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Measuring Nonlinear Selection

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A recent comprehensive review of empirical studies that measured the strength of selection concluded that there was little evidence for strong nonlinear selection in natural populations (Kingsolver et al. 2001). The median quadratic selection gradient identified by Kingsolver et al. (2001) was only 0.1, and gradients consistent with stabilizing or disruptive selection were found at a similar frequency and to be of similar magnitude. Stabilizing selection in particular is an important premise in many areas of evolutionary biology (Travis 1989), so this finding challenges our current understanding of how selection may operate in the wild (Conner 2001; Kingsolver et al. 2001). There is already some evidence that the strength and frequency of nonlinear selection identified in the review of Kingsolver et al. (2001) has influenced how evolutionary biologists view the potential role of stabilizing selection (Barton and Keightley 2002; Zhang et al. 2002).

Kingsolver et al. (2001) suggest a number of reasons why empirical studies may not find or may underestimate nonlinear selection, including an empirical bias toward selecting experimental systems that are likely to show directional selection. In addition, nonlinear selection gradients are often able to be estimated from data sets but are not published (Kingsolver et al. 2001), probably as a consequence of the paucity of significant individual gradients and the difficulty of interpreting the overall pattern of nonlinear selection from the large number of estimated gradients. Here, we demonstrate that the strength of non-

linear selection has been consistently underestimated in many studies as a consequence of the incomplete application of response surface methodology.

Response Surface Methodology

Nonlinear selection is routinely measured using second-order polynomial regression (Lande and Arnold 1983; Brodie et al. 1995). The representation of second-order polynomial regression most familiar to many biologists is

$$w = \alpha + \sum_{i=1}^n \beta_i z_i + 1/2 \sum_{i=1}^n \sum_{j=1}^n \gamma_{ij} z_i z_j, \quad (1)$$

where w is the fitness measure and z_i are the individual traits measured. Linear selection on individual traits is measured by using the partial linear regression coefficients, β_i . Quadratic regression coefficients (γ_{ii}) are used in empirical studies of selection to indicate convex selection (negative γ_{ii}) or concave selection (positive γ_{ii}) on individual traits, although they alone are not sufficient to establish that stationary points exist within the sampled space (Mitchell-Olds and Shaw 1987). If stationary points do exist within the sampled space, true stabilizing or disruptive selection are indicated by negative or positive γ_{ii} 's, respectively. Unfortunately, the full extent of nonlinear selection on a multivariate set of traits cannot be identified from the quadratic coefficients in isolation. The full second-order polynomial model also includes cross-product terms (γ_{ij}) that represent correlational selection on pairs of traits. Correlational selection gradients indicate nonlinear selection along axes that are not parallel to the axes represented by the individual traits. Of the 574 estimates of nonlinear selection identified by Kingsolver et al. (2001), only 109 were correlational selection gradients.

For convenience, model (1) may be represented in matrix form

$$w = \alpha + \mathbf{z}^T \boldsymbol{\beta} + \mathbf{z}^T \boldsymbol{\gamma} \mathbf{z}, \quad (2)$$

where \mathbf{z} is a vector of the traits on which selection is being measured, $\boldsymbol{\beta}$ is the vector of directional selection gradients,

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and γ is the matrix of quadratic and cross-product terms:

$$\gamma = \begin{bmatrix} \gamma_{11} & 1/2\gamma_{12} & \cdots & 1/2\gamma_{1j} \\ 1/2\gamma_{12} & \gamma_{22} & \cdots & 1/2\gamma_{2j} \\ \vdots & \vdots & \ddots & \vdots \\ 1/2\gamma_{1j} & 1/2\gamma_{2j} & \cdots & \gamma_{jj} \end{bmatrix}. \quad (3)$$

If correlational selection is present between pairs of traits, to interpret the form and strength of nonlinear selection acting on that set of traits (in contrast to individual traits), the major axes of the quadratic response surface need to be identified. Canonical analysis (Box and Wilson 1951; Box and Draper 1987) finds the major axes of the response surface by determining the normalized eigenvectors (\mathbf{m}_i), and their associated eigenvalues (λ_i), of γ . In other words, γ is rotated to eliminate the cross-product terms. The diagonalization of γ results in a matrix Λ :

$$\Lambda = \mathbf{M}^T \gamma \mathbf{M}, \quad (4)$$

where \mathbf{M} is a matrix that contains the normalized eigenvectors of γ as columns. The Λ matrix has the eigenvalues of γ along the diagonal and zeros off the diagonal since all cross-product terms have been eliminated:

$$\Lambda = \begin{bmatrix} \lambda_1 & 0 & 0 & 0 \\ 0 & \lambda_2 & 0 & 0 \\ 0 & 0 & \ddots & 0 \\ 0 & 0 & 0 & \lambda_i \end{bmatrix}. \quad (5)$$

The original second-order response surface in equation (2) can now be rewritten in canonical form:

$$w = \alpha + \mathbf{y}^T \boldsymbol{\theta} + \mathbf{y}^T \Lambda \mathbf{y}, \quad (6)$$

where individual traits (z_i) have been replaced by the new major (or canonical) axes of the response surface (y_i), and $\boldsymbol{\theta}$ is a vector that describes the slope of the surface along each new axis, just as $\boldsymbol{\beta}$ does for each original z_i . The eigenvalues of γ (the canonical coefficients) in Λ now replace the quadratic coefficients in γ as measures of the strength of convex or concave selection. It can be seen that each individual λ_i is a natural measure of the strength of nonlinear selection along each eigenvector, as when the y_i 's are placed back into a full second-order polynomial model, the values of the λ_i 's are returned as the quadratic coefficients (Bisgaard and Ankenman 1996). This useful property of the canonical coefficients does not appear to have been appreciated in selection analyses.

Phillips and Arnold (1989) gave a detailed introduction to the use of canonical analysis for investigating nonlinear selection, and we direct readers to that article for a com-

prehensive development of the technique for use in selection analyses. Unfortunately, although this article has frequently been cited, the appropriate canonical rotation of γ has been conducted infrequently in selection analyses to date (Simms 1990; Brodie 1992; Simms and Rausher 1993; Björklund and Senar 2001). Our purpose here is not only to reiterate the value of conducting a canonical analysis of the response surface but also to demonstrate how nonlinear selection will be underestimated in studies that do not conduct a canonical analysis that allows the strength and form of nonlinear selection to be determined from the canonical coefficients.

An Example: Sexual Selection on Male Color Traits in Guppies

Male guppies attract females by displaying colorful patterns that are made up of several different components: orange, black, and iridescent spots, and facultatively expressed areas of fuzzy black coloration (Houde 1997). The area of each of these four color attributes may be measured as a different trait, but it is unlikely that females make their choice by evaluating these four different aspects of coloration independently (Endler and Houde 1995; Brooks 1996; Brooks and Endler 2001). Rather, all aspects of male coloration are likely to contribute to the overall impression (e.g., the contrast) a male's color pattern makes, comprising his attractiveness (Endler and Houde 1995). Male attractiveness may thus be thought of as a composite trait of the individual color pattern measures.

Brooks and Endler (2001) demonstrated that there was significant linear sexual selection operating on male color patterns but did not consider nonlinear selection. Briefly, the attractiveness of 251 males to females was assessed in trials that consisted of allowing a single female to choose to spend time in the proximity of six males presented simultaneously to her. Male ornamentation was measured as the area covered by each of the four color types. Here, we reanalyze the four color variables measured on male guppies from that study to illustrate how the canonical rotation of γ can reveal concave or convex selection on a suite of traits that is not apparent from the quadratic coefficients. We estimated standardized nonlinear selection gradients using second-order polynomial regression to generate the γ matrix (Lande and Arnold 1983).

From the γ matrix (table 1), it could be concluded that there was little nonlinear selection on male coloration as all quadratic selection gradients were small and nonsignificant. Most selection analyses in the literature have stopped at this point without considering the correlational gradients (Kingsolver et al. 2001). All but one of the correlational selection gradients are nonsignificant as well, but note that the three correlational gradients between orange

Table 1: Matrix of standardized quadratic and correlational selection gradients (γ) for four male guppy color traits

	Black	Fuzzy	Iridescence	Orange
Black	.016			
Fuzzy	-.016	.00003		
Iridescence	-.028	.066	-.011	
Orange	.103	-.131*	-.099	.030

* $P = .039$.

and the other traits are quite large. The value of the canonical rotation of γ is displayed in table 2, where this complex set of correlational selection gradients (even with only four traits) has been reduced to a single canonical axis, m_1 , which displays a highly significant level of concave selection as λ_1 is positive. The composite trait represented by m_1 contrasts orange and black coloration with fuzzy black and iridescent coloration, which is consistent with the signs of the correlational selection gradients in γ . The results from the canonical analysis suggest that concave selection may play an important role in the evolution of male coloration by sexual selection, which is in direct contrast to the quadratic coefficients in γ that indicated no significant concave selection. Blows et al. (2003) present detailed analyses and visualizations of nonlinear selection on these traits and discuss how concave selection may help maintain polymorphism in male guppy ornaments.

The average size of the quadratic selection gradients in table 1 is only 0.014, and yet the strength of concave selection indicated along the m_1 axis is almost an order of magnitude larger ($\lambda_1 = 0.132$). Therefore, although there is little curvature along the axes parallel to the original traits, nonlinear selection is much stronger along the major axis of the response surface. It is important to remember, however, that the canonical rotation (table 2) has not uncovered any more selection than was already present in the γ matrix (table 1); rather, it is only the allocation of selection present in γ to the various coefficients that has been changed. This example serves to emphasize that the distinction between correlational and quadratic selection gradients is arbitrary; correlational selection can be transformed into concave or convex selection by the canonical rotation of γ . The arbitrary nature of nonlinear selection gradients mirrors the arbitrary nature of individual traits themselves when considered from a quantitative genetic perspective. Genetic correlations between traits indicate that individual trait phenotypes will not evolve independently but will be influenced by the patterns of genetic covariation between them (Lande 1979).

Large differences between the strength of nonlinear selection along major axes of the response surface and axes parallel to original traits will not always occur. For ex-

ample, the analysis of nonlinear selection of plant resistance to herbivores by Simms (1990) displayed roughly similar magnitudes of selection along the canonical and original trait axes (app. A, table A1) as a consequence of all but one of the γ_{ij} coefficients in γ being very small. In the extreme case, where all correlational selection gradients are zero, the γ matrix is equal to Λ , and so the canonical rotation would have no effect. Therefore, the canonical rotation may not provide substantial new insights into every situation, particularly when correlational selection is weak, in which case the coefficients in γ may be simpler to interpret biologically than the eigenvectors in M . Such a situation might commonly occur when traits that have very different functions are included in a single analysis.

Underestimation of Nonlinear Selection

To determine the extent to which nonlinear selection may have been underestimated in the studies surveyed by Kingsolver et al. (2001) as a consequence of ignoring nonlinear selection represented by the correlational selection gradients, we reconstituted γ from all studies in their database that had estimated quadratic and correlational selection gradients on three or more traits. The eigenvalues of each of 19 estimates of γ from seven studies (table A1) were then calculated using the EIGVAL function implemented in SAS IML2001. Although this approach allowed us to determine whether the λ_i 's were consistently larger than individual γ_{ii} 's, significance testing of the λ_i 's from zero was not possible without access to individual trait values. How the λ_i 's may be tested for significance when individual trait values are available, as will be the case in any empirical study, is discussed in detail in the next section.

In each of the 19 cases, the absolute size of the largest eigenvalue of γ (median $|\lambda| = 0.55$) was larger than the largest quadratic coefficient for an individual trait (median $|\gamma| = 0.37$). As in the case of Simms (1990), the difference was small in a number of cases (table A1), but overall the largest $|\lambda|$'s were significantly larger than the largest $|\gamma|$'s (Wilcoxon test: $Z = -3.823$, $n = 19$, $P < .001$). This re-

Table 2: M matrix of eigenvectors from the canonical analysis of γ for four male guppy color traits

m_i	λ_i	Black	Fuzzy	Iridescence	Orange
m_1	.132*	.390	-.467	-.389	.692
m_2	.006	.846	.467	.256	-.018
m_3	-.038	.011	-.487	.861	.149
m_4	-.064	-.363	.572	.206	.706

Note: The eigenvalue (λ_i) of each eigenvector (m_i) is given in the second column.* $P = .002$.

sult indicates two aspects about nonlinear selection in nature. First, correlational selection has a significant presence in those data sets that are currently available. The major axes of the response surfaces generally are not parallel to the axes defined by individual traits, as the rotations have on average found new axes that have significantly more curvature associated with them, which would not have been the case if all correlational gradients were effectively zero. Second, the strength of nonlinear selection has been underestimated. If one takes the largest quadratic selection gradient in these studies as the base for comparison, nonlinear selection has been underestimated by roughly a factor of 1.5. It is interesting to note that the median level of $|\gamma|$ for individual traits reported by Kingsolver et al. (2001) of 0.1 (which is the same for the subset of studies in table A1) is on average about five times less than the eigenvalue of the major axis of the response surface that displays the most curvature. Therefore, although nonlinear selection may well be generally weak on the individual traits included in any particular selection analysis as reported in many empirical studies, it may be much stronger on at least one of the composite traits that may be the actual target of nonlinear selection in many situations.

Using a Canonical Analysis in Future Empirical Studies

Although Phillips and Arnold (1989) introduced canonical analysis in the context of selection analyses in their seminal article more than a decade ago, it has had little impact on the way empirical studies of multivariate selection have been conducted in this regard. Below we outline how one can implement a canonical analysis, and we recommend a number of avenues for presentation of the results.

There are two readily available ways to conduct the canonical analysis after a second-order polynomial regression has been used to estimate the quadratic and cross-product coefficients comprising γ . As we have done with the previously published studies surveyed by Kingsolver et al. (2001), direct eigenanalysis of γ will return the eigenvalues (canonical coefficients) and eigenvectors (comprising \mathbf{M}) of this symmetrical matrix. If this method is to be used, note that the γ_{ij} coefficients from the quadratic regression need to be halved as in equation (3). Alternatively, the SAS RSREG procedure is perhaps the most efficient way to obtain a canonical analysis as it conducts the second-order model and the canonical analysis in the same routine (app. B). Here, it is important to be aware that PROC RSREG (SAS version 6 or higher) will, by default, recode the original variables before analysis to result in variables that range between -1 and 1 . Under this transformation, the λ_i 's will not equal the quadratic coefficients when the y_i 's are placed back into a full second-order polynomial model and are therefore of little use in estimating the strength of nonlinear

selection. The NOCODE option in the model statement needs to be used for the original traits to be analyzed. We have drawn attention to these potential mistakes because either may result in the overestimation of the strength of nonlinear selection.

The presentation of the results of an analysis of nonlinear selection should always include γ and \mathbf{M} , in addition to the λ_i 's. Presentation of γ will allow the reader to check that the canonical analysis was conducted correctly by direct eigenanalysis, while \mathbf{M} is required for the interpretation of the major axes of the response surface with regard to the original traits. Such an approach requires a considerable shift in emphasis from previous empirical studies that rarely considered or reported correlational selection gradients (Kingsolver et al. 2001).

Significance of the λ_i 's may be used to test for the presence of concave or convex selection along the major axes of the fitness surface. Simms (1990; Simms and Rausher 1993) suggested an intuitive way of testing the eigenvalues for significance that has been subsequently confirmed to be equivalent to more computationally demanding methods for the estimation of eigenvalue errors (Bisgaard and Ankenman 1996). The new traits in the canonical space (y_i) are simply placed back into a full second-order polynomial model. The quadratic coefficients in this model will equal the eigenvalues of γ as noted above, and the standard errors of the γ_{ii} 's will then approximate the standard errors of the λ_i 's. Therefore, significance of each λ_i may be assessed by the significance of the quadratic term associated with it in this new second-order model as we have done above for the guppy example. As Phillips and Arnold (1989) warn, no improvement in accuracy is gained by conducting this orthogonal rotation. If the nonlinear selection gradients in γ have been estimated with considerable error as a consequence of poor measurements, small sample size, or some other source of experimental error, the canonical coefficients are expected to display the same level of error as the original selection gradients.

Visualization of the fitness surface has always been of major importance in interpreting the form of selection, and it remains important even after the canonical analysis (Phillips and Arnold 1989; Blows et al. 2003). One of the purposes of the canonical analysis is to reduce the number of axes of the response surface that need to be considered when three or more traits are involved. When only two traits are measured in addition to fitness, the best quadratic approximation of the surface can reveal the major axes of selection, so the need for canonical analysis is less urgent. However, when more than two traits are involved, selection on the first two major axes of the response surface can be visualized in the same fashion (e.g., Simms and Rausher 1993). A less constrained surface, and perhaps a more complete indication of how selection may be operating,

may be gained by plotting the major axes using a thin-plate spline (Blows et al. 2003).

Conclusion

The canonical analysis of γ is a complication to the analysis of nonlinear selection that will be necessary in many instances. Selection will rarely act on single traits in isolation (Lande and Arnold 1983; Phillips and Arnold 1989; Schluter and Nychka 1994). Consequently, correlational selection is likely to be common (Schluter and Nychka 1994), particularly among sets of functionally related traits. It follows that estimates of stabilizing or disruptive selection based on quadratic coefficients from a second-order polynomial model will routinely underestimate the strength of

selection, and by a substantial amount in some cases. This is because the target of selection will generally not be the traits that empiricists see and measure but will be a combination of traits that may be elucidated by applying the multivariate tools of response surface methodology.

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APPENDIX A

Table A1: Comparative data set

n	Largest γ_{ii}	λ	Type of surface	Type of selection	Reference
5	.044	.062	Saddle	O	Mitchell-Olds and Bergelson 1990
4	-.457	-1.262	Saddle	F	Moore 1990
4	-.550	-.714	Saddle	M	Moore 1990
4	-.707	-1.093	Saddle	F	Moore 1990
4	-.498	-.729	Saddle	M	Moore 1990
4	.102	.155	Saddle	M	Moore 1990
4	-.538	-.650	Saddle	F	Moore 1990
4	-.122	-.273	Saddle	S	Brodie 1992
3	-.874	-.875	Saddle	F	Nunez-Farfan and Dirzo 1994
3	.370	.552	Saddle	F	O'Connell and Johnston 1998
3	1.180	1.709	Bowl	F	O'Connell and Johnston 1998
3	.770	1.124	Saddle	F	O'Connell and Johnston 1998
3	.260	.283	Saddle	F	O'Connell and Johnston 1998
3	.200	.305	Saddle	F	O'Connell and Johnston 1998
3	.23	.26	Saddle	F	O'Connell and Johnston 1998
5	.994	.999	Saddle	F	Simms 1990
3	-.019	-.021	Peak	S	Kelly 1992
4	.016	.027	Saddle	S	Kelly 1992
5	.112	.214	Saddle	F	Kelly 1992

Note: Analysis of nonlinear selection in 19 data sets identified by Kingsolver et al. (2001) involving three or more traits. We have presented the largest γ_{ii} and λ_i from each γ . The type of surface is based on the signs of all eigenvalues, following the descriptions used by Phillips and Arnold (1989); if eigenvalues were all negative, the surface has a peak; if all were positive, the surface is a bowl; and if some were negative and positive, the surface is a saddle. The type of selection follows the categories used by Kingsolver et al. (2001): S = survival, M = mating success, F = fecundity/fertility, O = other. n = number of traits measured in each study.

APPENDIX B

SAS Code for a Canonical Analysis

```
Proc RSREG data = SAS-data-set;
MODEL response = independents / NOCODE;
Run;
```

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