existing phenotypes and the frequency-weighted variance.

While equation (A6) shows us that we can impute non-existing data using whatever method we choose with no effect on our outcome (so long as we note which values are imputed using a), it may be useful to impute using the existing-data mean. Because $\bar{z} = \bar{z}_1$, we can standardize z by its mean to find Cov $(w, z^*) = p$ Cov (w, z). In other words, the simple covariance and the partial covariance definitions of phenotypic correlations converge. This makes sense because the phenotypic values (imputed and nonimputed) and the dummy variable are orthogonal. In principle, imputation with the mean can allow us to measure selection gradients without including the dummy variable. However, the dummy variable should be included in the model because it will account for part of the total opportunity for selection. Furthermore, imputation with the mean reduces the phenotypic variance by a factor of $1 - p$, meaning that selection can be measured directly using imputed data as $\mathrm{Cov}\,(w, z^*) = b_{wz}\sigma_z^2$. Note, however, that imputation does not increase sample size, and tests of significance must reflect the number of observations taken from individuals with existing data (pN).

Table 1

Selection on mating success, sex, and survival

Factor	$\boldsymbol{\beta}$	**b**	**Size of existing fraction, *p***	**Trait variance (existing fraction)**	$\mathbf{i}_z$
S	.022	−.068	1	.250	<|0.001|
L	1.183	1.180	1	.129	.181
M_m	1.062	1.039	.426	.443	.208
M_f	.724	.662	.422	.154	.031
$(M_m - \bar{M}_m)^2$	−.067	.224	.426	.545	−.003
$(M_\mathrm{f} - \bar{M}_m)^2$	−.460	−.395	.422	.228	.017
R_2					.650

Note: The total opportunity for selection is 0.667; the causal model explains 0.434 of this total. The structure of the table follows equation (7b), applied to the case with nonexistent data: the product of the first four numerical columns yields values in the far-right column.