

Adaptationism and Optimality

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Chapter 7

Is Optimality Over the Hill?

The Fitness Landscapes of Idealized Organisms

GEORGE W. GILCHRIST AND JOEL G. KINGSOLVER

Imagine a mountaineering enthusiast who decides to write a comprehensive guide for climbers. This would-be author spends many years climbing every peak throughout the world, gathering material for a book, and then starts to write. In the end, our enthusiast produces a guidebook, listing each peak, its longitude and latitude, and the number of climbers the author encountered at the summit.

Clearly, this guidebook is unlikely to make the best-seller list or even to become a citation classic. Readers of this guide would undoubtedly have many additional questions: What is the height of each peak? How steep is the approach to the summit from different directions? Are there ridges leading to the peak? Are there other peaks nearby? When asked about these questions, the author replies in defense, "Climbers climb peaks, so I wrote about peaks."

In our view, many (perhaps most) studies of optimality in biology seem similar to this guidebook. The primary questions of interest are "Where is the fitness peak?" and "Is the population or species of interest currently at or near the peak?" The rationale for this emphasis is that, because evolution by natural selection is expected (under certain conditions) to increase the mean fitness of a population, one might predict that populations would tend to reside at the peaks in a fitness landscape.

Although fitness peaks are interesting, we fear that an exclusive emphasis on them may generate an understanding of phenotypic selection and evolution that is as unsatisfying as our imaginary mountaineering guidebook. We suggest that a broader view that explores the topography of fitness landscapes may be useful. In this chapter, we address a series of questions that emerge naturally from the perspective of fitness topography in phenotypic space. What is

a fitness or adaptive landscape? When is a peak not a peak? What does the shape of the peak imply about adaptation? How bumpy are fitness landscapes? How does evolution by natural selection proceed on complex adaptive topographies? Such questions have scarcely been raised, much less answered, so our suggestions will be tentative and provisional. Our goal is simply to convince the reader that a view of fitness landscapes beyond the location and occupation of fitness peaks may enrich our understanding of phenotypic selection and evolution.

WHAT ARE FITNESS OR ADAPTIVE LANDSCAPES?

Sewall Wright's (1932) model of evolution on a fitness or adaptive landscape is one of the most widely used heuristic tools in evolutionary biology; however, at least three different versions of the model are currently in circulation. Wright (p. 315) originally conceived of this "surface of selective value" as depicting the fitness of individual multilocus genotypes within a certain environment. The often-reproduced figure shows a pair of axes representing a "field of gene combinations in two dimensions instead of many thousands," with dotted lines defining the contours of the fitness peaks and valleys. Unfortunately, this view is quite meaningless when applied to real organisms because there is no unique way to array multilocus genotypes along a pair of axes (Provine 1986). Wright's second version of the concept (e.g., Wright 1935) placed allele frequencies along the x- and y-axes. Because allele frequencies are properties of populations, this version depicts the fitness of populations, or demes, rather than that of individuals. The third version was outlined by Simpson (1944, 89); he saw the axes of the landscape as phenotypic values, with the peaks and valleys representing either individual or population fitnesses. Lande (1976) used quantitative genetics to provide a robust theoretical justification for this phenotypic version of evolution on the adaptive landscape for polygenic, quantitative traits.

Our interest here is with evolution and adaptation of phenotypic traits; therefore, our discussion focuses largely, although not exclusively, on the phenotypic version of adaptive landscape. Various authors have used *fitness landscape*, *adaptive landscape*, and similar terms in a variety of ways (Provine 1986). Here we use *individual*

performance or *fitness surface* to describe a map of individual phenotypes (occasionally genotypes) to individual performance or fitness, and *adaptive landscape* to describe a map of mean phenotype (or allele frequency) to the mean population fitness. Although an individual fitness surface and its corresponding adaptive landscape for a population are necessarily related, they are quite distinct. For example, the existence, location, and curvature of peaks and other features may be very different on the individual surface and the adaptive landscape, depending on the patterns and nature of phenotypic and genetic variation (e.g., Felsenstein 1979; Coyne et al. 1997). As discussed later ("How does evolution proceed on an adaptive landscape?"), only the adaptive landscape, relating mean phenotypes or allele frequencies to mean population fitness, can be directly related to models of evolutionary dynamics (Wright 1935; Lande 1976).

The consideration of optimality models in terms of individual fitness surfaces or adaptive landscapes can yield insight into the intensity and direction of natural selection. In the context of dynamic-programming models applied to behavioral traits, Mangel and Ludwig (1992) have also emphasized the value of considering the fitness consequences of deviations from optimality. Here we assume that the optimality model can be presented with individual or population fitness as a function of one or more individual or mean phenotypic trait values. When only one or two traits are studied, presentation of the model as a graphical landscape is straightforward. A larger set of traits requires the use of principle components or non-parametric methods (e.g., Schluter and Nychka 1994) to visualize the fitness surface.

Construction of a theoretical fitness surface or adaptive landscape can complement empirical studies, such as the estimation of directional and quadratic selection coefficients on some set of quantitative traits. These coefficients are necessary to predict the evolutionary response because they describe the effect of selection at the population level (Lande 1979), but they do not provide information that is comparable to a fitness surface, particularly if the phenotypes are not multinormally distributed (Mitchell-Olds and Shaw 1987; Schluter 1988). For example, from the selection coefficients alone one cannot generally tell whether a fitness peak lies within the range of observed phenotypes within a population. The construction of a fitness landscape provides the most direct means of visualizing

the correspondence between a model of fitness as a function of phenotype and the distribution of phenotypes in nature (Brandon and Rausher 1996).

WHEN IS A PEAK NOT A PEAK?

One critical issue in any model of phenotypic evolution is the role of unmeasured variables. Genetically or phenotypically correlated traits can alter the shape and location of the peaks on the fitness landscape. One might misidentify peaks that do not exist because of the interaction of the measured trait with a key unmeasured trait having a large effect on fitness (Lande and Arnold 1983; Mitchell-Olds and Shaw 1987). Here we present an example in which a two-dimensional fitness surface adapted from a "successful" one-dimensional optimality model (that is, the model predictions provide a good match to the mean value of the trait in nature) suggests that higher theoretical peaks might exist than those identified by the author.

This example concerns a quantitative prediction of optimal body size. Roff's classic paper (1981) on *Drosophila* body size used Euler's equation to describe the relationship between fitness, body size, and various life history components. Roff presented the result as a one-dimensional fitness surface, plotting fitness (modeled as the rate of increase, r) as a function of body size (Figure 7.1, after Roff 1981, Figure 1). The model predicts an optimal body size of 0.95 mm, which falls within the observed range of *D. melanogaster*. The fitness surface further suggests a fairly good correspondence between the observed variation and the small range of body sizes that fall near the flattened peak (Figure 7.1). The rapid drop-off in fitness outside the observed range implies that selection should maintain populations near the predicted optimum.

Ricklefs (1982) raised a potential problem with this model: Roff assumed a constant value of 3.0 for δ , the exponent relating body size to development time. Justification for this point included a sensitivity analysis for the range of δ between 3 and 4 (with development time slowing as δ increased) that showed little change in the optimal prediction. Ricklefs countered that the model was, in fact, sensitive to variation in δ ; however, the sensitivity decreased as δ increased. Therefore, smaller values of δ (an acceleration of growth rate) predict quite different optimal body sizes. Figure 7.2 shows contours of the

Is Optimality Over the Hill?

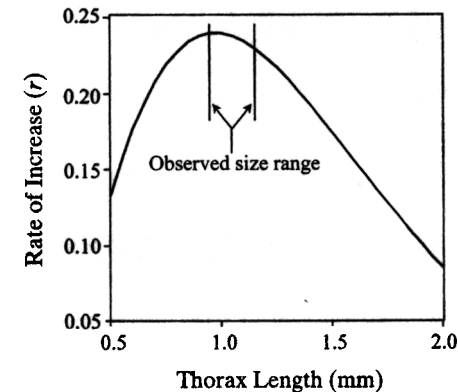


Figure 7.1. The fitness landscape of *Drosophila melanogaster* body size (measured as thorax length). After Roff (1981, Figure 1).

individual fitness surface as a function of both body size and the growth exponent. Note that the region above the dashed line (Roff's estimate of $\delta = 3$) indeed shows little variation in the optimal size as δ changes. Below the line, the optimal size increases as the growth exponent decreases, suggesting (not surprisingly) that being big and growing fast are good things to do. Roff argued (1983) that several other lines of evidence suggested that $\delta = 3$ was the appropriate value; however, he admitted that the problem could bear further investigation.

Our point here is not to argue whether Roff's model was or was not appropriate but rather to show that the two-dimensional fitness surface (Figure 7.2) raises important issues directing further investigation of this system. The model predicts a fitness plateau for δ 's ranging from 2.5 to 4, where the optimal body size is largely independent of growth rate. As growth rate accelerates (δ decreases), the optimal body size climbs and individual fitness increases. Clearly, higher fitness can be gained by growing faster and larger, but perhaps no *Drosophila* in nature occupy this region of the landscape. If this is the case, then clearly something is missing from the model. Perhaps ecological, metabolic, or structural constraints never allow such rapid growth rates. Furthermore, the model suggests that optimal body size should be more plastic over the range of conditions favoring rapid growth; under moderate growth conditions, body size should be relatively insensitive to growth rate variation.

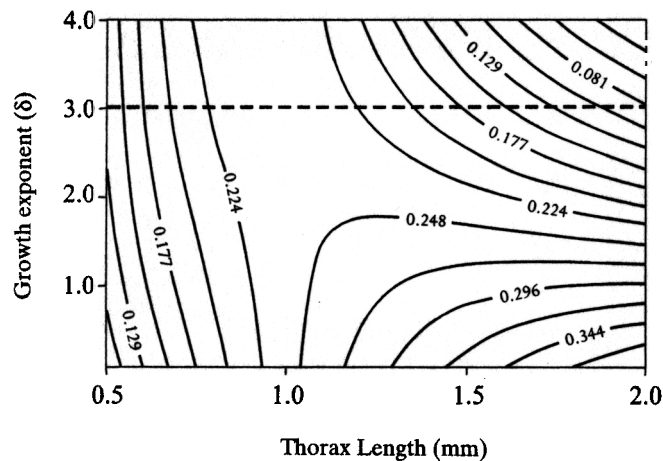


Figure 7.2. The fitness landscape of body size and the larval growth exponent from Roff's (1981) model. The cross section indicated by the broken line (at $\delta = 3$) is the fitness landscape in Figure 7.1. The highest fitness is toward the lower-right-hand corner.

WHAT DOES THE SHAPE OF THE PEAK IMPLY ABOUT ADAPTATION?

Fitness peaks can have an infinite variety of shapes. The fitness surface provides a picture of how strongly natural selection favors specific trait values. For example, asymmetry about a peak may reflect an asymmetrical relationship between the trait values and fitness and, in the case of a multivariate fitness surface, functional, genetic, or phenotypic correlations between pairs of traits. To determine how a specific population might evolve, one must construct an adaptive landscape, weighting the fitness landscape by the frequency of phenotypes or genotypes in the population. Lande's (1976) models for evolution on an adaptive landscape showed that selection tends to drive the population up the steepest slope on an asymmetric peak (Lande 1976; Lande and Arnold 1983). More-complex dynamics can occur, however, if ridges of high fitness dominate the landscape (Wagner 1984; Bürger 1986). To see what can be learned about adaptation from the topology of the landscape, we turn to our own work as an example of optimality models that predict ridged fitness landscapes.

Fitness Landscapes in Temporally Varying Environments

Gilchrist (1995) constructed fitness landscapes to identify the optimal performance curve, defined as the reaction norm of temperature-sensitive performance. Many optimality studies assume a temporally constant environment; however, in this case, the optimal phenotype would be the one that yielded the highest fitness over several generations in a variable environment. The geometric mean is an appropriate fitness measure when selection varies over time (Haldane and Jayakar 1963), at least for simple population genetic models. More-complex dynamics arise for multiple alleles and multiple loci (Turelli 1981), but genetic simulations show the geometric mean to be a good approximation, at least for these models (Gilchrist, unpublished data). Figure 7.3 shows contour plots of geometric mean fitness of individuals having different combinations of two traits: the breadth of the performance, indicating the degree of specialization, and the maximum temperature, which positions the curve along the temperature gradient.

The nine fitness landscapes in Figure 7.3 correspond to nine different patterns of temporal variation. From left to right, the within-generation component of variation increases; this corresponds to daily temperature variation for the multivoltine insects on which this model is based. From top to bottom, the among-generation component of variation increases, corresponding to the seasonal pattern of temperature variation. Within-generation variation is modeled as a normally distributed variable, whereas the among-generation component follows a sinusoidal trajectory. So the plot in the upper left represents a relatively constant environment, whereas the plot in the lower right represents an environment with substantial variation over within- and among-generation time scales. Although some of the variation in this model is patterned, completely stochastic variation of the same magnitude yields essentially identical results. The number in the upper-left-hand corner of each figure gives the distance between the contours in arbitrary fitness units. The model assumes Levins's (1968) principle of allocation; Gilchrist (1995) discusses the consequences of relaxing this assumption.

The optimal solution for a given pattern of environmental variation, indicated by a triangle on the fitness landscapes (Figure 7.3), represents the phenotype with the highest geometric mean fitness over a single cycle of variation. When there is no among-generation

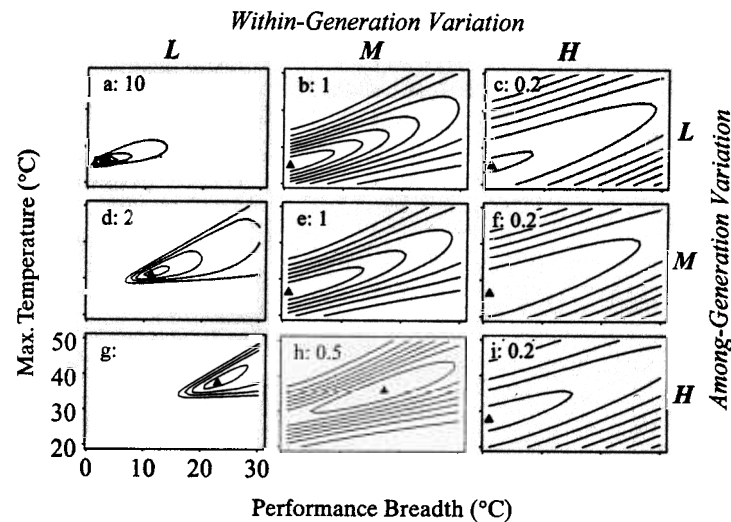


Figure 7.3. A contour plot of the fitness surface for low, medium, and high within-generation environmental variation crossed with low, medium, and high among-generation environmental variation. The triangle in each figure indicates the peak; the number in the upper-right-hand corner indicates the interval, in arbitrary fitness units, between the contour lines. After Gilchrist (1995, Figure 4).

variation in temperature, the optimal performance phenotype is a narrow, "specialist" curve (Figure 7.3a, b, c). Increasing the within-generation variation flattens the fitness landscape, but it does not change the optimum performance breadth. Selection for generalists with a broader performance curve increases with among-generation variation in temperature (Figure 7.3a, d, g). The interaction between temperature variation on the two time scales produces a surprising result: Narrow performance curves are the optimal phenotypes in environments with copious within- and among-generation variation (Fig 7.4i). A moment's reflection should resolve this enigma: The specialists are simply waiting until conditions are right and then performing like mad until conditions deteriorate again. If we were modeling tolerance curves using multiplicative fitnesses, as in the case of previous studies (e.g., Levins 1968; Lynch and Gabriel 1986; Lynch and Gabriel 1987), we would obtain a quite different result. Although organisms can delay feeding, ovipositing, and mating until

conditions improve, they cannot delay surviving without a significant loss of fitness, so increasing within-generation variation selects for broad tolerance curves.

Given the criterion of optimality, the performance curve in the preceding model should be narrow, regardless of the level of among-generation variation, and it should track the environment as conditions vary. Such tracking might be achieved by acclimation ability; however, acclimation is usually imperfect (Kingsolver and Huey 1998). Alternatively, the organisms could achieve higher fitness by evolving homeostasis (assuming that the potential metabolic costs were not restrictive) so that the conditions within the body are independent of the external environment. Indeed, the payoff for homeothermy, according to the performance model, is substantial: a specialist in a constant environment (Figure 7.3a) has maximum fitness nearly an order of magnitude higher than essentially the same phenotype in a fluctuating environment (Figure 7.3i). Gilchrist (1995) assumed isothermy between the organism and the environment and no acclimation ability (reasonable assumptions for many small insects), so these globally optimal solutions were beyond the scope of these models.

The optimal performance phenotype in a constant environment (Figure 7.3a), a specialist with narrow performance breadth, is almost identical to the optimal phenotype in an environment that varies greatly on both within- and among-generation time scales (Figure 7.3i). The fitness surface surrounding these two optima, however, is entirely different. The fitness peak in Figure 7.3a is a high, narrow pinnacle rising sharply above the low-fitness flatlands, whereas the "peak" in Figure 7.3i is a barely perceptible rise along a flattened ridge of high fitness. Natural selection is responsible for driving organisms toward either peak, but the chance of a specific population reaching that phenotype differs greatly in the two situations. Increasing either temporal component of variation in this model flattens the landscape, greatly reducing the selective advantage of individuals possessing the optimal phenotype. In fact, the ubiquity of environmental variation both within and among generations in nature suggests that flattened fitness landscapes might be the rule rather than the exception. If the optimal phenotype is little better than some range of alternative phenotypes, then natural selection may be too weak to overcome constraining forces such as genetic drift and indirect evolution due to selection pressures on

correlated traits. Note that the flattening of the individual fitness surface here is fundamentally different from the flattening of the adaptive landscape resulting from the reduction of mean fitness due to phenotypic variation within the population (see the later discussion).

The fitness surfaces pictured in Figure 7.3 also reveal the presence of a functional constraint (as opposed to a genetic constraint or correlation) that greatly slows the evolution of the performance traits (Bürger 1986). In any model where the performance curve or norm of reaction is asymmetric, the parameters describing that curve cannot evolve independently. (Exactly what biological parameters determine the degree of plasticity has been the subject of much debate. For a brief review, see Via et al. 1995). For example, in the preceding model one could fix one parameter – say, performance breadth – and determine the optimal location of the curve given by maximum temperature. If natural selection were to favor a slightly different performance breadth, selection would have to change both performance breadth and the location of the curve along the environmental gradient. Attaining the new optimum would require coordinated adaptive evolution of two traits and not just one. Details of the variance-covariance structure of the traits in question will have a large effect on the evolutionary outcome. On the other hand, a symmetric performance curve or reaction norm, perhaps following a Gaussian model, allows the position and breadth parameters to evolve independently. Biological systems are replete with various functional constraints, which are a subset of the “global constraints” mentioned in Orzack and Sober (1994b).

HOW BUMPY ARE FITNESS SURFACES AND ADAPTIVE LANDSCAPES?

Most published models consider fitness surfaces that are quite simple in form, consisting of one or several symmetric, Gaussian fitness peaks rising from an otherwise flat plain (e.g., Felsenstein 1979; Kirkpatrick 1982; Coyne et al. 1997). For example, this “volcanic peaks above the plains” topography is implicit in most considerations of the evolution of niche partitioning. Yet the topography of actual fitness surfaces is an empirical question that has received little serious attention. In the absence of such data, models can be valuable in exploring the kinds of fitness landscapes that may occur.

One approach to this issue is to consider highly idealized models that explore general properties of fitness surfaces. Kauffman (1993) has pioneered this approach to examine how interactions between loci, or between parts of a system, influence the ruggedness of individual fitness landscapes. In this idealized (NK) model, an organism has N gene loci (each with two alleles) that contribute to an individual's fitness. Let K be the average number of other loci that interact epistatically to influence the fitness contribution of each locus. When fitness contributions are assigned randomly among the N loci, how does the number of epistatically interacting loci (i.e., K) affect the topography of the fitness landscape? Kauffman's analysis of this simple model yields three interesting results. First, in the absence of epistasis ($K = 0$), there is a smooth fitness surface with a single, global peak. In this sense, a purely additive model for fitness implies a simple, smooth fitness surface. Second, as K increases to 2 (the fitness contribution of each locus is influenced on average by two other loci), multiple peaks arise, but these peaks tend to cluster together in the landscape of possible genotypes. Third, as K approaches $N - 1$ (the fitness contribution of each locus is influenced on average by every other locus), the fitness landscape consists of a very large number of widely dispersed peaks, but each peak is quite small. For our purposes, Kauffman's analysis makes two important points: Bumpy fitness landscapes can arise naturally as a result of the interactions among components of a system, and highly interconnected systems may have extremely bumpy landscapes with no high fitness peaks.

What about fitness surfaces for phenotypic traits? One approach is to consider models tailored for particular organisms or systems; this is the stuff of most optimality models for quantitative phenotypic traits. Although fitness is sometimes explicitly defined and modeled, in most cases the output from such models is expressed in terms of measures of performance (e.g., energy intake rate, locomotory speed, etc.) or fitness components (e.g., survival, egg production) that are assumed to be directly related to fitness. Optimal values for the traits of interest are then defined as those that maximize the performance of an individual. What do such performance surfaces look like? Here we describe briefly two biomechanical examples chosen to illustrate some possible complex topographies. Complexity in landscapes arises from nonlinear relationships between the components of the trait and performance or from the interaction of several correlated traits in a manner more like that envisioned by Kauffman (1993).

Recent analyses of the consequences of septal complexity in ammonoids, such as the chambered *Nautilus*, illustrate the first of these possibilities (Daniel et al. 1997). The shells of *Nautilus* and other externally shelled ammonoids have walls, or septa, that divide the shell into a series of chambers. In many ammonoids, these septa are folded or fluted in complex ways; increases in septal complexity were a prominent evolutionary trend within many ammonoid lineages. Many workers (e.g., Jacobs 1990) have proposed that complex septa function to buttress the chambered shell against hydrostatic pressure in deep water, reducing the risk of implosion. Daniel et al. (1997) used finite-element analysis to model how septa complexity (defined as the number and amplitude of waves in the surface of the septum; see Figure 7.4) affects the ability of the septum to resist breaking under high external pressure, indexed in terms of a safety factor. This measure of performance shows a complex dependence on both wave number and amplitude of the septum (Figure 7.4), yielding a complex surface characterized by several peaks separated by a saddle along a long ridge. Interestingly, the highest point on the landscape occurs for a simple, hemispherical septum, suggesting that the evolution of increased septal complexity cannot be generally explained in terms of increased resistance to breaking under high hydrostatic pressure at depth. Here the complexity of the performance surface is determined, not by the interactions among components but rather by how septal geometry affects the location of points of stress concentration within the septum that lead to mechanical failure.

Even more complex performance surfaces may arise when many components of a system interact. For example, Daniel et al. (1998) have explored how the mechanical properties of thick and thin filaments and cross-bridges within a muscle fiber contribute to force generation during contraction. Myosin "motors" occur at regular intervals along the thick filament. During the cross-bridge cycle, the myosin heads form cross-bridges to actin binding sites along the thin filament; contraction of the myosin motors generates force on the thin filament, leading to contraction of the muscle fiber as a whole. Increasing the mechanical stiffness of the myosin motor decreases the probability that a cross-bridge will form but increases the force generated by cross-bridge contraction. Similarly, the stiffness of the thin filament affects the spacing of binding sites relative to the cross-bridges and the transfer of force from the cross-bridge to the thin

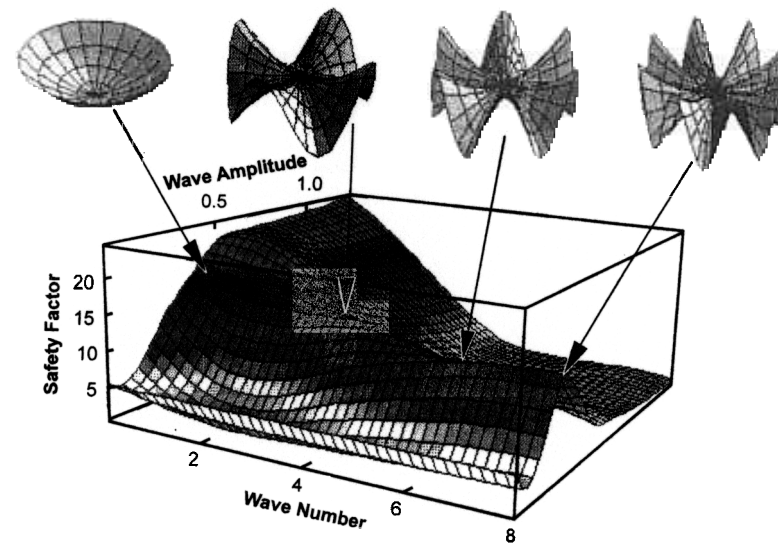


Figure 7.4. Safety factors against breaking for the septum of a *Nautilus* shell based on stress distributions predicted by finite-element analysis. The safety factor is plotted as a function of primary wave amplitude scale for dome-like septa (0 waves) and more-complex septa (4, 6, and 8 waves). From Daniel et al. (1997).

filament during cross-bridge contraction. Models for force generation for a filament pair containing many cross-bridges and binding sites reveal complex effects of cross-bridge and thin filament stiffness on force production (Figure 7.5). The performance surface possesses multiple peaks and ridges, with highest levels of performance occurring in two regions. In one region, both cross-bridge and thin filaments have very low stiffness (so that cross-bridges form at a very rapid rate but their contractions generate relatively little force transferred to the thin filament). In the second region, high performance occurs at intermediate stiffness of thin filaments and high stiffness of cross-bridges (so that cross-bridge contractions generate large forces, although cross-bridges form less frequently). As with Kauffman's (1993) idealized models of epistasis, the large number of interacting components in this simple muscle system generates a complex performance surface.

These examples illustrate that even quite simple systems can generate rather complex surfaces for individual performance. Such

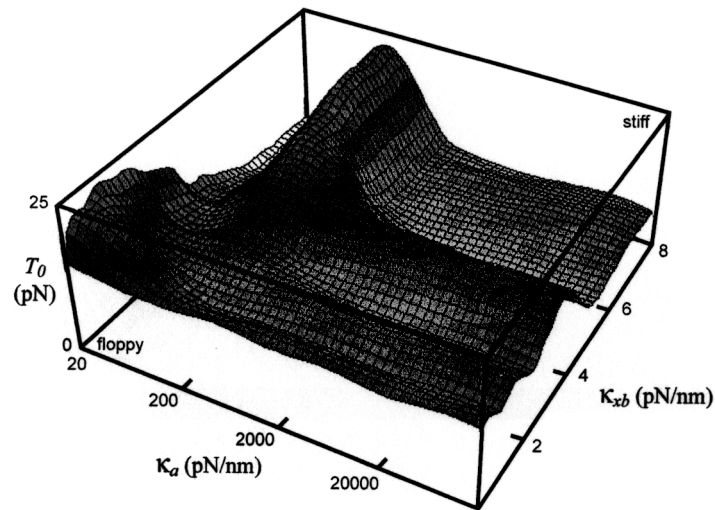


Figure 7.5. Mechanical tuning of a sarcomere in a muscle with compliant filaments. Tension is plotted against the thin filament spring constant (κ_a) and the cross-bridge spring constant (κ_{xb}). From Daniel et al. (1998).

landscapes contain multiple high points, long ridges, and many asymmetries. At the least, they provide no compelling support for the notion that fitness topographies with symmetric peaks or gently rolling hills are the norm. In her recent review of biomechanical performance in a variety of systems, Koehl (1996) has emphasized how the relationship between morphology and performance is frequently “nonlinear, context-dependent, and sometimes surprising,” as one might expect if performance surfaces are complex. Of course, performance is not fitness, and the force generated by a single muscle fiber, or even the safety factor for a *Nautilus* septum, is not necessarily related to fitness. However, we can think of no reason why one might generally expect individual fitness surfaces to be less bumpy than performance surfaces.

HOW DOES EVOLUTION PROCEED ON AN ADAPTIVE LANDSCAPE?

The performance and fitness landscapes just discussed describe the performance or fitness of an individual organism with a specified

phenotype. An optimality hypothesis predicts that, as a result of evolution by selection, the mean phenotype of a population of such individuals will occur at peaks on the adaptive landscape; that is, the adaptive landscape should be similar in topology to the underlying individual fitness surface. A growing literature discusses the ability of optimality models to predict long-term evolutionary equilibria. Optimality and ESS models often provide a good approximation of the equilibria predicted by genetic models (Hammerstein 1996; Eshel and Feldman, this volume), but cases exist in which the two types of models make dramatically different predictions (Weissing 1996). We focus our comments on the relationship between optimality models and quantitative-genetic approaches.

Optimality Models Versus Quantitative Genetic Approaches

As Wright (1932) originally noted, the precise path across the adaptive landscape followed by an evolving population depends on the starting point, the strength of selection (reflected by the topology of the fitness landscape), and the size of the population. Contemporary quantitative-genetic theory demonstrates that understanding the dynamics of evolution on an adaptive landscape generally requires some knowledge of the underlying constraints. The selection gradient gives the direction and intensity of selection on the phenotype. In the absence of genetic, functional, and demographic constraints, selection will drive the population up the steepest local slope (Lande and Arnold 1983) and a phenotypic model should be adequate. Genetic or functional correlations among the traits, however, will alter the evolutionary trajectory in ways that cannot be predicted without knowledge of the underlying variance-covariance matrixes (Lande and Arnold 1983; Bürger 1986). Evolutionary changes in the genetic variance-covariance matrix can further alter the trajectory of an evolving population on the adaptive landscape (Turelli 1984; Barton and Turelli 1987; Turelli and Barton 1994).

Although phenotypic models cannot generally predict the path of evolution on an adaptive landscape, they may be adequate for predicting the equilibrium value of the traits under study. In a strict sense, an optimality model for any quantitative, frequency-independent trait (say, z) typically predicts that all individuals in a population will have the identical (optimal) trait value z^* , occurring at maxima of the fitness function $w(z^*)$; there is no variance in the trait

value. Because variation among individuals in a population may be inevitable for any quantitative trait, optimality predictions are instead evaluated in terms of whether the mean trait value for a population (\bar{z}) is "close to" the optimal predicted value, relative to the variation in the trait (but see Orzack and Sober 1994a); in other words, that $z^* = \bar{z}$. An implicit assumption here is that evolutionary equilibrium occurs at points where $w(\bar{z})$ represents a local maximum. In contrast, evolutionary equilibria in quantitative-genetics model for frequency-independent traits occur at points where mean population fitness (\bar{w}) is locally maximized. However, mean population fitness is not necessarily maximized at the value of z that maximizes the individual fitness function, and thus optimality and quantitative genetic predictions of evolutionary equilibria may differ (Felsenstein 1979). For example, a one-dimensional individual fitness surface with two fitness peaks can generate an adaptive landscape (relating mean phenotype to mean fitness) with a single peak not located at either peak on the individual fitness surface (Felsenstein 1979; Kirkpatrick 1982).

Under what conditions do optimality and quantitative-genetic models predict different evolutionary outcomes? As discussed in detail by Gomulkiewicz (1998), there are three main issues. First, discontinuities in the individual fitness function, $w(z)$, can lead to different evolutionary predictions. For example, fitness functions involving thresholds (where $w(z)$ is discontinuous) may yield different evolutionary predictions for optimality and quantitative-genetic models.

Second, different evolutionary outcomes can occur when higher-order derivatives of the mean population fitness, \bar{w} , with respect to z cannot be neglected (specifically, when the Taylor series expansion of the mean population fitness, \bar{w} , at the equilibrium involves non-negligible higher-order derivatives). Two factors can contribute to the importance of such higher-order derivatives: the bumpiness of the individual fitness landscape, and the extent of phenotypic variation and covariation in the population. Phenotypic variation is important in this process because it determines the region of the fitness landscape that is "experienced" by the population. Bürger (1986) provides an analysis of the "corridor model" of evolution on a multi-peaked fitness landscape in which the higher-order terms are not negligible; in this model the phenotypes that maximize w are different from those that maximize \bar{w} in the absence of constraints.

Third, genetic constraints in the additive genetic variance-covariance matrix that are not apparent at the phenotypic level can cause optimality models and quantitative-genetic models to make different predictions. Often, phenotypic correlations provide an adequate estimate of the difficult-to-measure genetic correlations (Cheverud 1988); however, this is not always the case. Charlesworth (1990) showed that the phenotypic and genetic correlations of most quantitative traits may not have a simple relationship.

These considerations suggest that optimality predictions are most likely to diverge from predictions of quantitative-genetic models when fitness landscapes are bumpy, and when the magnitude of the phenotypic variances and covariances is large and not directly related to genetic variation and covariation. Yet most optimality models focus narrowly on the mean trait values and the location of peaks in the individual fitness function, thereby ignoring both the fitness landscape topography and patterns of phenotypic and genetic variation.

LOCAL VERSUS GLOBAL OPTIMALITY IN AN EMPIRICALLY DETERMINED ADAPTIVE LANDSCAPE

Deriving a fitness surface or adaptive landscape from a model shows a great deal about the nature of selection on the traits of interest. Testing adaptive hypotheses, however, requires data from natural populations. Few examples exist in which data on the frequency of phenotypes (or genotypes) and the fitnesses of individuals subject to natural selection are numerous enough to construct detailed adaptive landscapes. One of the best empirical examples of a landscape in terms of allele frequencies is the prevalence of the sickle-cell allele in West Africa (Cavalli-Sforza and Bodmer 1971). In this classic case of natural selection, the sickle-cell allele (the S allele) at the β -hemoglobin locus in humans confers resistance to malaria in the heterozygous state. When homozygous, this gene causes severe hemolytic anemia, usually leading to death before adulthood. Homozygotes for the predominant allele in all populations (the A allele) are free of the sickle-cell trait but are susceptible to malaria, so heterozygous carriers of the S allele have a selective advantage in areas where malaria is common. There is also a less-well-known third allele at this locus, dubbed the C allele. It confers resistance to malaria without the deleterious sickling of red blood cells but does so only in

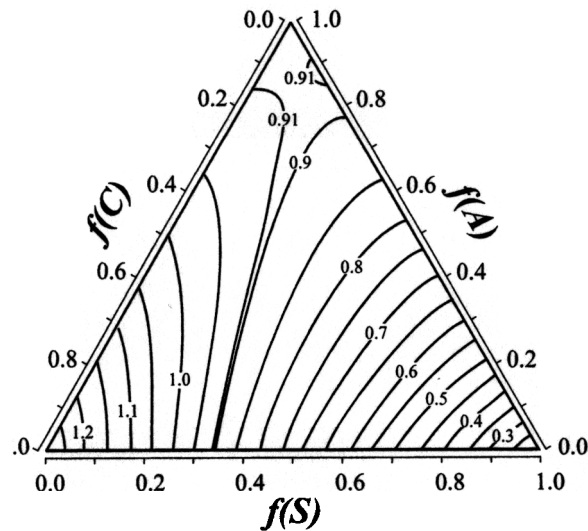


Figure 7.6. Fitness landscape for African human populations having various frequencies of the *S*, *A*, and *C* alleles of the sickle-cell locus. Most populations have allele frequencies that place them near the lower peak, located near the upper apex of the figure. The much higher peak, in the lower left, is essentially unoccupied because of the rareness of the *C* allele. After Templeton (1982).

the homozygous state. Individuals possessing the *CS* genotype have lower fitness than *AA* or *AS*, but higher than *SS*, genotypes.

Templeton (1982) used Cavalli-Sforza and Bodmer's (1971) estimates of fitness to show why the *C* allele remained rare in West Africa in spite of its adaptive advantage in the homozygous state. The adaptive landscape corresponding to the model is shown in Figure 7.6. Because the axes in this example are allele frequencies, the points on the landscape are populations. Most populations are at the lower peak, with $f(A) \approx 0.89$, $f(S) \approx 0.11$ and $f(C) \approx 0$, with a mean fitness of approximately 0.91. The much higher peak at the lower left, with populations fixed for the *C* allele, is essentially unoccupied by any natural population simply because the allele, and therefore the incidence of homozygotes, is rare and so its selective advantage is rarely expressed.

If one obtained the fitnesses of the various genotypes depicted in Figure 7.6 from an optimality model and knew nothing of the genetic constraints that confined populations to the lower optimum, one

might conclude wrongly that natural selection played little role within West African populations. However, any optimality model used in the testing of adaptation must also incorporate the relevant genetic, developmental, and functional constraints. As Templeton (1982) remarks, in reference to the sickle-cell example, "Thus, natural selection is *necessary* for adaptive evolution, but it is *not sufficient* to define an adaptive process, since other factors can and do influence the average excess (of fitness phenotypes). Thinking of adaptation only in terms of natural selection can be erroneous and misleading."

CONCLUSIONS: A TOPOGRAPHICAL PERSPECTIVE

The examples we've chosen show several pitfalls in potential studies of adaptation. In Roff's study, the empirically measured body size of *Drosophila melanogaster* coincides with a high point on the one-dimensional individual fitness surface. But if one examines variation in the growth exponent as well as size, that point turns out to be at a relatively low point along a ridge of high fitness. The question, then, is why the population's body size lies so far from the peak of high growth rate and large size (Figure 7.1) at the lower right. In this case, it may well be that *Drosophila* are physiologically unable to obtain such rapid growth rates, and hence a constraint must be incorporated into the model.

Gilchrist's work shows how a fitness landscape can be obtained for variable selection factors and illustrates how, for certain traits, the definition of fitness can greatly affect the topography of the landscape. Under some conditions, optimality models can be constructed that yield an optimal solution, but examination of the landscape topography reveals a large number of trait values that yield essentially equal fitness. An excellent empirical example of such a plateau of high fitness can be seen in Schluter and Nychka's (1994) paper on constructing empirical fitness surfaces; the survival probability of humans as a function of birth mass and gestation period forms a broad plateau (Figure 5 in Schluter and Nychka 1994). If the fitness surface contains a broad region of trait variation with statistically insignificant variation in fitness, what sort of quantitative test, matching phenotype to model optima, might one apply to populations falling on top of that plateau?

There have been few empirical attempts to uncover complex fitness surfaces (Schluter and Nychka 1994), but multi peaked

performance surfaces do emerge from physical models of complex interacting systems, such as Daniel et al.'s (1998) model of muscle mechanics at the cellular level. Complex surfaces also arise from traits that have nonlinear relationships with performance or fitness. And because the topographical relationship between individual fitness surfaces and adaptive landscapes – mean fitness in relation to mean phenotypes – is not simple, we are a long way from understanding how evolution might proceed on rugged adaptive landscapes for phenotypes.

Finally, the adaptive landscape of the alleles associated with the sickle-cell trait in West Africa show the importance of factors other than natural selection in determining the phenotypic or genotypic composition of the population. Natural selection is clearly responsible for maintaining the population at a local optimum, but another, higher fitness optimum is unattainable due to genetic constraints, even though the valley separating the two peaks is relatively shallow.

The graphical presentation of a fitness landscape conveys more information than a page of our hypothetical mountaineer's book of peaks. Knowing that the fitness surface is nearly a flat plateau instead of a towering Alp tells one more about the likelihood of finding a population perched atop its optimal point than even the most precise measurement of the altitude at that point. In this chapter, we have attempted to illustrate how fitness landscapes can be used to construct hypotheses about adaptation, and particularly how they can identify candidate systems for the application of more-rigorous testing.

The optimality of traits that form a flattened fitness surface, a ridge of high fitness values, or a rugged, multi-peaked surface may prove difficult to test by Orzack and Sober's (1994a) criteria. When a model yields a number of solutions of nearly identical fitness, it seems likely that correlated and random evolutionary forces on unmeasured traits will determine the position of a population on the fitness landscape. Yet even the simple case in which we observe concordance between a population's mean phenotype and a global peak on a fitness surface does not constitute a rigorous test of optimality. Manipulation of individual phenotypes or the distribution of phenotypes within the population of interest, followed by observation of the fitness consequences, always provides a more direct test. An optimality model can be used a priori to identify candidate traits or suites of traits for manipulation by examining the sensitivity of the fitness landscape to variation in those traits (Williams 1992; Lauder 1997).

Although it would be nice to have more tests of optimality (Orzack and Sober 1994b), the current shortage should not stop workers from studying adaptive processes. Indeed, we urge our mountaineer to keep writing, because a guidebook to the peaks of the world would be an interesting and important tool for anyone planning a future expedition. If our mountaineer were to include contour maps of the peaks, it would greatly increase the utility of the guide to other users. In the case of evolutionary biologists seeking systems to test adaptation, knowledge of the topography surrounding the adaptive peak would be essential in deciding whether such a test might have a reasonable chance of succeeding.

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