

COMBINING SELECTIVE EPISODES TO ESTIMATE LIFETIME NONLINEAR SELECTION

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Studies measuring natural selection acting via different components of fitness may provide insight into such central questions in evolutionary biology as the evolution of life histories and sexual dimorphism. It is often desirable to combine estimates of selection at different episodes to understand how they interact to produce total lifetime selection. When selective episodes are sequential, total directional selection may be calculated by summing directional selection across episodes. However, it is unclear whether lifetime nonlinear (e.g., stabilizing, disruptive, or correlational) selection may be similarly calculated using estimates of quadratic selection from sequential episodes. Here, I show that lifetime quadratic selection depends not only upon the sum total of quadratic selection across episodes but also upon the pattern of directional selection across episodes. In certain cases, the effects of directional selection across episodes may cancel one another, leading to no net directional selection but strong stabilizing selection. This result suggests that true stabilizing selection may be more common than previously thought, especially when the entire life cycle is considered. The equations derived here are easily applicable to empirical data, as is illustrated both with a simulated dataset and with a reanalysis of a study of quadratic selection in dark-eyed juncos.

KEY WORDS: Correlational selection, disruptive selection, life history, sexual dimorphism, stabilizing selection.

The methods for measuring phenotypic selection developed by Lande and Arnold (1983) have generated a wealth of data contributing to an understanding of how natural selection operates in the wild (Endler 1986; Kingsolver et al. 2001). Although selection acting via total lifetime fitness is most relevant for predicting the trajectory of phenotypic evolution (Lande 1979), lifetime fitness is notoriously difficult to measure. As a result, most studies measuring selection in the wild focus on one or a few components of fitness (Kingsolver et al. 2001). Despite their limited ability to fully quantify natural selection, however, measurements of selection obtained using components of fitness are often informative. For example, measuring and comparing selection via different fitness components such as survival and reproduction can provide insight into the evolution of life histories (Arnold and Wade 1984a,b; Schluter et al. 1991; Hoekstra et al. 2001). In addition, comparing selection via components of male and female fitness can shed light on the evolution of sexual dimorphism (Price 1984; Cox and Calsbeek 2009).

To explore how episodes of selection interact, investigators may wish to combine estimates of selection across episodes into a cumulative estimate of selection. The combination of estimates of directional selection is relatively straightforward. When fitness components are defined in such a way that they multiply to lifetime fitness, selection at each episode may be combined additively to achieve estimates of total lifetime selection (Arnold and Wade 1984a). Fitness can often be partitioned into such multiplicative components. For example, total offspring production may be separated into number of breeding seasons, number of mates per year, and number of offspring per mate. Arnold and Wade originally applied their results to both selection differentials (s), which measure the covariance between phenotypes and relative fitness, and selection gradients (β), which measure the direct relationship of traits to fitness when holding correlated traits constant. However, it was later shown that a correction for changes in the phenotypic variance–covariance matrix (\mathbf{P}) must be applied when adding selection gradients (Wade and Kalisz 1989). This

correction is necessary because the measurement of selection gradients at a particular episode relies on \mathbf{P} that may have been altered by selection at earlier episodes (Lande and Arnold 1983).

These methods for adding selection across episodes were derived solely for directional (linear) selection, not for nonlinear or quadratic measures of selection (e.g., stabilizing, disruptive, and correlational). Because the publication of a meta-analysis of selection studies, which showed that measurements of nonlinear selection, were relatively uncommon (Kingsolver et al. 2001), interest in quadratic selection has grown (Blows and Brooks 2003; Stinchcombe et al. 2008). Quadratic selection differentials (C) and gradients (γ) describe the curvature of the fitness function and are of particular interest because of their predicted effects on the evolution of genetic variance and covariance (Lande 1980b; Lande and Arnold 1983; Phillips and Arnold 1989). Few studies have attempted to measure nonlinear selection using multiple fitness components (e.g., Preziosi and Fairbairn 2000; McGlothlin et al. 2005), but studies such as these are likely to be particularly illuminating because of the intimate relationships between genetic correlations (which may be shaped by correlational selection) and life-history trade-offs (which may be shaped by variation in selection across the life cycle). Thus, a method for adding estimates of nonlinear selection is desirable.

Here, I derive equations relating lifetime nonlinear selection to selection that occurs via components of total fitness. This derivation produces a method that can be used to add episodes of selection to estimate lifetime nonlinear selection that is similar to the current methods used for directional selection (Arnold and Wade 1984a,b; Wade and Kalisz 1989), with one important difference. Namely, the analysis here shows that directional selection across episodes contributes to total quadratic selection, even when net directional selection is zero. I demonstrate how to employ this method using two examples: a simulated dataset with four consecutive selective episodes and a reanalysis of data from a long-term study of dark-eyed juncos (McGlothlin et al. 2005).

Adding Nonlinear Selection

Arnold and Wade (1984a) derived a generalized method for adding selection across episodes, showing that phenotypic change due to selection in one generation, $\mathbf{s}_{\text{total}}$ (a column vector of consisting selection differentials, s_i for each trait i) could be partitioned into additive components due to selection in each episode k of m total selective episodes. Expressed symbolically,

$$\mathbf{s}_{\text{total}} = \sum \mathbf{s}_k, \tag{1}$$

where

$$s_{i,k} = \frac{1}{\bar{W}_k} \text{Cov}(z_{i,k}, W_k) \tag{2}$$

and W_k is a component of absolute fitness at episode k . Selection differentials may be added in this way if the components of fitness at each episode multiply to give lifetime fitness, W_{total} .

Unlike selection differentials, the estimation of selection gradients, which estimate the direct relationship between traits and fitness when controlling for correlated traits, depends upon the pattern of variance and covariance in \mathbf{P} . Wade and Kalisz (1989) demonstrated that it is necessary to correct for changes in \mathbf{P} across the life cycle to estimate the total selection gradient. The total selection gradient is thus given by

$$\boldsymbol{\beta}_{\text{total}} = \mathbf{P}_0^{-1} \sum \mathbf{P}_k \boldsymbol{\beta}_k, \tag{3}$$

where \mathbf{P}_0 is the phenotypic (co)variance matrix before all selection and \mathbf{P}_k is the phenotypic (co)variance matrix before selection episode k . Because nonlinear selection gradients are measured using the same multiple regression method as is used for directional selection, changes in \mathbf{P} are also likely to be important for estimating lifetime nonlinear selection.

To derive equations for relating lifetime quadratic selection differentials (C_{total}) and gradients (γ_{total}) to their components, I will follow an approach similar to that used by Arnold and Wade (1984a). I begin by partitioning the total change in \mathbf{P} due to selection across the life cycle into the sum of changes at each episode,

$$\Delta \mathbf{P}_{\text{total}} = \sum \Delta \mathbf{P}_k. \tag{4}$$

Lande and Arnold (1983) showed that this change can be expressed as a function of selection differentials,

$$\Delta \mathbf{P}_{\text{total}} = \mathbf{C}_{\text{total}} - \mathbf{s}_{\text{total}} \mathbf{s}_{\text{total}}^T, \tag{5}$$

where \mathbf{C} represents a square matrix of quadratic selection differentials C_{ij} and T denotes matrix transposition. Similarly, change in \mathbf{P} at the k th episode of selection can be expressed as

$$\Delta \mathbf{P}_k = \mathbf{C}_k - \mathbf{s}_k \mathbf{s}_k^T \tag{6}$$

Substituting equations (5) and (6) into equation (4) and rearranging, one finds

$$\mathbf{C}_{\text{total}} = \sum \mathbf{C}_k - \sum \mathbf{s}_k \mathbf{s}_k^T + \mathbf{s}_{\text{total}} \mathbf{s}_{\text{total}}^T, \tag{7}$$

or equivalently,

$$\mathbf{C}_{\text{total}} = \sum \mathbf{C}_k + \sum_{k \neq l} \mathbf{s}_k \mathbf{s}_l^T. \tag{8}$$

The analogous equation for selection gradients may be solved by noting that by definition (Lande and Arnold 1983),

$$\mathbf{s} = \mathbf{P}\boldsymbol{\beta} \tag{9a}$$

and assuming multivariate normality of z ,

$$\mathbf{C} = \mathbf{P}\boldsymbol{\gamma}\mathbf{P}. \tag{9b}$$

By using equations (9) to define \mathbf{s}_k , $\mathbf{s}_{\text{total}}$, \mathbf{C}_k , and $\mathbf{C}_{\text{total}}$ as a function of selection gradients, substituting these terms into equation (7), and rearranging, it can be shown that

$$\boldsymbol{\gamma}_{\text{total}} = \mathbf{P}_0^{-1} \left[\sum \mathbf{P}_k (\boldsymbol{\gamma}_k - \boldsymbol{\beta}_k \boldsymbol{\beta}_k^T) \mathbf{P}_k \right] \mathbf{P}_0^{-1} + \boldsymbol{\beta}_{\text{total}} \boldsymbol{\beta}_{\text{total}}^T, \quad (10)$$

or equivalently,

$$\boldsymbol{\gamma}_{\text{total}} = \mathbf{P}_0^{-1} \left[\sum (\mathbf{P}_k \boldsymbol{\gamma}_k \mathbf{P}_k) + \sum_{k \neq l} \mathbf{P}_k \boldsymbol{\beta}_k \boldsymbol{\beta}_l^T \mathbf{P}_l \right] \mathbf{P}_0^{-1}. \quad (11)$$

Mathematica notebooks for performing the necessary calculations to add selection differentials and gradients are provided as Supporting Information.

It is clear from equations (7–8) and (10–11) that total nonlinear selection is not simply the sum of nonlinear selection gradients at each episode. Rather, directional selection in each episode contributes to the total curvature of fitness function, creating a nonzero $\mathbf{C}_{\text{total}}$ or $\boldsymbol{\gamma}_{\text{total}}$ even when all \mathbf{C}_k or $\boldsymbol{\gamma}_k$ equal zero. Using equation (8), consider the single-trait case with two episodes pure directional selection (all $\mathbf{C}_k = 0$). It is easy to see that when s_1 and s_2 are of the same sign, the total quadratic selection differential will have a disruptive character ($\mathbf{C}_{\text{total}} > 0$), but if s_1 and s_2 are of opposite signs, it will have a stabilizing character ($\mathbf{C}_{\text{total}} < 0$). In the special case where $s_1 = -s_2$, there will be no total directional selection (eq. 1), but $\mathbf{C}_{\text{total}}$ will be less than zero, leading to true stabilizing selection across the life cycle.

Lifetime correlational selection may also arise from directional selection acting on two traits in different episodes. One instructive case to consider is when directional selection acts in opposite directions but identical magnitudes in two sequential episodes ($\mathbf{s}_1^T = [s, -s]$, $\mathbf{s}_2^T = [-s, s]$). This situation leads to zero net directional selection, but net stabilizing selection on both traits and positive correlational selection on the combination of the traits,

$$\mathbf{C}_{\text{total}} = \begin{bmatrix} -2s^2 & 2s^2 \\ 2s^2 & -2s^2 \end{bmatrix}.$$

If one wishes to use canonical rotation to interpret $\boldsymbol{\gamma}_{\text{total}}$ (Blows and Brooks 2003; Blows 2007), effects of changes in \mathbf{P} and of directional selection should be taken into account before canonical rotations are performed, as both factors will influence the eigenvalues and eigenvectors of $\boldsymbol{\gamma}_{\text{total}}$.

Assigning statistical confidence to calculations performed using equations (7–8) and (10–11) is not straightforward. In general, testing statistical significance of measures of selection presents a problem because fitness components are almost never normal, leading to violation of the assumptions of statistical testing in ordinary least squares regression (Mitchell-Olds and Shaw 1987). Although using generalized linear models and resampling methods may circumvent this problem for individual analyses,

adding measures of selection presents additional complications, in that the error of a summed selection differential or gradient depends upon the cumulative error of multiple analyses. One solution is to use the addition of selection gradients as a heuristic tool to interpret results, leaving statistical testing to the individual components (as is commonly done for the predicted response to selection, e.g., McGlothlin et al. 2005). A second newly available solution is to use aster models to estimate the strength and form of total selection (Geyer et al. 2007; Shaw et al. 2008). Aster models explicitly model statistical dependence of sequential episodes and use compound distributions to assign statistical confidence to the total fitness landscape (Shaw et al. 2008). If both parameter estimates (differentials or gradients) and the shape of the fitness landscape are of interest, aster analyses may be performed alongside the calculations presented here.

Selection in Males and Females

Another common application of Lande and Arnold’s method involves measuring selection acting separately on males and females (reviewed in Cox and Calsbeek 2009). When male and female traits are quite different, it is often useful to consider them as separate traits. However, if the male and female traits are fairly similar, one may wish to treat them as the same trait and to add selection on males and females (e.g., McGlothlin et al. 2005).

Adding selection in males and females is not strictly the same as adding selection across the life cycle, as male fitness and female fitness do not multiply to total fitness, and selection on the sexes occurs simultaneously rather than sequentially. To address this, I consider Lande’s (1980a) model for the evolution of sexual dimorphism:

$$\begin{bmatrix} \Delta \bar{\mathbf{z}}_m \\ \Delta \bar{\mathbf{z}}_f \end{bmatrix} = \frac{1}{2} \begin{bmatrix} \mathbf{G}_m & \mathbf{B} \\ \mathbf{B}^T & \mathbf{G}_f \end{bmatrix} \begin{bmatrix} \mathbf{P}_m^{-1} \mathbf{s}_m \\ \mathbf{P}_f^{-1} \mathbf{s}_f \end{bmatrix}, \quad (13)$$

where m denotes male, f denotes female, and \mathbf{B} is the matrix of cross-sexual genetic covariance, and the multiplier $1/2$ arises because each offspring has one father and one mother. To treat male and female traits as the same traits, several assumptions are necessary. First, one must assume that $\mathbf{G}_m = \mathbf{G}_f$. A measurement of \mathbf{G} independent of sex can be obtained by including sex as a fixed effect in an animal model (McGlothlin et al. 2005). In addition, one must estimate a common \mathbf{P} for the two sexes and assume that genetic correlations between the sexes are large ($r_{mf} \approx 1$), so that $\mathbf{G}_m = \mathbf{G}_f = \mathbf{B}$. Making these assumptions,

$$\begin{bmatrix} \Delta \bar{\mathbf{z}}_m \\ \Delta \bar{\mathbf{z}}_f \end{bmatrix} = \frac{1}{2} \begin{bmatrix} \mathbf{G} & \mathbf{G} \\ \mathbf{G} & \mathbf{G} \end{bmatrix} \begin{bmatrix} \mathbf{P}_0^{-1} \mathbf{s}_m \\ \mathbf{P}_0^{-1} \mathbf{s}_f \end{bmatrix}. \quad (14)$$

Multiplying,

$$\Delta \bar{\mathbf{z}}_m = \Delta \bar{\mathbf{z}}_f = \frac{1}{2} \mathbf{G} \mathbf{P}_0^{-1} (\mathbf{s}_m + \mathbf{s}_f) = \frac{1}{2} \mathbf{G} \mathbf{P}_0^{-1} (\mathbf{P}_m \boldsymbol{\beta}_m + \mathbf{P}_f \boldsymbol{\beta}_f). \quad (15)$$

Noting that $\Delta \bar{\mathbf{z}} = \frac{1}{2} (\Delta \bar{\mathbf{z}}_m + \Delta \bar{\mathbf{z}}_f) = \mathbf{G} \mathbf{P}_0^{-1} \mathbf{s}_{\text{total}}$, the total force of selection on males and females can thus be written as

$$\mathbf{s}_{\text{total}} = \frac{1}{2} (\mathbf{s}_m + \mathbf{s}_f), \quad (16)$$

or

$$\boldsymbol{\beta}_{\text{total}} = \frac{1}{2} \mathbf{P}_0^{-1} (\mathbf{P}_m \boldsymbol{\beta}_m + \mathbf{P}_f \boldsymbol{\beta}_f). \quad (17)$$

A similar approach can be followed to find the total effect of nonlinear selection using the equation for within-generation change in \mathbf{G} . Making the same assumptions,

$$\begin{bmatrix} \Delta \mathbf{G}_m \\ \Delta \mathbf{G}_f \end{bmatrix} = \frac{1}{2} \begin{bmatrix} \mathbf{G} & \mathbf{G} \\ \mathbf{G} & \mathbf{G} \end{bmatrix} \left(\begin{bmatrix} \mathbf{P}_0^{-1} (\mathbf{C}_m \mathbf{P}_0^{-1}) & \mathbf{0} \\ \mathbf{0} & \mathbf{P}_0^{-1} (\mathbf{C}_f \mathbf{P}_0^{-1}) \end{bmatrix} - \begin{bmatrix} \mathbf{P}_0^{-1} (\mathbf{s}_m \mathbf{s}_m^T) \mathbf{P}_0^{-1} & \mathbf{0} \\ \mathbf{0} & \mathbf{P}_0^{-1} (\mathbf{s}_f \mathbf{s}_f^T) \mathbf{P}_0^{-1} \end{bmatrix} \right) \begin{bmatrix} \mathbf{G} & \mathbf{G} \\ \mathbf{G} & \mathbf{G} \end{bmatrix}. \quad (18)$$

Expanding, it can be shown that

$$\Delta \mathbf{G}_m = \Delta \mathbf{G}_f = \frac{1}{2} \mathbf{G} \mathbf{P}_0^{-1} (\mathbf{C}_m + \mathbf{C}_f - \mathbf{s}_m \mathbf{s}_m^T - \mathbf{s}_f \mathbf{s}_f^T) \mathbf{P}_0^{-1} \mathbf{G}. \quad (19)$$

Noting that $\Delta \mathbf{G} = \frac{1}{2} (\Delta \mathbf{G}_m + \Delta \mathbf{G}_f) = \mathbf{G} \mathbf{P}_0^{-1} (\mathbf{C}_{\text{total}} - \mathbf{s}_{\text{total}} \mathbf{s}_{\text{total}}^T) \mathbf{P}_0^{-1} \mathbf{G}$, the total effect of nonlinear selection on males and females is

$$\mathbf{C}_{\text{total}} = \frac{1}{2} (\mathbf{C}_m + \mathbf{C}_f - \mathbf{s}_m \mathbf{s}_m^T - \mathbf{s}_f \mathbf{s}_f^T) \mathbf{P}_0^{-1} + \mathbf{s}_{\text{total}} \mathbf{s}_{\text{total}}^T. \quad (20)$$

or

$$\boldsymbol{\gamma}_{\text{total}} = \frac{1}{2} \mathbf{P}_0^{-1} [\mathbf{P}_m (\boldsymbol{\gamma}_m - \boldsymbol{\beta}_m \boldsymbol{\beta}_m^T) \mathbf{P}_m + \mathbf{P}_f (\boldsymbol{\gamma}_f - \boldsymbol{\beta}_f \boldsymbol{\beta}_f^T) \mathbf{P}_f] \mathbf{P}_0^{-1} + \boldsymbol{\beta}_{\text{total}} \boldsymbol{\beta}_{\text{total}}^T. \quad (21)$$

This derivation arrives at the same result as equations (7) and (10) except that here, nonlinear selection in each sex is averaged instead of summed. These can equivalently be expressed as

$$\mathbf{C}_{\text{total}} = \frac{1}{2} (\mathbf{C}_m + \mathbf{C}_f) - \frac{1}{4} (\mathbf{s}_m - \mathbf{s}_f) (\mathbf{s}_m - \mathbf{s}_f)^T \quad (22)$$

and

$$\boldsymbol{\gamma}_{\text{total}} = \frac{1}{2} \mathbf{P}_0^{-1} [\mathbf{P}_m \boldsymbol{\gamma}_m \mathbf{P}_m + \mathbf{P}_f \boldsymbol{\gamma}_f \mathbf{P}_f - \frac{1}{2} (\mathbf{P}_m \boldsymbol{\beta}_m - \mathbf{P}_f \boldsymbol{\beta}_f) (\mathbf{P}_m \boldsymbol{\beta}_m - \mathbf{P}_f \boldsymbol{\beta}_f)^T] \mathbf{P}_0^{-1}. \quad (23)$$

In contrast to the equation for summing selective episodes, this formulation shows that directional selection does not give rise to curvature unless it acts differently on males and females.

For a single-trait case, any sex difference in directional selection creates stabilizing selection, which should tend to reduce available genetic variance.

By a similar process, one could derive equations summing simultaneous selection on the same traits in different environments, assuming no genotype-by-environment interaction (Via and Lande 1985). In this case, selection in each environment would be weighted not by $1/2$ but by the frequency with which each environment occurs.

Simulated Data

To illustrate how directional selection in different episodes can give rise to nonlinear selection, I used PASW Statistics 17 (SPSS Inc, Chicago, IL) to simulate a population of 1000 individuals with a single phenotype z with an expected normal distribution of $\mu = 0$ and $\sigma^2 = 1$. The resulting simulated sample was distributed as $\bar{z} = 0.017$, $s^2 = 0.926$. I then applied four sequential episodes of viability selection by generating at each episode a second variable proportional to z and an error term, which was added so that the fitness function would not represent truncation selection. In episodes 1 and 3, the top 80% was selected to survive, and in episodes 2 and 4, the bottom 80% was selected to survive. Fitness was assigned as 1 or 0 based on survival and divided by average fitness to calculate relative fitness (w). Then, I measured selection in each episode as $s_k = \text{cov}(w_k, z_k)$ and $C_k = \text{cov}[w_k, (z_k - \bar{z}_k)^2]$ and total selection as $\mathbf{s}_{\text{total}} = \text{cov}(w_{\text{total}}, z_1)$ and $\mathbf{C}_{\text{total}} = \text{cov}[w_{\text{total}}, (z_1 - \bar{z}_1)^2]$. Total relative fitness (w_{total}) was calculated based on survivorship through all episodes. Similarly, directional selection gradients (β) were measured using univariate linear regressions and stabilizing selection gradients (γ) were measured using bivariate linear regressions that included z and $(z - \bar{z})^2$. The regression coefficient from the squared deviation term was doubled to give γ (Lande and Arnold 1983; Stinchcombe et al. 2008). Measured total selection was compared to total selection calculated using equations (1), (3), (7), and (10).

Results are presented in Table 1, with cubic spline fits from glms version 4.0/glmsWIN version 1.0 (Schluter 1988) shown in Figure 1. For all totals except γ , the calculated value was identical to the measured value to three decimal places. The estimates for γ were further apart, likely because there tended to be some collinearity between z and $(z - \bar{z})^2$, creating error in estimating the quadratic term. Inspection of these results indicates that oscillating directional selection across episodes canceled out, leading to no total directional selection. Total selection was strongly stabilizing. Some of this effect was due to the sigmoid fitness functions in each episode, which all had negative curvature ($\sum C_k = -0.325$). However, variation in directional selection also contributed to stabilizing selection, decreasing C_{total} by 0.123. The reason for this is clear. When viability selection fluctuates in direction

Table 1. Means, variances, and measurements of linear and nonlinear selection for a simulated population of 1000 individuals subject to four episodes of viability selection. See text for definition of variables.

k	\bar{z}	P	s	C	β	γ
1	0.017	0.926	0.221	-0.110	0.239	-0.139
2	0.238	0.767	-0.211	-0.132	-0.275	-0.190
3	0.027	0.591	0.142	-0.037	0.240	-0.084
4	0.169	0.534	-0.142	-0.046	-0.266	-0.193
Final	0.027	0.468				
Total (measured)			0.010	-0.458	0.011	-0.547
Total (calculated)			0.010	-0.458	0.011	-0.523

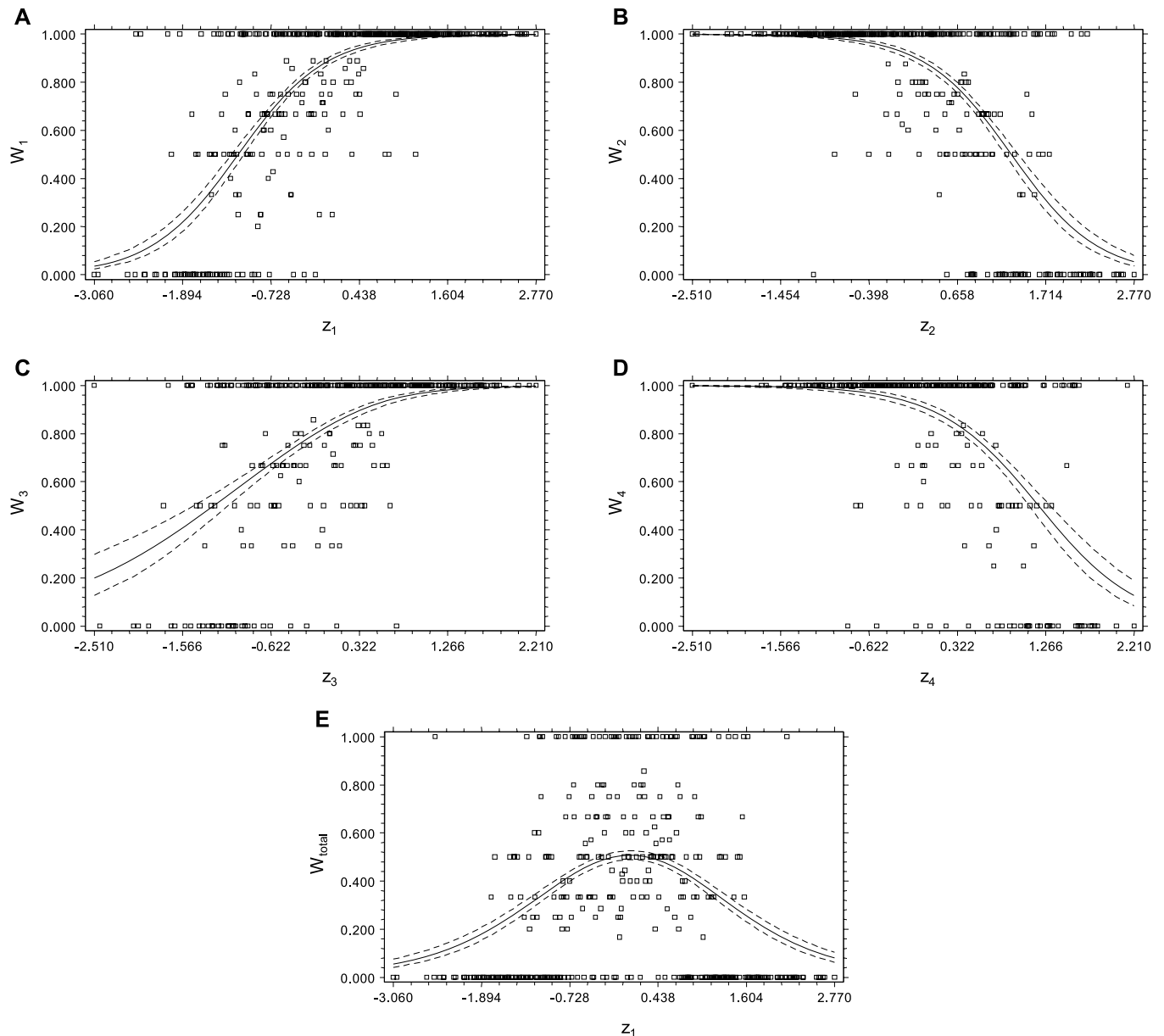
**Figure 1.** Cubic spline representations of four episodes of viability selection from a simulated population of 1000 individuals (A–D) and the cumulative effect of selection (E). Fitness (W) was assigned as either zero or one. Data points between zero and one represent average fitness of individuals with the same phenotype. The solid line shows predicted fitness, and the dashed lines represent ± 1 SE calculated with bootstrapping.

Table 2. Off-diagonal elements (P_{ij}) of phenotypic (co)variance matrices (\mathbf{P}) from a study of selection in dark-eyed juncos. The diagonal elements of each matrix are equal to unity because traits were standardized before each analysis. The consensus matrix for males and females is calculated from a multivariate animal model with sex as a fixed effect (McGlothlin et al. 2005). All other matrices are from subsets of the population upon which each episode of selection was measured.

Analysis	P_{ij}		
	Wing/ Tail	Wing/ Tail white	Tail/ Tail white
Consensus	0.460	0.090	0.090
Male juvenile survival	0.496	-0.014	0.012
Male adult survival	0.514	-0.019	-0.006
Male mating success	0.627	0.158	-0.048
Male fecundity/mate	0.652	0.038	-0.090
Female juvenile survival	0.423	-0.019	0.040
Female adult survival	0.408	-0.030	0.025
Female mating success	0.453	0.029	0.097
Female fecundity/mate	0.433	0.039	0.145

across episodes, individuals in the middle of the phenotypic distribution will tend to be more likely to survive the entire time span.

This simulation also illustrates the importance of correcting for changes in phenotypic variance when calculating estimates of γ_{total} . Simply adding the values of γ_k would overestimate the strength of stabilizing selection ($\sum \gamma_k = -0.605$). This problem would be exacerbated if the contribution of directional selection were added without taking change in \mathbf{P} into account ($\sum \gamma_k + \sum_{k \neq l} \beta_k \beta_l = -0.861$).

Selection in Dark-Eyed Juncos

To show how the method of adding quadratic selection gradients may be applied to real data, I present a reanalysis of a study of selection in male and female dark-eyed juncos (*Junco hyemalis*) (McGlothlin et al. 2005). Selection was measured separately in each sex at four different episodes: juvenile survival, adult survival, mating success, and offspring per mate. The selection gradients were originally reported in Table 3 of McGlothlin et al. (2005). As required for quadratic selection analysis, the diagonal elements of γ were calculated by doubling coefficients from squared terms in the multiple regression (Lande and Arnold 1983; Stinchcombe et al. 2008). One of these terms was reported incorrectly in the original paper (correct value for $\gamma_{\text{wing length}^2} = -0.022$), but the correct value was used in further calculations in that paper. Standard errors for each analysis were estimated using delete-one jackknifing.

To investigate the total effect of selection, directional and nonlinear gradients were originally added without using the correction factor of Wade and Kalisz (1989) or the method derived here. As shown above, this can lead to inaccurate estimates of total nonlinear selection. I recalculated the summed gradients for each sex using equations (3) and (10) and for sexes combined using equations (17) and (21). Values for \mathbf{P} are given in Table 2, and newly calculated summed selection gradients are shown in Table 3. As statistical testing is not of primary interest here, I reproduce the estimated standard errors from the original paper. Standard errors for the summed selection gradients for males and females were calculated from the jackknifed standard errors as $\sqrt{\sum SE_k^2}$. The standard errors for the combined analysis of males and females were miscalculated in the original paper, leading to overconfidence in these estimates. Here, they are shown as $\frac{1}{2}\sqrt{SE_m^2 + SE_f^2}$.

Table 3. Summed selection gradients for males, females, and sexes combined from a study of dark-eyed juncos. Selection gradients from Table 3 in McGlothlin et al. (2005) were added using the equations derived in this article. See text for calculation of standard errors.

	β	γ		
		Wing length	Tail length	Tail white
Males ($n=1431$)				
Wing length	0.104±0.143	0.114±0.316		
Tail length	-0.030±0.144	0.061±0.287	0.025±0.360	
Tail white	0.117±0.108	0.270±0.159	-0.064±0.164	0.111±0.188
Females ($n=1329$)				
Wing length	-0.150±0.111	0.305±0.188		
Tail length	0.264±0.133	-0.087±0.175	0.186±0.216	
Tail white	0.085±0.103	0.121±0.131	-0.185±0.157	0.074±0.161
Sexes combined ($n=1380$)				
Wing length	-0.042±0.091	0.169±0.183		
Tail length	0.123±0.098	0.005±0.168	0.095±0.210	
Tail white	0.099±0.074	0.167±0.103	-0.127±0.114	0.070±0.124

Table 4. Evolutionary predictions from combined-sex selection gradients in Table 3 and an estimate of \mathbf{G} from McGlothlin et al. (2005).

	$\Delta\bar{z}$	$\Delta\mathbf{G}$		
		Wing length	Tail length	Tail white
Wing length	0.041	0.034		
Tail length	0.054	0.031	0.042	
Tail white	0.045	0.025	0.002	0.045

In general, directional selection was weak, and the results using the Wade–Kalisz correction did not differ substantially from the originally reported results. Nonlinear selection gradients were more strongly affected by correcting for changes in \mathbf{P} and the contribution of β . Because of the overall weakness of directional selection in this study, most of this effect arose from correcting for changes in \mathbf{P} ; recalculating the values in Table 3 without β led to an average absolute difference of only 0.011.

For males, correlational selection acting on wing length and tail white, which provided the major result from the original paper, was still quite strong, but the value was slightly lower than the value reported in the original paper ($\gamma = 0.346$). The other correlational selection gradients were also weaker than the originally reported results. For females, the changes in γ were not as large, most likely because \mathbf{P} did not vary as much across selection episodes (Table 2). When examining selection summed across both sexes, the differences between the two studies largely reflected the effects of selection on males.

Despite the differences between the estimates of β and γ , the predicted responses to selection using the estimate of \mathbf{G} from the original paper and the equations $\Delta\bar{z} = \mathbf{G}\beta_{\text{total}}$ and $\Delta\mathbf{G} = \mathbf{G}(\gamma_{\text{total}} - \beta_{\text{total}}\beta_{\text{total}}^T)\mathbf{G}$ (which predicts within-generation change in \mathbf{G} , Phillips and Arnold 1989) did not differ substantially from the original results (Table 4).

Discussion

The equations derived here and their application to simulated and real data show the importance of considering changes in the phenotypic (co)variance matrix and the effects of directional selection when adding quadratic selection gradients across episodes of selection. As is the case for directional selection (Wade and Kalisz 1989), correcting for changes in \mathbf{P} has the effect of diminishing the importance of later episodes of quadratic selection, as is illustrated by the junco dataset.

Perhaps the most interesting result, however, is that directional selection acting in different episodes can lead to net quadratic selection, even in the absence of quadratic selection at

each episode. It was already well known that purely directional fitness functions can lead to the measurement of quadratic gradients that may be incorrectly interpreted as stabilizing or disruptive selection were the fitness function not plotted (Schluter 1988; Brodie et al. 1995). However, the ability of fluctuating directional selection to generate true stabilizing selection has not generally been appreciated. For example, in an exploration of the net effect of male–male competition and female mate choice, Hunt et al. (2009) suggest that opposing directional selection through these two components of sexual selection may maintain variance in the sexually selected traits. The equations here suggest that this situation should lead to net stabilizing selection, which should have the effect of reducing, rather than maintaining, genetic variance.

This analysis may also explain why strong stabilizing selection is rarely measured in natural populations (Kingsolver et al. 2001). Most studies of natural selection measure selection acting via one or a few components of fitness because of the difficulty of estimating lifetime fitness. Directional selection seems to be very common when selection is measured in natural populations, whereas quadratic selection is generally found to be weak (Kingsolver et al. 2001). Furthermore, disruptive selection gradients are found as often as stabilizing selection, despite theoretical predictions that stabilizing selection should be common in populations well-adapted to their current environmental conditions (Travis 1989; Kingsolver et al. 2001; Hansen and Houle 2004; Estes and Arnold 2007)

As I have shown here, the commonality of directional selection acting via components of fitness does not negate the possibility of stabilizing selection over the entire life cycle. It is possible that directional selection that fluctuates across the life cycle, due to environmental variation or life-history trade-offs, for example, predominates in natural populations. If so, stabilizing selection should be common when total lifetime selection is measured.

The equations derived here also demonstrate that fluctuating directional selection may give rise to lifetime correlational selection, which is predicted to affect the evolution of genetic correlations between traits (Lande 1980b; Brodie 1989; Phillips and Arnold 1989; Brodie 1992; Sinervo and Svensson 2002; McGlothlin et al. 2005). Life-history trade-offs are often characterized by conflicting directional selection pressures at different stages of the life cycle (Schluter et al. 1991). The physiological mechanisms, such as hormones, that underlie life-history trade-offs are also often responsible for integrating suites of correlated traits (Ketterson and Nolan 1992, 1999; Adkins-Regan 2005). Correlational selection has been suggested as an evolutionary mechanism for the maintenance of such suites (McGlothlin and Ketterson 2008). The results presented here suggest that such correlational selection may tend to arise as a consequence of life-history trade-offs.

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Supporting Information

The following supporting information is available for this article:

Adding_selection_differentials. Mathematica notebook for performing the calculations in the text.

Adding_selection_gradients. Mathematica notebook for performing the calculations in the text.

Supporting Information may be found in the online version of this article.

Correction made after 1/10/2010 publication: Equations 13, 14, and 23 had formatting errors in the previous version.

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Correction for McGlothlin (2010)

In a recent paper (McGlothlin 2010), I extended the method of combining selection gradients from multiple episodes of selection, first developed by Arnold and Wade (1984) and Wade and Kalisz (1989), to include nonlinear selection gradients. A mistaken assumption led to an error in the section of that paper regarding selection on males and females. My original equation (18) made the implicit assumption that the total change in the phenotypic (co)variance matrix \mathbf{P} could be expressed as an average of the change in each sex, or

$$\Delta\mathbf{P}_{\text{total}} = \frac{1}{2}(\Delta\mathbf{P}_m + \Delta\mathbf{P}_f). \quad (1)$$

This assumption, which led to the initial conclusion that sexually antagonistic directional selection should create negative curvature in the fitness surface, can be shown to be incorrect using an extreme case with strong sexually antagonistic selection. Consider a population consisting of two equally frequent morphs that do not differ between the sexes. Scoring the phenotypic values of the two morphs as 0 and 1, the phenotypic variance before selection is $P_{\text{total}} = P_m = P_f = 0.25$. If all males with $z = 0$ and all females with $z = 1$ survive and the rest die, viability selection removes all variance within each sex, and so $\Delta P_m = \Delta P_f = -0.25$. However, assuming an equal sex ratio, the overall variance in the population does not change because each morph is still equally common; thus $\Delta P_{\text{total}} = 0$, disproving equation (1). Further, the selection differentials in this example are $s_m = -0.5$, $s_f = 0.5$, and $\mathbf{s}_{\text{total}} = 0$, suggesting that the change in variance due to directional selection should be a function of s_{total} . Indeed, the correct portion of $\Delta\mathbf{P}_{\text{total}}$ due to sex-specific directional selection, given as a multivariate equation for generality, is simply $-\mathbf{s}_{\text{total}}\mathbf{s}_{\text{total}}^T$ or $-\frac{1}{4}(\mathbf{s}_m + \mathbf{s}_f)(\mathbf{s}_m + \mathbf{s}_f)^T$ (Lande 1980; McGlothlin 2010).

Through a trivial derivation using the definition of covariance, the total contribution of nonlinear selection in males and females can then be shown to be simply

$$\mathbf{C}_{\text{total}} = \frac{1}{2}(\mathbf{C}_m + \mathbf{C}_f), \quad (2)$$

where each \mathbf{C} is a matrix of quadratic selection differentials. Expressed using nonlinear selection gradients ($\boldsymbol{\gamma}$) instead of differentials,

$$\boldsymbol{\gamma}_{\text{total}} = \frac{1}{2}\mathbf{P}_0^{-1}(\mathbf{P}_m\boldsymbol{\gamma}_m\mathbf{P}_m + \mathbf{P}_f\boldsymbol{\gamma}_f\mathbf{P}_f)\mathbf{P}_0^{-1}. \quad (3)$$

Equations (2) and (3) are exact only when the sex-specific phenotypic means are equal or are transformed to be so. Equation (2) replaces original equations (20) and (22) from McGlothlin (2010), and equation (3) replaces original equations (21) and (23). Original equations (20–23) had suggested a contribution of directional selection to total nonlinear selection, which is clearly not the case in equations (2) and (3). The correction in equation (3) also slightly affects my reanalysis of a dataset from McGlothlin et al. (2005). The results of these new calculations are presented in Table 1.

Using Lande and Arnold's (1983) equation $\Delta\mathbf{P}_{\text{total}} = \mathbf{C}_{\text{total}} - \mathbf{s}_{\text{total}}\mathbf{s}_{\text{total}}^T$, the total change in phenotypic variance due to sex-specific quadratic and directional selection expressed in differentials is then

$$\Delta\mathbf{P}_{\text{total}} = \frac{1}{2}(\mathbf{C}_m + \mathbf{C}_f) - \frac{1}{4}(\mathbf{s}_m + \mathbf{s}_f)(\mathbf{s}_m + \mathbf{s}_f)^T \quad (4)$$

or expressed in gradients,

$$\Delta\mathbf{P}_{\text{total}} = \frac{1}{2}(\mathbf{P}_m\boldsymbol{\gamma}_m\mathbf{P}_m + \mathbf{P}_f\boldsymbol{\gamma}_f\mathbf{P}_f) - \frac{1}{4}(\mathbf{P}_m\boldsymbol{\beta}_m + \mathbf{P}_f\boldsymbol{\beta}_f)(\mathbf{P}_m\boldsymbol{\beta}_m + \mathbf{P}_f\boldsymbol{\beta}_f)^T, \quad (5)$$

where \mathbf{P}_0 is the consensus phenotypic (co)variance matrix before selection. Equations (4) and (5) are not derivable from the false equation (1) because of the interaction between male and female directional selection.

Unlike sequential episodes of selection, variation in directional selection does not contribute to $\mathbf{C}_{\text{total}}$ or $\boldsymbol{\gamma}_{\text{total}}$ when selection acts differently on males and females. The difference between the two cases arises because when selection episodes are sequential, the fitness of a given phenotype may differ between episodes, and these fitness effects accrue across the life cycle. When selection fluctuates in its direction, the phenotypes in the middle of the distribution do the best because it is better to always be average rather than to

Table 1. Recalculation of total (male + female) nonlinear selection gradients and predicted change in the G matrix from a study of dark-eyed juncos (McGlothlin et al. 2005; McGlothlin 2010). These results replace the original Table 3 (section 3) and Table 4 (section 2) in McGlothlin (2010).

	γ_{total}		
	Wing length	Tail length	Tail white
Wing length	0.187		
	± 0.183		
Tail length	-0.015	0.119	
	± 0.168	± 0.210	
Tail white	0.169	-0.129	0.070
	± 0.103	± 0.114	± 0.124
	$\Delta \mathbf{G}_{\text{total}}$		
	Wing length	Tail length	Tail white
Wing length	0.034		
Tail length	0.031	0.044	
Tail white	0.025	0.001	0.046

be extremely good sometimes and extremely bad at other times. The cumulative effects of directional selection that fluctuates in its direction thus create stabilizing selection (McGlothlin 2010). However, an analogous effect does not occur in sex-specific selection because a given phenotype never experiences both male-specific and female-specific selection, only one or the other. The effects of opposing sex-specific selection thus cancel each other out instead of creating curvature.

As a result, sexually antagonistic selection will not tend to decrease genetic variation as I argued in the original paper. The implication of equations (4) and (5) is that sexually antagonistic directional selection in males and females will tend to ameliorate the diminishing effect of directional selection on overall genetic variance, thus tending to preserve polymorphism in some cases as predicted by population genetic theory (e.g. Kidwell et al. 1977; Hedrick 1999; Rice and Chippindale 2001). This is a classic prediction for environmental variation as well (e.g., Hedrick et al. 1976). As suggested in the original paper, the total effect of environment-specific nonlinear selection can be estimated by modifying the sex-specific equation, replacing $1/2$ with the frequency that an environment is experienced. However, the corrections introduced here indicate that, as expected by population genetic theory, differences in directional selection in simultaneously experienced environments do not create a stabilizing effect.

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