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Performance Surfaces and Adaptive Landscapes[1]

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SYNOPSIS. In an earlier characterization of the relationship between morphology, performance and fitness, I focused only on directional selection (Arnold, 1983). The aim of this article is to extend that characterization to include stabilizing and other forms of nonlinear selection. As in the earlier characterization, this more general description of the morphology-performance-fitness relationship splits empirical analysis into two parts: the study of the relationship between morpholgy and performance, and the study of the relationship between performance and fitness. From a conceptual standpoint, my goal is to specify the relationship of performance studies to the adaptive landscape. I begin by reviewing the adaptive landscape concept and its importance in evolutionary biology. A central point emerging from that review is that that key descriptors of the adaptive landscape can be estimated by measuring the impact of selection on the means, variances and covariances of phenotypic traits. Those descriptors can be estimated by making a quadratic (regression) approximation to the selection surface that describes the relationship between the phenotypic traits of individuals and their fitness. Analysis of the effects of morphology on performance follows an analogous procedure: making a quadratic approximation to the individual performance surface and then using that approximation to solve for the descriptors of the performance landscape. I conclude by discussing the evolution of performance and adaptive landscapes. One possibility with biomechanical justification is that the performance landscape evolves along performance lines of least resistance.

INTRODUCTION

An adaptive landscape for phenotypic characters was first proposed by Simpson (1944, 1952). This landscape characterization of evolution was derived from Wright's concept of an adaptive landscape in which population fitness is a function of gene frequencies (Wright, 1932). In Wright's landscape, mean fitness in the population, $\bar{W}$, is a function of the frequency, p, of an allele. Simpson (1944) used phenotypic adaptive landscapes to successfully argue that the results of paleontology could be reconciled with geneticist's view of population evolution (Wright, 1945). Lande (1976, 1979) showed that properties of an adaptive landscape for phenotypic traits specified the force of selection in equations for change in the means, variances and covariances of the traits. In Lande's landscape, the natural log of population mean fitness, $\ln\bar{W}$, is a function of the average values of one or more continuously distributed phenotypic traits, $\bar{z}$. As in Wright's landscape, the population mean tends to evolve in an uphill direction on this phenotypic landscape (Lande, 1979). These theoretical developments merged Simpson's idea of an adaptive landscape with concepts of inheritance that had been developed in the field of quantitative genetics.

The importance of the adaptive landscape as an integrating concept has long been appreciated. This importance is reflected in the long history of the landscape and related concepts in the evolutionary literature (Pearson, 1903; Fisher, 1930; Wright, 1931; Dobzhansky, 1937; Simpson, 1944; Schmalhausen, 1949). The power of the landscape idea is that it ties together many of the fundamental ideas in evolutionary biology (modes of selection, responses to selection, adaptation, speciation, adaptive radiation). Because of their power, landscapes have been sought for various kinds of traits (*e.g.*, proteins, RNA) with varying degrees of success (Govindarajan and Goldstein, 1997; Fontana and Schuster, 1998; Bornberg-Bauer and Chan, 1999). The most common kind of failure in landscape pursuit is inability to find empirically accessible aspects of traits that can in turn be related to a property, such a population mean fitness, that governs evolutionary trajectories. Against the background of these unsuccessful quests, the tangible existence of an adaptive landscape for phenotypic traits shines like a beacon across the field of evolutionary biology. We have succeeded here, so perhaps we can succeed elsewhere.

THE ADAPTIVE LANDSCAPE FOR PHENOTYPIC TRAITS

Success in specifying a useful adaptive landscape for phenotypic traits rests on a foundation of three assumptions (Lande, 1976, 1979; Lande and Arnold, 1983). (a) Phenotypic traits are normally distributed within populations, or are approximately normal after suitable transformation. (b) The function that relates the trait values of individuals to their expected individual fitness can plausibly assumed to be smooth and continuous. In other words, we can specify its first and second derivatives. (c) Fitness is frequency-independent in the sense that the fitness of individuals is affected by their own trait values, but not by the trait values of other individuals in the population. Although these assumptions somewhat restrict our domain of application, they grant enormous conceptual power.

How can we tap into the conceptual power of the adaptive landscape? Many authors have assumed that

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TABLE 1. *Nomenclature for surfaces and landscapes*

Name of surface or landscape	Dimensions Vert.	 Hori.	Slope[1]	Curvature[2]
Individual selection surface (selection surface)	$w(z)$	z	β	γ
Adaptive landscape for morphology (adaptive landscape)	$\ln \bar{W}$	$\bar{z}$	β	$\gamma - \beta\beta^T$
Individual performance surface (performance surface)	$f(z)$	z	β_f	γ_f
Performance landscape for traits (performance landscape)	$\ln \bar{F}$	$\bar{z}$	β_f	$\gamma_f - \beta_f\beta_f^T$
Individual selection surface for performance (selection surface for performance)	$w(f)$	f	β_w	γ_w
Adaptive landscape for performance (performance adaptive landscape)	$\ln \bar{W}$	$\bar{f}$	β_w	$\gamma_w - \beta_w\beta_w^T$

[1] The symbol represents the average slope in the case of individual surfaces.

[2] The symbol represents the average curvature in the case of individual surface.

the adaptive landscape is merely a metaphor (Eldredge and Cracraft, 1980; Provine, 1986; Dawkins, 1996). These authors have ignored the possibility that the adaptive landscape—like mutation, drift, and inheritance—is an object for empirical study. The adaptive landscape for phenotypic traits is accessible to us because of the immediate changes that it induces in the means, variances and covariances of traits within a generation. The features of the landscape that cause changes in means, variances and covariances are its slope and curvature, its first and second derivatives. The first and second derivatives of the landscape also play a fundamental role in predicting how the population mean, $\bar{z}$, will change from one generation to the next in respond to selection, and how the inheritance matrix, G, will change within a generation in response to selection;

$$\Delta\bar{z} = GP^{-1}(\bar{z}^* - \bar{z}) = G\frac{\partial \ln \bar{W}}{\partial \bar{z}} \qquad (1)$$

$$\Delta_s G = GP^{-1}(P^* - P)P^{-1}G = G\frac{\partial^2 \ln \bar{W}}{\partial \bar{z}^2}G \qquad (2)$$

(Lande, 1979, 1980; Lande and Arnold, 1983). In these equations $\bar{z}$ and P are, respectively, a column vector of phenotypic means and their variances and covariances (P is a matrix; P^{-1} is its inverse) before selection; asterisks denote these same parameters after selection within a generation. G is the inheritance matrix (additive genetic variance-covariance matrix) that translates the effects of phenotypic selection into genetic values, either across generations (1) or within a generation (2). These equations also show that the first and second derivatives of the adaptive landscape can be estimated from the changes that selection causes in the first and second moments of the phenotypic distribution. In other words, the slope of the adaptive landscape can be inferred from the shift that selection causes in the phenotypic mean. The curvature and orientation of the adaptive landscape can be inferred from the expansions and contractions that selection causes in phenotypic variances and covariances. Quadratic regression is a useful tool for accomplishing these inferences (Lande and Arnold, 1983; Phillips and Arnold, 1989; Brodie *et al.*, 1995; Stinchcombe *et al.*, 2002).

In our empirical quest for the adaptive landscape it will be useful to recognize an important way station known as the individual selection surface. Our approach will be to first characterize this individual selection surface and then use theoretically-derived connections between this surface and the adaptive landscape to make inferences about the adaptive landscape. What is the individual selection surface?

The individual selection surface (Pearson, 1903) is the relationship between the relative fitness of individuals in a population and the values of a set of phenotypic traits. The adaptive landscape is a function of mean trait values; the selection surface is a function of individual trait values (Table 1). Using data on the fitness of individuals and their phenotypic traits, we could use any of a variety of curve-fitting approaches to estimate the individual selection surface. A popular approach is to use the method of cubic splines, which is capable of matching the shape of a wide variety of surfaces in one or more character dimensions (Schluter, 1988; Schluter and Nychka, 1994). The goal in such an exercise is to accurately describe the shape of the selection surface. Our goal, however, is different and so demands another approach. Our goal is to characterize the selection surface in a way that will give us straightforward insights about the adaptive landscape. The cubic spline approach will not accomplish this goal because the connections between cubic splines and the adaptive landscape are unknown and may not exist. In other words, it has not been established that the first and second derivatives in equations (1) and (2) can be estimated with cubic splines. Although cubic splines will not get us to our goal, another approach will. That approach is called quadratic approximation. In this approach, second-order (quadratic) rather than third-order (cubic) polynomials are used to approximate the individual selection surface.

A quadratic approximation to the individual selection surface can be made by using a least-squares regression approach (Lande and Arnold, 1983). For convenience we will assume from here on that the values of individual values for traits, z, have been standardized so that their means are zero, and relative fitness, w, has been standardized so that its mean is one. We will use the following multiple regression model to relate the individual values of multiple traits, z, to relative fitness, w

$$w = \alpha + \beta^T z + \frac{1}{2} z^T \gamma z + \varepsilon, \tag{3}$$

using the notation of Phillips and Arnold (1989). In this multivariate version of the model, z is a column vector of individual traits values, z^T is the row vector version of that same vector (the transpose of z). The intercepts in the model are α (a column vector) and errors or residuals are ε (a column vector). The point of this model is to estimate the linear directional selection gradients β (a column vector) and the nonlinear selection gradients γ (a matrix). The factors of ½ in (3) serve the role of making the γ coefficients equivalent to second derivatives.

Why are we interested in β and γ? One point of interest is that these coefficients correct for the effect of trait correlation and so can help us identify the targets of selection. We shall return to that point shortly. The other point of interest—the primary one in our present discussion—is that we can infer the first and second derivatives of the adaptive landscape from β and γ. The relationship of β to the adaptive landscape is straightforward. β is the average slope of the individual selection surface, $w(z)$, but it is also the direction of steepest uphill slope on the adaptive landscape, $\ln \bar{W}$, in the vicinity of the phenotypic mean, $\bar{z}$,

$$\beta = \int p(z) \frac{\partial w(z)}{\partial z} \, dz = \frac{\partial \ln \bar{W}}{\partial \bar{z}}, \tag{4}$$

where $p(z)$ are the frequencies of the phenotypic values z in the population before selection (Lande and Arnold, 1983). The relationship of γ to the adaptive landscape is slightly more complicated. In parallel with the first expression in (4), γ is the average curvature of the individual selection surface,

$$\gamma = \int p(z) \frac{\partial^2 w(z)}{\partial z^2} \, dz \tag{5}$$

(Lande and Arnold, 1983). The curvature of the adaptive landscape, however, is a function of both γ and β,

$$\frac{\partial^2 \ln \bar{W}}{\partial \bar{z}^2} = \gamma - \beta\beta^T \tag{6}$$

(Lande, 1979; Phillips and Arnold, 1989). One way to understand this more complicated relationship, is to notice that, whereas the elements in γ represent just the effects of nonlinear selection on the variance or covariance of characters (Lande and Arnold, 1983, eq. 14a), the elements in the matrix $\partial^2 \ln \bar{W} / \partial \bar{z}^2$ represent both the effects of linear and nonlinear selection on variances and covariances. The matrix $\beta\beta^T$ represents just the effects of linear selection on variances and covariances.

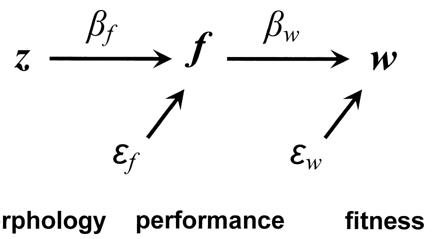

FIG. 1. Path diagram corresponding to the linear approximation (7) to the individual selection surface for a set of morphological traits (morphology), denoted z. The effects of morphology on fitness, w, are mediated through a set of performance variables, f. The performance gradient, β_f, is the slope of the fitted performance surface. The fitness gradient is β_w.

SELECTION ON MORPHOLOGY VIA EFFECTS ON PERFORMANCE AND FITNESS

Performance is a measure of whole organism capacity (Bartholomew, 1958; Bennett, 1980). Depending on the traits and ecological circumstance of interest, performance might take the form of seed dispersal ability, shell-crushing capacity, swimming speed, or tree-climbing ability. Performance in its various guises is a central issue in ecological morphology, physiological ecology, functional morphology and other disciplines poised at the interface of phenotype and ecology (Wainwright and Reilly, 1994).

The relationship of performance to selection theory can be visualized with path diagrams that portray selection surfaces (Arnold, 1983). In such a diagram (Fig. 1) we see performance interposed between morphology and fitness. In the discussion that follow 'morphology' will be used as a shorthand for biochemical, physiological, behavioral and morphological attributes that affect performance. Turning to the regression equations, the interposition of performance means that the equation that relates morphology to fitness can be decomposed into two equations: one that relates morphology to performance and one that relates performance to fitness:

$$f_i = \alpha_{fi} + \beta_{fi}^T z + \varepsilon_{fi} \qquad w = \alpha_w + \beta_w^T f + \varepsilon_w \tag{7}$$

where f denotes various measures of performance (a column vector) and f_i denotes an element in that vector. The total selection gradient β in the linear version of equation (3),

$$w = \alpha + \beta^T z + \varepsilon \qquad w = \alpha + \beta_w \beta_f^T z + \varepsilon, \tag{8}$$

is a product of the performance gradient β_f and the fitness gradient β_w (Arnold, 1983). Eq.(7) can be used to estimate β_f and β_w even if the performance surface or the fitness surface is curvilinear. In these instances of curvilinearity, however, we need a more complicated model than (7) to estimate curvature itself. We shall now turn to that more complicated model.

If the performance surface is curved we can approximate its curvature with a quadratic function. In this quadratic approximation, performance is a function of quadratic variables, zz^T, which represent the

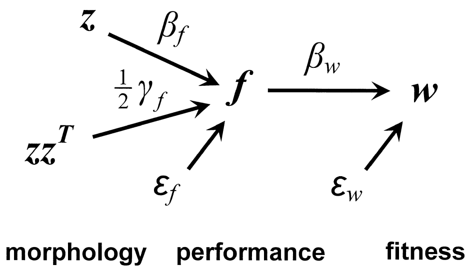

FIG. 2. Path diagram corresponding to the quadratic approximation (9) to the individual selection surface for morphology. The nonlinear performance gradient γ_f is the curvature of the fitted surface. Other conventions as in Figure 1.

squares and products of trait values, as well as the trait values themselves,

$$f = \alpha_f + \beta_f^T z + \frac{1}{2} z^T \gamma_f z + \varepsilon_f. \qquad (9)$$

γ_f is a matrix of nonlinear performance gradients. We can also visualize this equation with a path diagram (Fig. 2). In the two trait case,

$$f = \alpha_f + \beta_{f1} z_1 + \beta_{f2} z_2 + \frac{1}{2}\gamma_{f11} z_1^2 + \frac{1}{2}\gamma_{f22} z_2^2 + \gamma_{f12} z_1 z_2 + \varepsilon_f \qquad (10)$$

where γ_{11} and γ_{22} describe curvature in character dimensions z_1 and z_2, respectively, and γ_{12} describes the orientation of the surface. Quadratic surfaces can take a limited variety of shapes in two dimensions. The range of possibilities is shown in Figure 3. In three trait dimensions the range is considerably greater (Fig. 4).

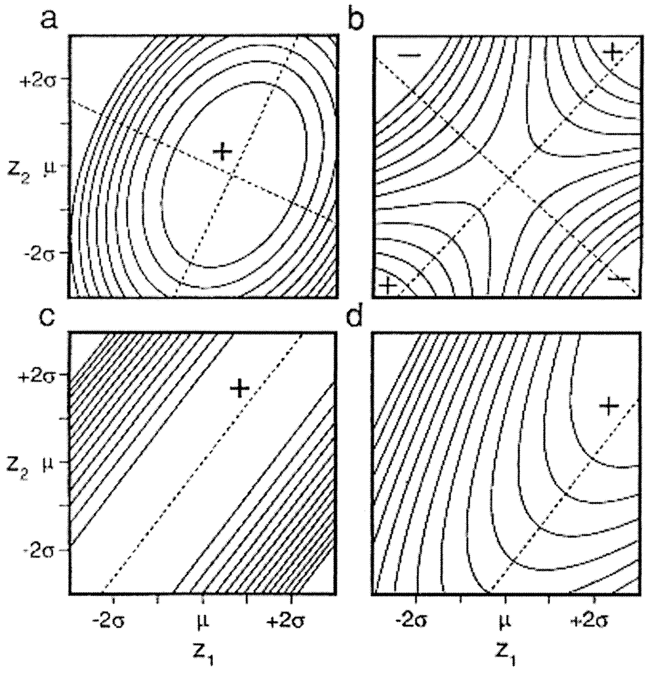

FIG. 3. Various shapes for quadratic performance surfaces for two traits, z_1 and z_2. High and low points on the surface are indicated by + and −, respectively. Dotted lines indicate performance lines of least resistance (eigenvectors or principal axes). (a) A surface with a peak. (b) A surface with a saddle. (c) A surface with a ridge. (d) A surface with a rising ridge. These surfaces differ only in their coefficients for correlational performance, γ_{f12}. From Phillips and Arnold (1989) reproduced with permission.

What is the relationship of this quadratic surface to the actual performance surface, which might—after all—have a more complicated shape? Regardless of the shape of the actual performance surface, β_f will estimate its average slope and γ_f will estimate its average curvature (Fig. 5). β_f will also estimate its slope of the performance landscape in the vicinity of the

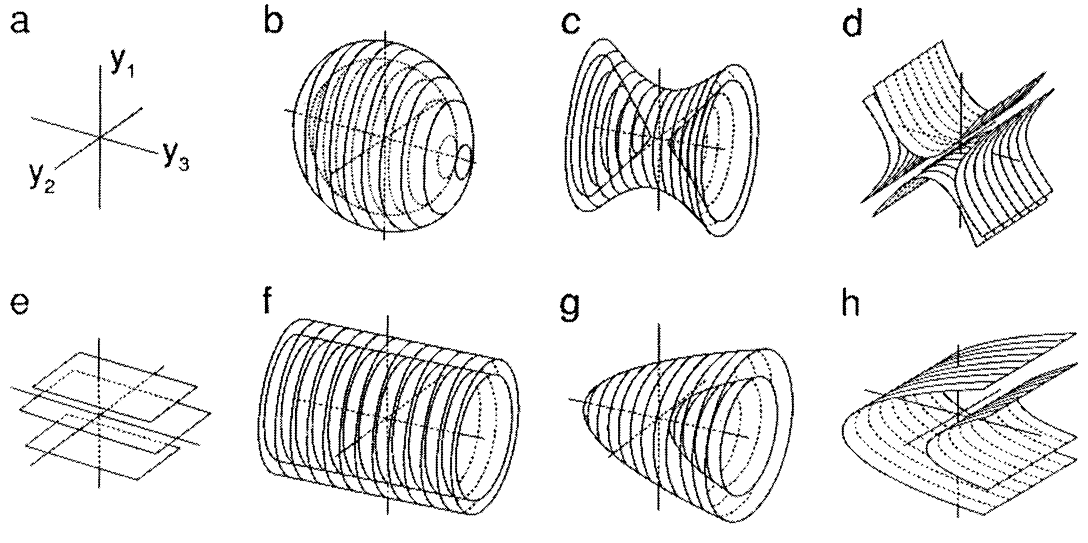

FIG. 4. Various shapes for quadratic performance surfaces for three traits (y_1, y_2, y_3) plotted on their principal axes (dotted lines). Each figure is a contour representation of a four-dimensional surface. Performance is the fourth axis and is represented by a surface of higher performance nested within a surface of lower performance. Dotted lines represent performance lines of least resistance. Axis labels are shown in (a). The regions of highest performance are the origin in (b) and (c), a line in (d) and (f), a plane in (e) and a curved surface in (g) and (h). From Phillips and Arnold (1989), reproduced with permission.

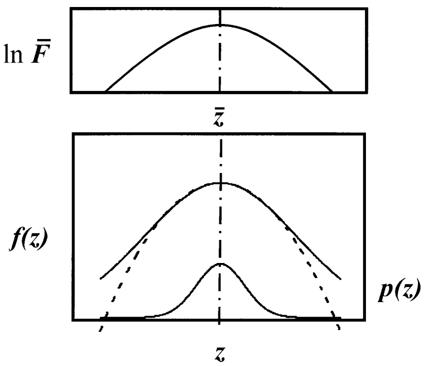

FIG. 5. The individual performance surface (lower panel) and the performance landscape (upper panel) for a single morpological trait. In the lower panel, the bottom solid curve represent the distribution, $p(z)$, of the morphological variable z; the upper solid curve represents the individual performance surface, $f(z)$; the dashed curve represents the quadratic approximation to the individual performance surface. In the upper panel, $\log_e$ mean performance, $\ln \bar{f}$, is a function of mean morphology, $\bar{z}$, in the population. The vertical dotted line marks the position of $\bar{z}$. Note that the mean lies at the optimum of the performance landscape. After Phillips and Arnold (1989).

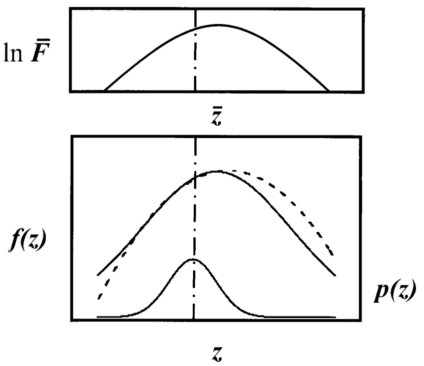

FIG. 6. The individual performance surface (lower panel) and the performance landscape (upper panel) for a single morpological trait when the mean morphology does not lie at the optimum of the performance landscape. In this situation, the curvature of the quadratic approximation to the individual performance surface, γ_f, evaluated at the morpological mean, overestimates the curvature of the performance landscape, $\gamma_f - \beta_f\beta_f^T$. Conventions as in Figure 3. After Phillips and Arnold (1989).

population mean, $\bar{z}$, but in general the curvature of the performance landscape at that point is $\gamma_f - \beta_f\beta_f^T$ (Fig. 6). Note that this last formula is a the general one for the curvature of the performance landscape, because in those instances in which the permformance means lies directly under the optimum of the landscape (Fig. 5), $\beta_f = 0$ and so $\beta_f\beta_f^T = 0$ (Phillips and Arnold, 1989).

It is useful to characterize the performance surface in terms of its principal axes, which represent performance lines of least resistance. The eigenvectors (or principal components) of the performance surface can be calculated from the matrix γ_f (Phillips and Arnold, 1989). The leading eigenvector of matrix γ_f represents the performance line of least resistance. Of all the lines that we might draw on the performance surface, movement along this line causes the smallest change in performance. The next best orthogonal line in this sense of least change in performance is the second eigenvector. The first and second eigenvectors of quadratic surfaces in Figure 3 are shown with dotted lines. To calculate the performance line of least resistance for the performance landscape we need to take the leading eigenvalue of the matrix $\gamma_f - \beta_f\beta_f^T$.

What about the total nonlinear selection gradient for a trait or a pair of traits? If we assume that the relationship between performance and fitness can be approximated with a linear fitness gradient, viz.,

$$w = \alpha_w + \beta_w^T f + \varepsilon_w, \tag{11}$$

then the total individual selection surface can be approximated by

$$w = \alpha + \beta_w^T\beta_f^T z + \frac{1}{2}\beta_w^T z^T \gamma_f z + \varepsilon. \tag{12}$$

Notice that the total nonlinear selection gradient for the traits is a function of the linear fitness gradient, β_w, and the nonlinear performance gradient, γ_f. Using (3–6), the curvature of the adaptive landscape for the traits in the vicinity of the population mean is β_w^T ($\gamma_f - \beta_f\beta_f^T < 1$, we can conclude that the curvature of the adaptive landscape will be less than the curvature of the performance landscape (Fig. 7).

SELECTION ON PERFORMANCE

In the preceding discussion we focused on morphology and how selection on morphology was mediated by its effects on performance. Our perspective was to view fitness from the perspective of fitness, with performance an intervening variable (Fig. 1). To consider selection on performance, we need a new perspective. We need to view fitness from the perspective of performance (Fig. 8). Turning to the issue of how selection acts on performance, we have two surfaces to consider: the individual selection surface for performance (or the selection surface for performance), in which individual fitness is a function of individual values for performance (Fig. 9, bottom), and the adap-

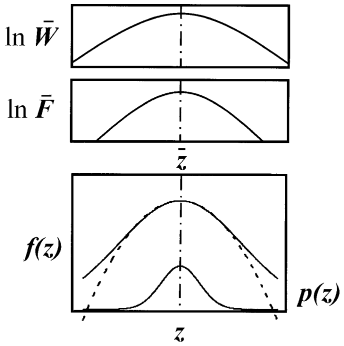

FIG. 7. The individual performance surface (lower panel) and the performance landscape (middle panel), and the adaptive landscape (upper panel) for a single morpological trait when the mean morphology lies at the optimum of the performance and adaptive landscapes. In the upper panel, $\log_e$ mean fitness, $\ln \bar{W}$, is a function of mean morphology, $\bar{z}$. Other conventions as in Figure 5.

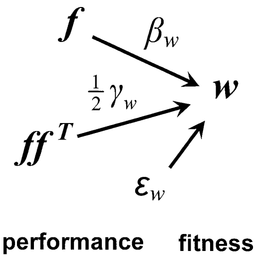

FIG. 8. Path diagram representing the quadratic approximation (13) to the individual selection surface for performance.

tive landscape for performance (or the performance adaptive landscape), in which the average value of fitness is a function of the population's average values for performance (Fig. 9, top). We can estimate the coefficients of the individual selection surface for performance using the quadratic approximation

$$w = \alpha_w + \beta_w^T f + \frac{1}{2} f^T \gamma_w f + \varepsilon_w. \tag{13}$$

This model is the same as (3); we are merely considering performance, f, to be the trait of interest. To fit this model we would need data on performance and fitness for a series of individuals in a population (Arnold, 1983, 1986). β_w is the average slope of the individual selection surface for performance, as well as the slope of the adaptive landscape for performance in the vicinity of average performance,

$$\beta_w = \int p(f)\frac{\partial w(f)}{\partial f}\,df = \frac{\partial \ln \bar{W}}{\partial \bar{f}}. \tag{14}$$

γ_w is the average curvature of the individual selection surface for performance,

$$\gamma_w = \int p(f)\frac{\partial^2 w(f)}{\partial f^2}\,df. \tag{15}$$

The curvature of the adaptive landscape for performance (Fig. 9, top) in the vicinity of mean performance is

$$\gamma_w - \beta_w\beta_w^T = \frac{\partial^2 \ln \bar{W}}{\partial \bar{f}^2}. \tag{16}$$

EVOLUTION OF THE PERFORMANCE SURFACE AND THE ADAPTIVE LANDSCAPE

It is the adaptive landscape, in conjunction with quantitative inheritance, that governs trait evolution, eq. (1). In the short term, we can consider the adaptive landscape to be a fixed entity, with constant slope and curvature, but in the long term we need to consider the possibility that the landscape itself might evolve. That evolution might reflect change in abiotic conditions, relationships with other species or trait interactions. Before we consider landscape evolution, however, we need to consider our vision of the landscape itself.

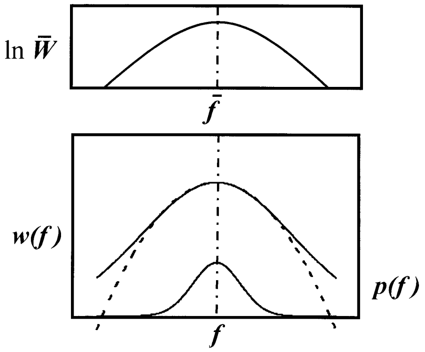

FIG. 9. The individual selection surface (lower panel) and the adaptive landscape (upper panel) for a single performance variable. In the lower panel, the bottom solid curve represent the distribution, $p(f)$, of the performance variable f; the upper solid curve represents the individual selection surface, $w(f)$; the dashed curve represents the quadratic approximation to the individual selection surface. In the upper panel, $\log_e$ mean fitness, $\ln \bar{W}$, is a function of mean morphology, $\bar{f}$, in the population. The vertical dashed line marks the position of $\bar{f}$. Note that when the mean lies at the optimum of the adaptive landscape, as in this portrayal, there is no directional selection on performance. After Phillips and Arnold (1989).

The most tractable vision of the adaptive landscape is one that is restricted to the immediate vicinity of a population's mean (Arnold *et al.*, 2001). This local vision is a practical one, because—as we have seen—we can use the tool of quadratic approximation to characterize the slope, curvature and orientation of the landscape in the vicinity of $\bar{z}$ or $\bar{f}$. We can have local visions of multiple landscapes. To visualize multiple populations or species, we superimpose their landscapes and view them all at once in a space of average trait or performance values (Arnold *et al.*, 2001, Fig. 9). The textbook vision of an adaptive landscape differs from this local vision of individual or multiple landscapes. A complex, rugged topography is often depicted in textbooks. Arnold *et al.* (2001) called it the global view of the landscape, for it portrays features near and far from the population mean. Dawkins (1996) has called it Mt. Improbable. The quandary of a population stuck on a local summit, down slope from the summit of Mt. Improbable, is a carry over from Wright's (1931, 1932) landscape in a space of gene frequencies. It is not clear, however, that a rugged topography, and the quandries resulting from local peaks, apply in the case of phenotypic characters. More importantly, we have no device that can tell us about landscape features far from the population's average. Mt. Improbable is, after all, Mt. Unknowable. This is the sense in which the local vision of the landscape is the most tractable. We have devices to give us a local vision. But if we adopt a local vision, how can the population ever evolve on the landscape? The answer is that the landscape's peak can move in evolutionary time (Simpson, 1944), causing the average trait or performance values to track that movement in response to directional selection.

A variety of models have been proposed for the evolution of the adaptive landscape (Arnold *et al.*, 2001;

Hansen and Martins, 1996). The simplest models all share the feature that the curvature and orientation of the landscape remains constant. Only the position of the landscape's peak evolves. With these provisos, we can recognize four broad categories of possibilities: (a) the peak undergoes random (*e.g.,* Brownian) motion, (b) peak movement is selectively constrained about a fixed or moving point, (c) the peak moves at a consistent rate and in a particular, characteristic direction, (d) peak movement is episodic rather than steady. Obviously, there are other possibilities and even the ones listed could be combined in various ways. I want to focus on just one possibility because of its apparent relevance to the comparative study of performance. I want to consider the issue of whether the peak moves in ways that can be deduced by studying performance within populations. Is the movement of the adaptive landscape selectively constrained?

The position of the adaptive landscape may tend to evolve along performance lines of least resistance. The basis of this prediction is the proposition that the performance lines of least resistance arise from fundamental biomechanical relationships. The major features of the performance surface distill these fundamental relationships within populations. In a study of garter snakes, for example, Arnold and Bennett (1988) found that the performance surface that relates crawling performance to body and tail vertebral numbers had a major axis that promoted a positive correlation between these two parts of the vertebral column. Thus, the snakes with the fastest crawling speeds tended to lie close to the performance line of least resistance. A change in vertebral numbers that moved a hypothetical snake along the line had relatively little effect on performance; a change that moved a snake off the line lowered performance. An unknown biomechanical law that gives a performance premium to well proportioned snakes presumably underlies these results. Even though the biomechanical law is unknown in this case, it's domain of operation might transcend the limits of vertebral variation in a single population. Our proposal is then that the peak of the performance landscape tends to evolve along the performance line of least resistance. Changed ecological circumstances cause the position of the adaptive landscape to change, but that evolutionary movement is selectively constrained by the same biomechanical laws that prevail within populations. A particularly evocative prospect is presented by the model of trivariate stabilizing selection shown in Figure 4f. Movement of this surface (or its corresponding landscape) along the selective line of least resistance would correspond to concentric series of pipes sliding simultaneously along their long axes. This proposal is different from Schluter's (1996) proposition that evolution occurs along genetic lines of least resistance. Schluter's lines correspond to the principal axes of the G-matrix in (1–2). See Arnold *et al.* (2001) for a discussion and comparison of the two proposals.

Can we explain adaptive radiations by movement of adaptive (or performance) peaks along a selective line of least resistance? In other words, is this model capable of generating the elongate clusters of population or species means that typically characterize interspecific allometry or morphospace? One point that emerges from models of peak movement is that movement along a selective line of least resistance probably must be sustained rather than random to explain the most common kind of patterns in trait space. For example, consider a Brownian motion model in which trait evolution is constrained in the same multivariate pattern that constrains performance-based selection within populations. Because movement of the peak is about a fixed point, the long term expectation is for no correlation in species or population means. For simplicity, assume that the performance surface is the same among all descendant populations in a radiation and takes the form of a Gaussian surface so that

$$f(z) = \exp\left[-\frac{1}{2}(z - \theta_f)^T\omega_f^{-1}(z - \theta_f)\right],$$

where ω_f is a matrix of coefficients, analogous to variances and covariances, that describes the shape and orientation of the performance surface, and θ_f is the peak of that surface. Suppose that the peak of the surface undergoes selectively-constrained Brownian movement. The peak moves as a normally distributed random variable with mean 0 and a variance-covariance matrix $k\omega_f$, where k is a scalar constant of proportionality (Arnold *et al.*, 2001). Each population tends to track its moving peak, and so, after some elapsed number of generations, the population means have a dispersion pattern that reflects the shape and orientation of the performance surface. Using results from Lande (1979) and Hansen and Martins (1996), the covariance of population means of the populations after t generations is

$$COV(\bar{z}) = Q(t)(k\omega_f)Q^T(t),$$

where $Q(t) = \exp[-tG(\omega_f + P)^{-1}]$. Under some conditions this model predicts correlation in population means. Such patterns of covariance will be aligned with the major axes of the ω-matrix, which can in turn be estimated by the major axes of the γ-matrix. These patterns of population covariance, however, decay very rapidly. Under plausible sets of parameter values, the covariance in population means decays to virtually nothing in less than 10,000 generations. Although the peak of the performance surface undergoes Brownian motion in a pattern that reflects the shape and orientation of the selection surface, the long term expectation is for population means to be close to the original position of the peak. In other words, Brownian motion seems unlikely to produce elongate patterns in population or species means. Our exploration of this model suggests that the position of the peak must move along selective lines of least resistance, rather than hover about a fixed point, to produce a radiation that reflects the within-population performance surface.

Comparative data can be used to test for selectively-constrained movement of the adaptive landscape. In the ideal case, we would have estimates of the performance surface from different populations or species. With those data we could test for homogeneity among populations in the γ-matrix. If variation in γ were not too great, we could estimate the pattern of dispersion of optima to see if that pattern coincides with the average line of selective least resistance within populations (*i.e.*, with the average leading eigenvector of the γ-matrix). Such an ideal case might require estimates of ten or more performance surfaces to accurately describe the multivariate dispersion of optima. If only one estimate of the performance surface is available, we might assume that mean of each population is close to its performance optimum, and then use the dispersion of population means as a surrogate for the dispersion of optima. Comparing the leading eigenvectors of the among-population variance-covariance matrix and the performance surface (γ-matrix) provides a test for evolution along selectively-constrained lines of least resistance. The garter snake test case was of this kind and yielded remarkably strong correspondence between the leading eigenvectors of the among-population dispersion matrix ($n = 9$ populations) and the γ-matrix for crawling speed; the vector correlation was 0.995. Thus, vertebral numbers in garter snakes evolve along performance lines of least resistance.

The perspective that the performance surface is curved and related to the adaptive landscape highlights two unresolved, empirical issues: (a) What is the time scale for the evolution of the curvature and orientation of the performance surface? The usefulness of the performance surface in understanding the evolution of morphology depends on the evolutionary stability of the surface. Because the surface springs from underlying components of the organism and their interactions, it seems likely that the performance surface and morphology evolve on the same time scale. Comparative studies of surfaces could test this proposition directly. (b) What are appropriate models for the evolution of the performance optimum? Evolution of the optimum along performance lines of least resistance is obviously just one possibility. Nevertheless, this proposal represents a simple hypothesis that cuts through the tangle of other possibilities (Emerson and Arnold, 1989). Here again, comparative studies of surfaces are a vital step in validating our models of surface and landscape evolution.

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