

Visualizing and quantifying natural selection

Edmund D. Brodie III, Allen J. Moore and Fredric J. Janzen

Natural selection is one of the primary mechanisms driving organic evolution. A thorough comprehension of the occurrence, form and significance of selection in natural populations is therefore critical to our understanding of the evolutionary process. Accordingly, one of the major foci of current evolutionary research is the detection, demonstration and description of selection in nature¹. Most studies of selection have concentrated on documenting its existence. Many different techniques can be implemented to achieve this goal¹⁻³. However, selection can be a complicated process, and the publication of a seminal paper by Lande and Arnold⁴ stimulated considerable interest in the details of selection. For the first time, empiricists were provided with tractable statistical machinery to dissect selection into components that target

specific traits. Furthermore, selection could be described using parameters⁵ that integrate into equations that describe intergenerational evolutionary change. These parameters also can be used to visualize selection, allowing a more intuitive understanding of the relationship between phenotypes and relative fitness. Subsequent innovations increased the generality and flexibility of the graphical approach to examining selection⁶⁻⁸.

With these modern approaches has come a wave of new logistical considerations from the collection of relevant data to statistical caveats to interpretation of parameters^{3,6,9-11}. Empiricists now have a bewildering array of choices for analyzing the details of selection, most of which yield different types of information. We hope to offer some guidance toward the use of statistical and graphical techniques to describe the targets and mode of selection by focusing on the most widely used methods.

Natural selection as a function

Selection is a phenomenon that affects the phenotypic distribution of a population (Box 1), but the mechanism of selection works on individuals through the effect of an individual's phenotype on its fitness. Most biologists immediately think of selection as a process affecting character states or the mean value of a trait ('directional' or 'linear' selection), but selection also can change variances ('stabilizing', 'disruptive' or 'univariate nonlinear' selection) and even covariances between two traits ('correlational' or 'bivariate nonlinear' selection). This can be a confusing perspective because selection acts on individuals, not on moments of a

Modern methods of analysis are enabling researchers to study natural selection at a new level of detail. Multivariate statistical techniques can identify specific targets of selection and provide parameter estimates that fit into equations for evolutionary change. A more intuitive understanding of the form of selection can be provided through graphical representation of selection surfaces. Combinations of quantitative and visual analyses are providing researchers with new insights into the details of natural selection in the wild.

Edmund Brodie III is at the Center for Ecology, Evolution and Behavior, T.H. Morgan School of Biological Sciences, University of Kentucky, Lexington, KY 40506-0225, USA; Allen Moore is at the Center for Ecology, Evolution and Behavior, Dept of Entomology, University of Kentucky, Lexington, KY 40546-0091, USA; Fredric Janzen is at the Dept of Zoology and Genetics, Iowa State University, Ames, IA 50011-3223, USA.

distribution – the action of selection differs from the effect of selection.

Selection affecting a mean is easily understood as selection acting on individual trait values. However, to evaluate the influence of selection through individuals on variances and covariances, we must express individual traits as deviations from the mean phenotype ($\bar{z} = z - \bar{z}$) (Ref. 4). With trait values transformed to a mean of zero, it becomes trivial to examine selection targeting the extreme phenotypes (i.e. greatest deviations from the mean), and thereby estimate the modes of selection that affect variances and covariances (see below).

Natural selection therefore can be viewed as the covariance between trait values and their expected relative fitnesses. The mathematical function describing this relationship can easily be derived by regression analysis of data

on individual phenotypes and fitness (Table 1, Boxes 2,3). Elements of selection functions can provide quantification of the strength of different modes of selection (Box 1), selection targeting specific traits and the intensity of total selection (of all modes) experienced by a trait. Some of these elements can be used to further evaluate selection by graphically representing the relationship between fitness and phenotype.

Measures of selection related to quantitative genetics

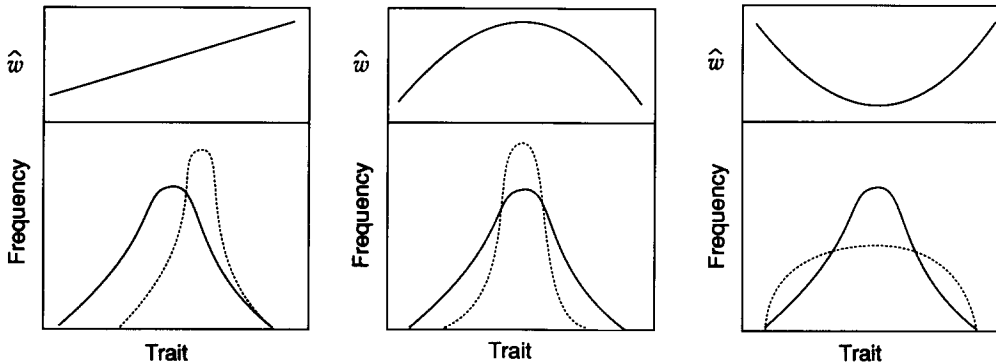
In the mid-1980s, a group of researchers that has since become known as the 'Chicago School' of evolutionary biology¹² advanced an approach to studying selection and response to selection that had long been used by plant and animal breeders. The parameters estimated in this quantitative genetic approach – opportunities, differentials and gradients – provide a hierarchy of information about selection. The appeal of these parameters comes from the explicit biological interpretation and simple statistical estimation of each type of coefficient (Table 1). The relevance of selection to the evolutionary process can be formally understood through these parameters because each one fits into the equations for intergenerational change originally developed by domestic breeders and adapted to evolutionary biology¹³.

The total potential for selection to act in a population is estimated by the opportunity for selection (I) (Refs 14–16). This parameter is useful as an upper bound on how strong selection could be, but is not especially satisfying because it does not describe any relationship between fitness and a trait.

Box 1. Modes of natural selection

We can distinguish the process of **natural selection**, which is a change in the phenotypic distribution within a generation, from its outcome, **evolution**, which is a change in the phenotypic distribution across generations^{32,33}. Inheritance is the biological mechanism that transmits the effects of selection across generations, thereby causing evolutionary change. Biologists have most commonly and profitably studied natural selection without demonstrating or quantifying inheritance.

Selection is a covariance between phenotypes and expected relative fitness (\hat{w}) and can be categorized based on its impact on phenotypic distributions. Illustrations show the view of selection as a function (above), and the within-generation change in the phenotypic distribution (below; solid curves before selection, dashed curves after selection).



Directional selection: linear selection for higher or lower phenotypic values, detected by an association between the mean of a trait and fitness. Directional selection increases (positive) or decreases (negative) the trait mean.

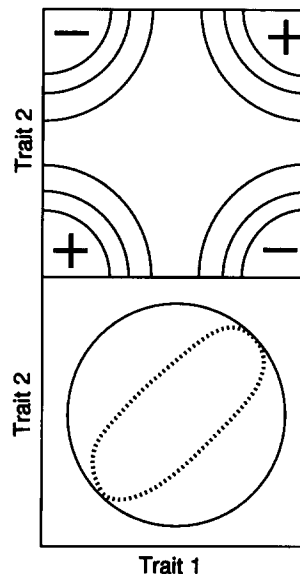
Stabilizing selection: concave nonlinear selection against extreme phenotypes, detected by a negative relationship between the second moment of a distribution and fitness. Stabilizing selection decreases the variance of a trait.

Disruptive selection: the opposite of stabilizing selection – convex nonlinear selection against intermediate phenotypes detected by a positive relationship between the second moment of a distribution and fitness. Disruptive selection increases the variance of a trait.

The use of the same terms to describe selection surfaces as well as statistical relationships can be misleading because it is not always clear where one form of selection ends and another begins^{4,6,8,9}. Directional, stabilizing and disruptive selection, as described above, fit the traditional interpretations of features of selection surfaces including peaks, valleys and saddles. These same terms also have been used to identify various selection coefficients. However, these quantitative measures of selection describe precise statistical relationships between fitness and moments of phenotypic distributions (e.g. means, variances), but not necessarily distinct topographical features. To avoid misinterpretations, we suggest labels that more accurately reflect the graphical information contained in the coefficients estimated from formal statistical analyses.

Linear coefficients (previously 'directional'^{4,6}) describe selection that affects the mean of a trait, while **nonlinear coefficients** (previously 'quadratic'⁶ or 'stabilizing/disruptive' and 'correlational'⁴) describe selection that affects second (and higher) moments of distributions such as variances and covariances. We can further distinguish **univariate nonlinear** coefficients from **bivariate nonlinear** coefficients, because the latter specifically describe selection simultaneously acting on two different traits, such as would describe correlational selection. The extent that linear or nonlinear selection corresponds with traditionally defined modes of selection can be determined using a univariate or multivariate visualization technique^{6,8}.

Correlational selection: nonlinear selection on combinations of traits, detected by a relationship between the second moment of a bivariate distribution for a pair of traits and fitness. Correlational selection changes the covariance between two traits. (Fitness function shown as a saddle-shaped contour plot with highest expected fitness marked as '+'.)



deviations from the mean (\bar{z}) to estimate these parameters. After subtracting the influence of the linear selection differential^{4,6}, the difference in the variance of a trait before and after selection is the univariate nonlinear selection differential, whereas the difference in a covariance is the bivariate nonlinear selection differential.

A useful comparative measure of the strength of total selection experienced by any single trait is the intensity of selection (i) (note that Crow¹⁵ originally called his 'opportunity for selection' the 'intensity for selection', I , but the terminology has since been changed to avoid confusion)^{4,14}. Intensity is nothing more than a selection differential measured on standardized traits ($\bar{z} = 0$, $SD = 1$). The resultant differentials, or intensities, are all of the same scale and are directly comparable among traits or populations as measures of the relative strength of a given mode of selection. A second measure of overall strength of selection, also called intensity (V), is derived from a non-parametric regression analysis⁸ (see below, 'Graphical representations of selection'). This 'total selection intensity' is similar to Manly's index of selection², and reflects the strength of selection on a trait considering all modes of selection simultaneously.

Selection gradients are measures of the link between fitness and a particular trait, independent of other measured correlated traits, and are obtainable as partial regression coefficients from a multiple regression^{4,6}. As with any regression analysis, the

The simplest measure of selection on a particular trait is the selection differential, which measures total change resulting from selection^{4,6,14}. Differentials do not distinguish between changes resulting from selection that directly links a trait with fitness (direct selection) and changes resulting from correlations with other traits affecting fitness (indirect selection). Linear selection differentials (S) measure changes in trait means. Nonlinear selection differentials (C) measure changes in the variance of a trait or the covariance between two traits independent of the effects of linear selection (which itself can cause changes in variances and covariances⁴). Again, selection does not act directly on moments of a distribution, so we use individual traits measured as

partial regression coefficients, or gradients, only measure the effect of a variable independent of the other variables included in the model^{4,9}. To the extent that all relevant traits are analyzed, gradients measure selection directly on a trait or combination of traits. Linear selection gradients (β) can be combined with estimates of genetic variances and covariances to predict the multivariate response to selection, taking into account the effect of selection on correlated traits and thereby providing a more accurate picture of short-term evolution than univariate analyses^{4,6,17,18}.

Quadratic forms of variables can be used to describe curvature of a function or surface and estimate the nonlinear selection gradients (γ). A quadratic regression provides

Table 1. Quantitative measures of selection

Parameter ^a	Symbol	Determined by:	Formula	Interpretation
Opportunity for selection ^{14,15}	I	Variance in relative fitness.	$\text{VAR}\left(\frac{W}{\bar{W}}\right)$	Upper limit of the strength of selection.
Intensity of selection ^{7,8,b}	V	Variance in expected relative fitness [$\hat{f}_w(z)$], where \hat{f} is estimated from nonparametric regression.	$\text{VAR}\left(\frac{\hat{f}(z)}{\bar{W}}\right)$	Overall strength of selection (linear and nonlinear combined).
Selection differential – linear selection ^{4,6,14}	S_i	Difference in trait means (\bar{z}_i) before and after selection, or covariance between relative fitness and trait.	$(\bar{z}_i)_{\text{after}} - (\bar{z}_i)_{\text{before}}$ $\text{COV}(w, z)$	Total change in the mean phenotype within a generation (total linear selection).
Selection differential – univariate nonlinear selection ^{4,6,14}	C_{ii}	Difference in trait variance before and after selection, or covariance between relative fitness and squared deviation (\bar{z}^2).	$\text{VAR}(z_i)_{\text{after}} - \text{VAR}(z_i)_{\text{before}} + S_i^2$ $\text{COV}(w, \bar{z}^2)$	Total change in the variance of a trait within a generation after adjusting for directional selection (total nonlinear selection).
Selection differential – bivariate nonlinear selection ^{4,6,14}	C_{ij}	Difference in trait covariance before and after selection, or covariance between relative fitness and cross-product of deviations ($\bar{z}_i \bar{z}_j$).	$\text{COV}(z_i, z_j)_{\text{after}} - \text{COV}(z_i, z_j)_{\text{before}} + S_i S_j$ $\text{COV}(w, \bar{z}_i \bar{z}_j)$.	Total change in the covariance of two traits within a generation after adjusting for directional selection (total nonlinear selection on a combination of traits, i.e. correlational selection).
Selection gradient – linear selection ^{4,6,9,14}	β_i	Multiple regression (purely linear model).	Partial regression coefficient for \bar{z}_i .	Partial change in the phenotypic mean (direct linear selection).
Selection gradient – univariate nonlinear selection ^{4,6,9,14}	γ_{ii}	Multiple regression (full model including linear, squared and cross-product terms).	Partial regression coefficient of squared term (\bar{z}_i^2).	Partial change in the variance of a character (direct nonlinear selection).
Selection gradient – bivariate nonlinear selection ^{4,6,9,14}	γ_{ij}	Multiple regression (full model including linear, squared and cross-product terms).	Partial regression coefficient of cross-product term ($\bar{z}_i \bar{z}_j$).	Partial change in the covariance between two characters (direct nonlinear selection on a combination of traits).

^aParameters estimated from statistical procedures may or may not correspond directly to the qualitative aspects of the processes of interest (Box 1). However, in all cases, the statistical measures are more general than the qualitative descriptors and therefore embody classical processes.

^bA second measure of the 'intensity of selection' (i) is the selection differential measured on traits standardized to $\bar{z} = 0$, $sd = 1$.

coefficients that describe selection affecting the variances and covariances of traits independent of other analyzed traits^{4,6}. The γ values are usually estimated from a regression that is separate from that used to estimate the β values because of correlations between linear and quadratic variables^{3,4}. Partial regression coefficients of squared deviations from the mean (\bar{z}^2) describe nonlinear selection directly acting to reduce the variance when negative, and increase the variance when positive. Univariate nonlinear selection gradients describe only convexity ($\gamma < 0$) and concavity ($\gamma > 0$) of a function, not necessarily an intermediate peak or valley. For this reason, γ values do not necessarily describe traditional stabilizing or disruptive selection (Box 1, Fig. 1)^{6,9}. Coefficients that relate fitness to the product of two traits expressed as deviations ($\bar{z}_i \bar{z}_j$) describe selection that directly targets specific combinations of the two traits simultaneously. These bivariate nonlinear selection gradients may be roughly interpreted as favoring similar combinations of traits when positive, or opposite combinations of traits when negative^{6,19}. The precise interpretation of selection on two traits requires knowledge of all linear and nonlinear gradients and is most readily obtained through graphical representation⁶ (Figs 1,2).

Path analyses of selection

A complementary approach to revealing the direct relationships between traits and fitness is path analysis^{10,20,21}. A 'path' diagram is constructed based on an *a priori* understanding of the causal interactions among traits and fitness, and multiple regression is employed to calculate path co-

Box 2. Data collection for analysis of selection

Describing selection requires estimating a function that relates phenotypic values to expected fitness. Longitudinal data that include measures of fitness and trait values on multiple individuals provide the best estimates of fitness functions⁴. Linear aspects of selection functions are much easier to detect than curvature, peaks and valleys. The precise sample sizes required depend on the subtleties of the function, but samples of hundreds of individuals are likely to be needed to reveal nonlinear selection in many studies (Figs 1,2)¹⁹. Multivariate studies of selection should attempt to measure all relevant correlated traits that might affect the fitness component under study. This will minimize the problem represented by unmeasured characters when interpreting the results of regression analyses. Of course, real data sets often will violate assumptions of parametric significance testing, so alternative methods, including jackknife, bootstrap and randomization tests, or probit or logistic regression, should be used to evaluate the statistical significance of parameter estimates^{4,9,19,28,34,35}. Other statistical considerations, including problems of highly correlated phenotypic traits, have been discussed elsewhere^{3,4,9}.

Cross-sectional data do not include individual measures of fitness and so cannot be analyzed with the statistical and graphical techniques described herein. However, comparisons between phenotypic distributions of different age groups sampled at a single point in time can be used to calculate some parameters, including selection differentials and intensities⁴. Under a set of restrictive assumptions, cross-sectional data sometimes can be used to calculate selection gradients through the basic equations provided by Lande and Arnold⁴.

efficients that illustrate the effect of one trait on the variation in another. Resulting paths are completely dependent upon the *a priori* model chosen, so path analysis is most useful as a tool to test competing hypotheses of trait interactions²². Path analysis further assumes that all relationships are linear and so is only appropriate when all selection acting is directional

Box 3. Measuring fitness

All studies of selection rely on measures of fitness. However, fitness is not measured directly, but estimated by quantifying related traits including fitness components. For example, fertility and/or fecundity (e.g. number of offspring produced), survival (e.g. alive or dead following an event or interval) and mating success are frequently used as estimates of fitness in selection studies¹¹. Other traits, such as growth rate or access gained to limited resources, are sometimes argued to reflect fitness differences among individuals^{17,35}. Although lifetime measures are ideal, researchers often can measure only a portion of the individual's lifetime reproductive success, such as territory success or survival as an adult. Interpretations of descriptions of selection should consider the limitations of the fitness measure employed. The best fitness measure is one that is based on the biology behind the question being investigated, and one that generates testable predictions for natural populations.

Continuous and discrete measures of fitness can be accurately analyzed using standard statistical methods, though nonparametric significance tests are generally required^{4,9,11}. When fitness is measured categorically (e.g. mating success, age of death), a strong biological rationale must underlie the numerical assignment of fitness values (e.g. fitness values of 0, 1, 2 will give different quantitative parameters than 1, 2, 3)¹¹. When fitness is measured at multiple life stages or in different episodes, a partitioned study of selection can be performed^{14,36}. Such an approach can reveal how a particular character experiences different selection during different life stages, or how a trait can have opposing effects on different fitness components. For example, dragonflies experience linear selection on body size as it affects territorial success, but nonlinear selection on body size as it affects fertilization success³⁵.

and linear. Because paths are obtained by multiple regression on standardized variables, they are equivalent to standardized linear selection gradients (β) in path models where all traits directly affect fitness¹⁰.

Path analysis is also useful when simultaneously studying selection on phenotypic traits and organismal performance²³. Some traits may be expected to affect fitness directly, or through an intervening performance measure, and path analysis can reveal such relationships. Additionally, the importance of unmeasured traits (as a part of the unexplained variation in fitness) can be considered by including paths for unmeasured variables¹⁰.

Graphical representations of selection

The parameters for quantifying selection, mentioned above, present many benefits for understanding the strength, form and targets of selection, but the numerical values may not lead to intuitive descriptions of selection. Perhaps the greatest advantage of modern selection analysis techniques is the ability to generate visual depictions of the form of selection (e.g. Figs 1,2). The metaphor of a landscape or surface of selection is quite useful for understanding the connection between traits and expected fitness. The distinctions among types of fitness surfaces have been neatly summarized by Phillips and Arnold⁶.

Selection gradients obtained from a quadratic regression can be used to construct the selection surface that describes the relationship between an individual's phenotype and its expected fitness. Gradients describe the average slopes (β) or curvatures (γ) of the selection surface. Because of the constraints of quadratic regression, this surface is only the 'best quadratic approximation' of the true selection surface⁶. By simply plotting the response surface described by the gradients, either univariate or bivariate views of the selection surface can be obtained.

True selection surfaces may be much more complex than the smooth functions estimated by quadratic regression. Also, some combinations of phenotypic distributions and directional selection can yield misleading quadratic gradients that describe curvature of a function where none exists. These considerations led Schluter⁸ to propose nonparametric regression as an alternative means of estimating the mode of selection that would allow for the estimation of complex functions with multiple peaks and valleys. The original form of this visualization technique, known as

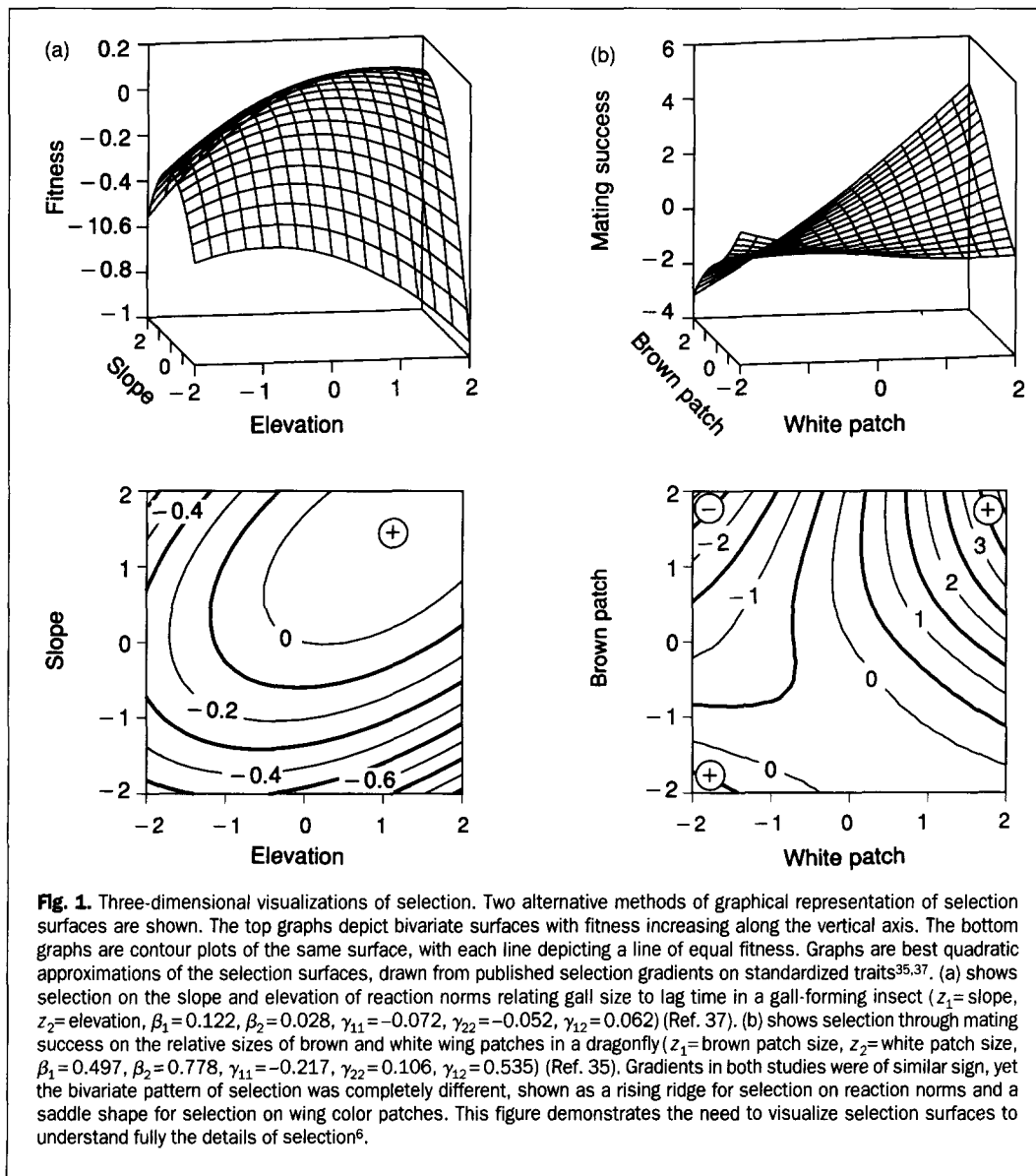


Fig. 1. Three-dimensional visualizations of selection. Two alternative methods of graphical representation of selection surfaces are shown. The top graphs depict bivariate surfaces with fitness increasing along the vertical axis. The bottom graphs are contour plots of the same surface, with each line depicting a line of equal fitness. Graphs are best quadratic approximations of the selection surfaces, drawn from published selection gradients on standardized traits^{35,37}. (a) shows selection on the slope and elevation of reaction norms relating gall size to lag time in a gall-forming insect (z_1 = slope, z_2 = elevation, $\beta_1 = 0.122, \beta_2 = 0.028, \gamma_{11} = -0.072, \gamma_{22} = -0.052, \gamma_{12} = 0.062$) (Ref. 37). (b) shows selection through mating success on the relative sizes of brown and white wing patches in a dragonfly (z_1 = brown patch size, z_2 = white patch size, $\beta_1 = 0.497, \beta_2 = 0.778, \gamma_{11} = -0.217, \gamma_{22} = 0.106, \gamma_{12} = 0.535$) (Ref. 35). Gradients in both studies were of similar sign, yet the bivariate pattern of selection was completely different, shown as a rising ridge for selection on reaction norms and a saddle shape for selection on wing color patches. This figure demonstrates the need to visualize selection surfaces to understand fully the details of selection⁶.

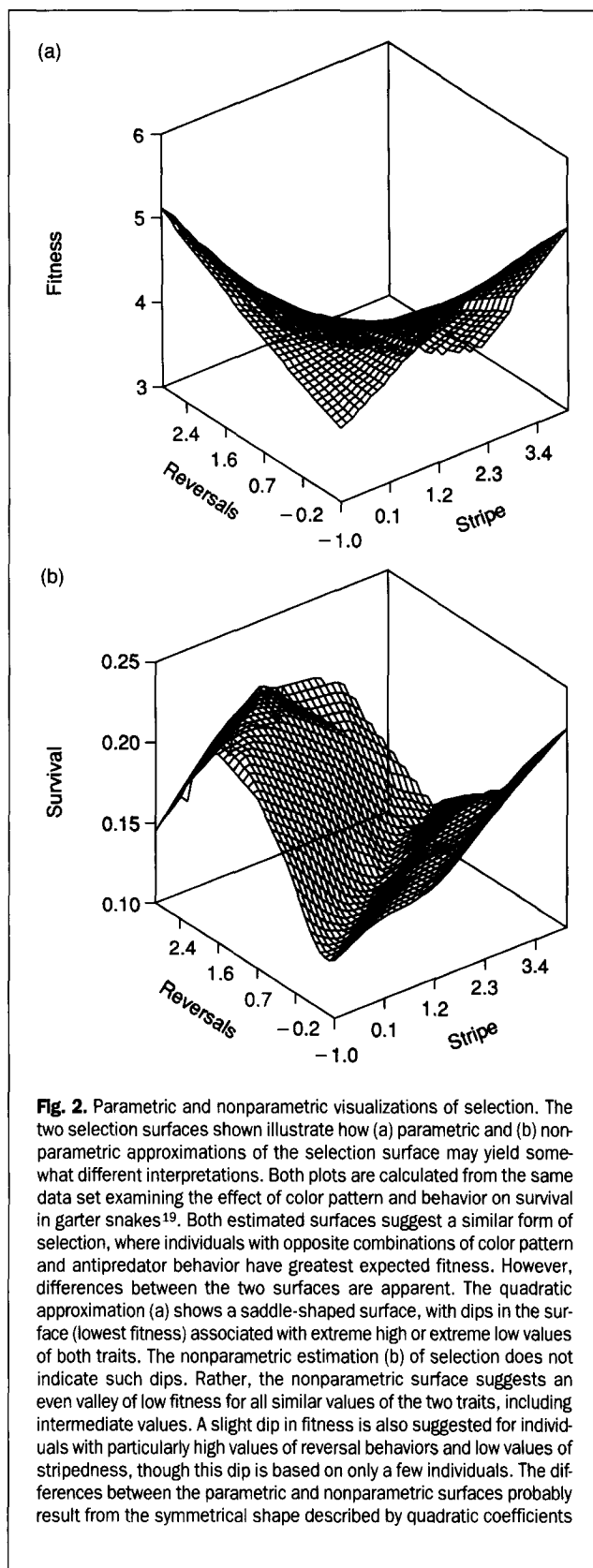


Fig. 2. Parametric and nonparametric visualizations of selection. The two selection surfaces shown illustrate how (a) parametric and (b) nonparametric approximations of the selection surface may yield somewhat different interpretations. Both plots are calculated from the same data set examining the effect of color pattern and behavior on survival in garter snakes¹⁹. Both estimated surfaces suggest a similar form of selection, where individuals with opposite combinations of color pattern and antipredator behavior have greatest expected fitness. However, differences between the two surfaces are apparent. The quadratic approximation (a) shows a saddle-shaped surface, with dips in the surface (lowest fitness) associated with extreme high or extreme low values of both traits. The nonparametric estimation (b) of selection does not indicate such dips. Rather, the nonparametric surface suggests an even valley of low fitness for all similar values of the two traits, including intermediate values. A slight dip in fitness is also suggested for individuals with particularly high values of reversal behaviors and low values of stripedness, though this dip is based on only a few individuals. The differences between the parametric and nonparametric surfaces probably result from the symmetrical shape described by quadratic coefficients

the 'cubic spline', was limited to univariate analyses, and so could not reveal correlational selection on combinations of traits. A recent advance⁷ has extended this approach to multiple traits, and it is now possible to estimate functions that can describe complicated multivariate fitness surfaces. These nonparametric techniques are useful both to qualitatively describe the selection surface and to quantify expected fitnesses of phenotypes in the population, which can be used to calculate the overall selection intensity (V) (Table 1).

Graphical representation of selection is generally limited to considering one or two traits at a time^{6,7} because of the difficulty of visually depicting more than three axes simultaneously. Selection acting simultaneously on multiple traits can be considered by performing a principal components analysis on a suite of traits and plotting selection as a function of the principal components^{4,6,8}. However, it is not clear that selection ever acts on principal axes of phenotypic variation and it is difficult to translate from selection on principal components to selection on the original traits.

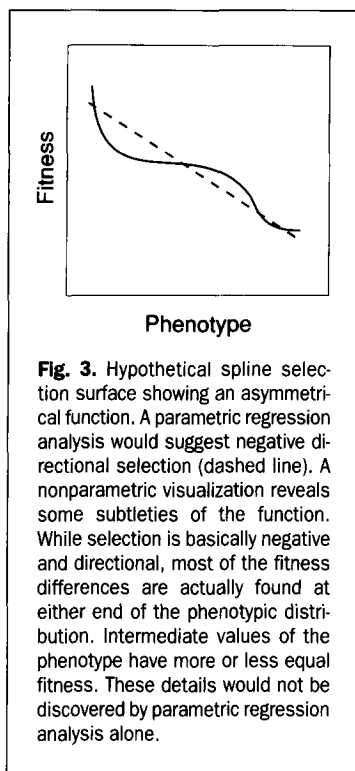
Selection on three traits can be visualized as a series of nested three-dimensional solids using a canonical analysis technique^{6,24,25} to transform the original traits to the major axes of the selection surface so that bivariate curvature (correlational selection) is no longer an issue. This transformation differs from principal components because the major axes of the selection surface *per se*, not of phenotypic variation, are determined. Thus, the transformed variables should accurately describe major targets of selection (in contrast to principal components), but the interpretation of such surfaces is problematic because axes no longer correspond to the original traits. For the adventurous, Phillips and Arnold⁶ also point out that a third or fourth trait can be visualized by animating the surface, where time becomes the fourth axis.

Schluter and Nychka⁷ take a similar (but nonparametric) approach to visualizing the relationship between fitness and multiple traits. They recommend projection pursuit regression as a complement to the univariate spline. This technique assumes that most selection acts on one or a few phenotypic dimensions. The analysis defines a vector of traits (a 'projection' or 'direction') that experiences the strongest selection. These new directions are comprised of various loadings of the original traits and can be used to examine selection on any number of variables, though visualizations are still restricted to three-dimensional surfaces. One advantage of this approach is that the multivariate vectors studied are those experiencing the strongest selection, not arbitrary rotations of phenotypic space such as principal components⁷.

Limitations and combinations of approaches

Each of the selection analysis techniques mentioned above offers trade-offs between the two main goals of selection analysis – estimation of quantitative selection coefficients and functional interpretation of the force of selection. Accordingly, the most complete and revealing studies of natural selection will use combinations of these approaches^{26,27}. The choice of analytical technique should be dictated by the goals of the specific research and the available data. When individual measures of phenotype and fitness are not available, researchers can still demonstrate selection using traditional methods^{1,2} and sometimes even can calculate opportunities or differentials (see Box 2). More complete data sets provide more options for analysis, and decisions should be based on the importance of revealing specific modes, targets and details of selection. Fortunately, these methods are not exclusive and all are performed easily on personal computers with simple software packages.

The nonparametric visualization techniques pioneered by Schluter^{7,8} provide the most flexible approximations of selection surfaces, and thereby present the most-detailed pictures of total selection affecting a particular trait or combination of traits (Figs 2,3). These are the only methods currently available to detect selection functions that are asymmetrical, or that have multiple peaks²⁸ or sudden changes in fitness (e.g. step-functions). Nonparametric



analyses can be further employed to suggest appropriate models for subsequent parameter estimation. The multivariate spline also allows researchers to visualize selection on more than two traits and to disentangle direct from indirect selection by considering the loading of original traits on the major axes of the selection surface. Quantitative measures of particular modes of selection (e.g. linear versus nonlinear) that can be used to statistically compare selection among characters, episodes or populations are not provided by nonparametric analyses. However, splines can be used to investigate the importance of different modes of selection by constraining the shape of the estimated function⁸.

When a quadratic function is suggested by nonparametric analysis, Lande–Arnold-style gradient analyses can be justifiably

implemented. One of the greatest advantages of the gradient approach is that the measures of selection obtained are variables in the multivariate equations describing evolutionary change, allowing researchers to make explicit and quantitative predictions about the effect of selection. Differentials and gradients also provide quantification of particular modes of selection that may be used in comparisons. Numerical values of gradients are not easily interpreted, however, because they describe subtleties of curvature, not peaks and valleys (Figs 1,2). Graphical representation is recommended to reveal the precise form of selection^{6,19}. Spline and quadratic surfaces visually describe different subsets of selection (total and direct, respectively) and therefore are not redundant. Path analysis represents an even more in-depth dissection of linear causal relationships among traits and fitness, and can be used to test specific *a priori* functional hypotheses²².

The techniques we have described are general, and represent a powerful set of tools to apply to problems of interest. Some basic questions about natural selection in the wild¹ are ideally addressed through the implementation of visualization and quantification approaches. Selection is unlikely to be constant on either temporal or spatial scales, and the techniques described herein allow for both qualitative and quantitative assessments of variability in selection. The ability to partition selection into separate components also enables researchers to examine the ubiquity of particular modes of selection (e.g. linear versus nonlinear, directional versus stabilizing) operating in nature. It is also likely that theoretical and practical advances will be made in the analytical techniques themselves that will improve our handling and understanding of real-world data. Generalized linear models (e.g. logistic regression) are more appropriate for some data sets than linear regression¹¹, but the coefficients from such models are not yet interpretable in the context of equations for evolutionary change. Nonparametric approaches have proven invaluable in both description of selection (e.g. splines) and significance testing (e.g. bootstrap and jackknife tests), but to date only a few possible techniques²⁹ have been investigated.

Despite the elegance of multivariate visualizations of selection, it is crucial to remember that surfaces and parameters only *describe* selection. In fact, only the relationship between phenotype and fitness is described. It is important to realize specific traits may covary with fitness as a result of non-causal phenomena such as environmental covariances^{30,31} and inbreeding. The exploration of what causes natural selection – the forces, agents, biotic and abiotic interactions that result in a relationship between phenotypes and fitness – is another issue. Mechanisms of selection sometimes may be inferred from descriptive studies, but only experimental studies can reveal the hows and whys driving natural selection^{1–3,6,19}. Regression analysis and visualization of selection are powerful methods for generating testable hypotheses about the causal agents of selection.

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