



The Adaptive Surface in Ecology

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MINI- REVIEW

Minireviews provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

The adaptive surface in ecology

Karen K. Fear and Trevor Price

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We review the adaptive surface as it applies to the kinds of continuously varying traits studied in ecology and behaviour. The adaptive surface is a plot of the mean fitness of a population against the mean phenotype, and can be used to predict directions of evolution. Under frequency-independent selection the mean phenotype of a population evolves to an equilibrium position near a peak in the adaptive surface. However, under other forms of selection, peaks in the adaptive surface often do not coincide with evolutionary equilibria. Even when selection does drive a population toward peaks, the peaks may bear little relationship to measures of population “fitness”, such as population size. Nevertheless the concept of an adaptive surface is heuristically useful because shifts between alternative locally stable states are likely to be a common mechanism of evolution. Furthermore, modelling peak shifts using the frequency-independent case indicates how easily different kinds of evolutionary transitions can occur. Theoretical models of peak shifts indicate that they most easily occur in response to the fluctuating selection pressures associated with environmental change, and are very unlikely to occur in response to genetic drift. Other mechanisms of peak shifts include environmental induction and mutations of large effect. The measurement of adaptive surfaces in nature is becoming increasingly common, although typically the individual fitness function rather than the true adaptive surface is measured, and frequency dependence is ignored. We suggest that more attention needs to be paid to the distinction between the individual fitness function, the adaptive surface, and the positions of evolutionary equilibria. If this is done, the value of the general concept will increase, and mechanisms of evolutionary transitions become further clarified.

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In 1932, Sewall Wright introduced diagrams of “adaptive surfaces” to illustrate his evolutionary theory. The diagrams plot some measure of a population’s fitness against gene frequency. Because the same level of fitness may be achieved by different combinations of genes, adaptive surfaces typically contain multiple

peaks of high fitness separated by valleys of low fitness. Wright (1932) showed that under some circumstances a population is expected to evolve close to a peak in the adaptive surface. Because the peak arrived at by the population may be one which has low fitness with respect to other peaks, the means by which populations

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cross valleys to new, possibly higher, peaks has been viewed as a critically important question in evolution (Wright 1932, Coyne et al. 1997).

Wright was originally concerned with genetic fine-tuning within one adaptive zone, without much phenotypic evolution (Wright 1959, Lande 1980). However, the concept of the adaptive landscape has since been expanded and used to envisage the relationship between distinct phenotypes. For example, in his discussion of the evolution of horses Simpson (1944) pointed to two discrete adaptive zones associated with browsing and grazing habits and suggested that intermediate forms might be at a selective disadvantage. Browsing and grazing represent peaks in the adaptive landscape, except here fitness is plotted against phenotype, rather than genotype, and peaks are treated as "ecologically possible phenotypes instead of local optima in gene frequency space" (Weber 1996). It is in this formulation that the adaptive surface is most useful when investigating the kind of continuously varying traits commonly measured in ecological studies, and it is this concept which we review.

Even with the focus of discussion restricted to ecological applications, the adaptive surface has been used in a variety of contexts: in heuristic descriptions, in empirical measurements of fitness, and in rigorous theoretical modeling. According to Provine (1986: 316), the "majority of evolutionary biologists have believed Wright's 1932 diagrams of the adaptive landscape to be the most heuristically valuable diagrams in all of evolutionary biology". To establish a framework for this review, we begin with a definition of the adaptive surface from theory and show how the adaptive surface relates to various measures of population and individual fitness. We then consider examples where the peaks and valleys in the adaptive surface do not correspond to directions of evolution and positions of equilibria. Despite its failure to predict evolutionary equilibria under many circumstances, the adaptive surface concept is valuable in both theoretical and empirical work because it can be used to explore the ease with which "peak shifts" between alternative adaptive zones, such as browsing and grazing, can occur. Past discussions of this process have been heavily influenced by Wright's views on the importance of genetic drift. In fact, genetic drift appears to be of minor importance (Coyne et al. 1997), and several other mechanisms have been relatively neglected. Finally, we consider the value of measuring adaptive surfaces in ecology.

Adaptive surfaces

Wright (1932) defined an adaptive surface for genotypes which relates some measure of the average fitness of an individual or population to its genotype or gene fre-

quency. Wright drew plots of both individual and mean fitness surfaces. The individual fitness surface describes individual fitness as a function of genotype. Individual fitness is typically used in one of two ways: the fitness of a single individual in a population, or the average fitness of all individuals of a given genotype (or phenotype). The latter definition is most commonly used, particularly in theoretical studies, and is the definition used to construct the individual fitness surface. Because genotypes are discrete entities, the individual fitness surface for genotypes is not continuous and therefore is not easily envisaged. Nonetheless, this definition is used in some theoretical applications (Gavrilets 1997).

The mean fitness of a population is calculated as the average fitness of all individuals in a population; this is equivalent to averaging the fitness of the genotypes, weighting each genotype by its frequency in the population. The adaptive surface describes the mean fitness of a population as a function of its gene frequency. Because gene frequency can vary continuously from 0 to 1, the adaptive surface is continuous and therefore easily envisaged. In practical situations, the measure of fitness used is invariably a component of total fitness, such as the number of eggs an individual lays, its survival over a specified time period, or the number of mates it obtains; occasionally a measure approximating total fitness (e.g. the product of survival and fecundity) is obtained. When defined with respect to total fitness, Wright showed that in the absence of frequency-dependent selection, populations come to equilibrium near peaks in this adaptive surface, although slight displacements from the peak are expected due to recurrent mutation and, with many loci, recombination (Coyne et al. 1997).

For continuously varying traits, such as body size, both the individual and mean fitness surfaces are plotted as a function of phenotype rather than genotype or gene frequency. Because the individual fitness surface is now defined relative to a continuous variable, it can be readily envisaged. The mean fitness surface describes the average fitness a population would have as its mean phenotype varies (Fig. 1) and is usually calculated by assuming that the distribution of phenotypes is normal and that the phenotypic variance remains constant as the mean phenotype changes. Because it is calculated by integrating over the individual fitness of all members of the population, the mean fitness surface is typically flatter than the individual fitness surface (Fig. 2). Lande (1976) quantitatively studied the mean fitness surface for phenotypes and showed that in the absence of frequency-dependent selection, the population evolves close to a maximum on this surface. Peaks and valleys in the individual and mean fitness surfaces need not coincide; for example, a few small individuals of very high fitness may have little influence on the course of evolution if, on average, larger individuals survive better than small ones (Fig. 1). Because of its relevance to

evolution, we refer to the mean fitness surface as the adaptive surface for phenotypes.

Mean fitness and population size

Evolution towards a peak in the mean fitness surface will not necessarily cause an increase in population size, and may even lead to a decrease (Wilson 1968, Prout 1980). For example, consider an adaptive surface describing average fecundity as a function of phenotype. As a population climbs a peak on this surface, the number of young produced will increase. However, if

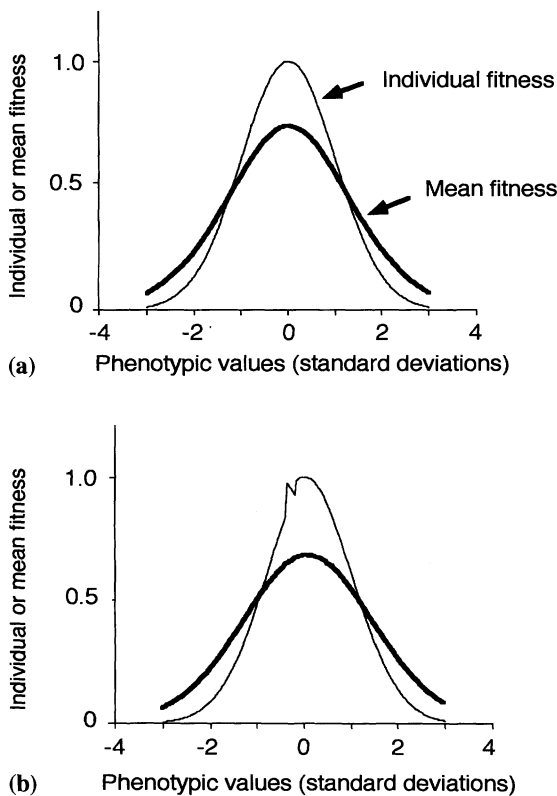


Fig. 1. An illustration of the relationship between the individual and mean fitness surfaces. a) The mean fitness surface (thick line) is flatter and broader than the individual surface (thin line). This is because mean fitness is calculated by integrating the individual fitness surface over the phenotype distribution. The mean fitness surface describes the average fitness of a hypothetical population varying in its mean phenotype, but with fixed phenotypic variance. The mean fitness surface in each figure was calculated assuming that the phenotypic distribution is normal with a variance, $\sigma_p^2 = 1.0$. The individual fitness function is Gaussian with parameters corresponding to a normal distribution with mean, $\theta = 0$ and variance, $\omega^2 = 1.0$. b) Discontinuities in the individual fitness surface (thin line) are smoothed out in the mean fitness surface. Peaks in the two surfaces need not coincide. The same phenotypic variance is assumed as in (a), and numerical integration was used to obtain the surface. The scale on the X-axis refers to phenotype (for the individual fitness function) or mean phenotype (for the mean fitness surface).

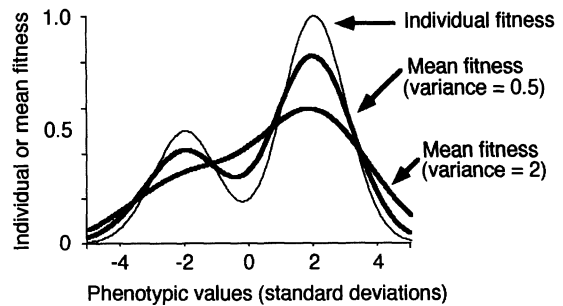


Fig. 2. An example of the effects of phenotypic variance on the adaptive surface when the individual fitness function is bimodal (thin line). The individual fitness function was generated by summing two Gaussian functions, each with a variance parameter, $\omega^2 = 1.0$, and means of -2 and $+2$. The left function was set to half the height of the right function. Two adaptive surfaces for this individual fitness function are shown, one where the phenotypic variance, $\sigma_p^2 = 0.5$ and the other where $\sigma_p^2 = 2$. Note that the adaptive surface is bimodal in the former case, and unimodal in the latter case. The scale on the X-axis refers to phenotype (for the individual fitness function) or mean phenotype (for the adaptive surface).

the population is subject to density-dependent mortality, the total number of young that survive to reproduce may actually decline, as a result of intraspecific competition between them.

Even if an adaptive surface represents the total lifetime fitness, there may be no increase in mean fitness (and hence population size) as a peak is climbed. This occurs if the population is evolving in a deteriorating environment (Fig. 3). Such deterioration can result from a change in either the abiotic or biotic environ-

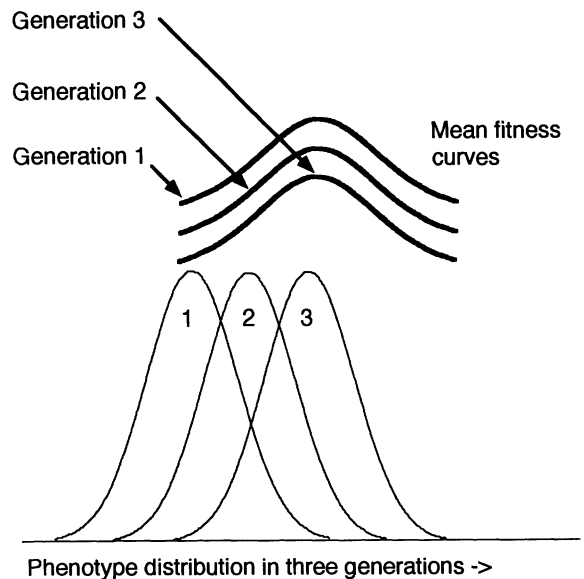


Fig. 3. In a deteriorating environment mean fitness may not increase even as a peak is climbed. Shown here is an example for three successive generations. Given the distribution of phenotypes in each generation (thin lines), and the depicted adaptive surfaces, the population mean fitness (indicated by an arrow for each generation) does not change.

ment. The biotic environment, including interspecific competition, provides particularly interesting examples of this phenomenon, because the deterioration is brought about as a direct result of the peak climbing process. For example, co-evolutionary arms races, such as between predators and their prey or parasites and their host, result in the deterioration in the environment of one species (e.g. a predator) as a consequence of counter adaptations in the species with which it interacts (Price 1972, van Valen 1973).

The adaptive surface as a guide to equilibria

In many biological situations, the mean phenotype of a population does not come to equilibrium at a peak in the adaptive surface. Mutation and recombination may result in small displacements from a peak (Coyne et al. 1997), but these may not be detectable in empirical studies of phenotypes. When dealing with fitness components, as empiricists usually are, trade-offs between different components will often cause a peak in the adaptive surface for one component of fitness to not coincide with a peak in the adaptive surface for total fitness; it is the latter which guides the direction of evolution. Large discrepancies between the average phenotype of the population and the position of a peak in the adaptive surface are usually attributed to such trade-offs (e.g. Armbruster 1990).

Even when the adaptive surface describes total fitness, selection often does not drive a population toward a maximum in the adaptive surface, but to some other equilibrium. In these cases mean fitness is not maximized; rather, the equilibria can lie on the sides of or even in valleys in the adaptive surface. We consider three mechanisms by which the mean phenotype of a population may be displaced from an adaptive peak.

1) Genetic constraints

It is possible that a lack of heritable variation in a trait will prevent its evolution, which could result in a substantial displacement from the peak. Although most traits seem to show some heritability, high negative genetic correlations between traits can prevent evolution to a peak in the fitness surface, because of an absence of heritability in some directions in multivariate space (Dickerson 1955, Kirkpatrick and Lofsvold 1992). A possible example of such a genetic constraint on evolution was demonstrated by Armbruster (1990), who found constraints between floral characters in *Dalechampia* blossoms which may render them unable to achieve the morphology which would maximize pollination efficiency.

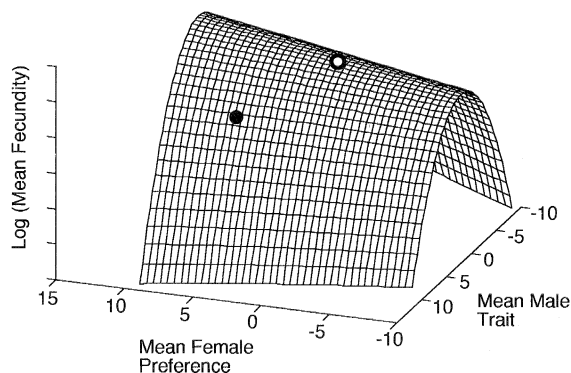


Fig. 4. When two traits, such as tail length and preference, are co-evolving in males and females of a species, mean fitness at evolutionary equilibrium may be significantly less than the mean fitness at an adaptive peak. This figure shows the mean fecundity surface for a male trait and female preference for that trait. The mean fecundity achieved in the absence of sexual selection (indicated by the open circle) is higher than the equilibrium mean fitness under sexual selection (indicated by the closed circle). For details, see text and Price et al. (1993a).

2) Co-evolution of the sexes

We noted previously that co-evolution between species may create a deteriorating environment and lower the mean fitness of the focal species. Similarly, because each sex is part of the biotic environment of the other sex (Rice 1996), adaptation in one sex can decrease the fitness of the other. This in turn can lead to a deterministic decline in the mean fitness of both sexes. An example comes from sexual selection theory (Price et al. 1993a). Suppose females use an indicator trait, such as tail length, to identify high condition males. Females who choose long-tailed males will have increased fecundity, perhaps because parasites are fewer in the longest-tailed males. Suppose further that males provide parental care in this species, an activity which is hampered by a long tail. Consequently, offspring survival is reduced. As a result of females choosing long tails, tail length evolves away from the fecundity optimum, and the average fecundity of the population declines (Fig. 4).

3) Frequency dependence

Under frequency-dependent selection, an individual's fitness depends on the phenotypes of the other members present in the population. The individual fitness surface is a function of both the phenotype of an individual and the mean phenotype of the population (recall that the phenotypic variance is assumed to be constant, so the phenotypic distribution is completely described by its mean). Therefore, the shape of the individual fitness surface changes as the mean phenotype changes. The mean fitness function is defined in exactly the same way

as in the frequency-independent case. Because the mean fitness of a population is calculated by integrating the individual fitness function *for that population* over its phenotypic distribution, there is still a single adaptive surface which can be drawn relating the mean phenotype of a population to its mean fitness, despite the fact that the shape of the individual fitness surface changes as the mean phenotype changes.

A simple example of frequency dependence is truncation selection, where a constant proportion of the population is culled across each of many generations. If the smallest 30% of individuals in a population are culled, then the fitness of an individual of a given size is dependent upon the frequency of smaller individuals in the population. In such a population, the mean fitness (average survival) would be constant at 0.7: the adaptive surface is a flat line, although evolution is proceeding. Under many forms of sexual selection the average mating success of males does not change as the male trait evolves: again the mean fitness surface is a flat line. Thus, when fitness is frequency dependent, the mean fitness surface will often not provide an accurate depiction of the selective forces to which a population is subject (Wright 1959).

Under frequency-dependent selection a population can evolve to a lower mean fitness (e.g. Wright 1959, Wilson and Turelli 1986, Creswell and Galen 1991). There are many examples of such a decline in game theory, such as in the hawk-dove game. In this game individuals adopt either a dove (non-fighting) or hawk (fighting) strategy (Maynard-Smith 1982). The mean fitness of a population comprised only of doves is higher than that of a population containing hawks because hawks expend energy fighting. However, a hawk mutation will invade and spread in a population of doves because the hawk strategy is favoured when it is at low frequency.

Frequency dependence arises in many situations, e.g. mimicry, sexual selection, predator-prey interactions, and intraspecific competition, and is perhaps present to some extent in all biological examples of selection. Taper and Case (1992) studied frequency-dependent intraspecific competition. Individuals were assumed to be competing for a resource which is normally distributed with respect to size. If larger individuals have a competitive advantage over smaller ones, e.g. because they are more aggressive, the population will evolve to a relatively large size and lie to the right of the peak in the resource distribution (Fig. 5). Although mean fitness depends on additional parameters not specified in the model, the results suggest that mean fitness may decline as evolution proceeds. For example, although larger animals have access to more of the resource distribution, they also require more resources simply to survive. For the same quantity of resources, there will be fewer surviving individuals if they are large than if they are small. Alternatively, the mere presence of large

individuals could inhibit the use of resources by smaller individuals, even if large individuals do not require more food for survival. In this case, some portion of the resource distribution goes un-utilized, resulting in lower mean fitness in the population.

The examples illustrate that the adaptive surface may not be a good guide to the positions of evolutionary equilibria. Equilibria reached under frequency-dependence have been termed 'selective' peaks by Wright (1959) to distinguish them from adaptive peaks. Selective peaks can bear little correspondence to peaks in the adaptive surface. In such situations numerical analysis will usually be needed to investigate a 'selective surface' describing 'selective peaks' and 'selective valleys' (stable and unstable equilibria), and the strength of selection away from such 'valleys' toward 'peaks' (Wright 1959). This perhaps explains why several of Wright's discussions were largely heuristic: he was attempting to draw selective surfaces, for which analytical formulae are often impossible to obtain. He has been criticized for depicting both individual and mean fitness surfaces, especially because a continuous individual fitness surface for genotypes does not exist. However, under frequency-dependent selection a peak in the individual fitness function, when measured at equilibrium, will correspond to the evolutionary equilibrium, whereas a peak in the mean fitness function need not. While the distinction between selective peaks and adaptive peaks has long been recognized (Dobzhansky 1968, Mourao and Ayala 1971), it has usually been ignored in recent

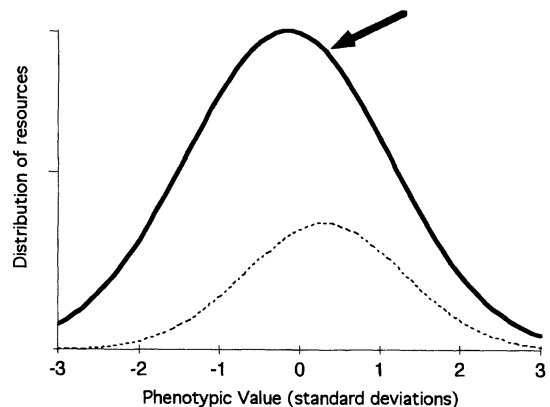


Fig. 5. Taper and Case (1992) showed that when there is asymmetric competition for resources, the population does not come to equilibrium under the peak of the resource curve. In their model, resources are distributed as a Gaussian function with standard deviation σ_k , and phenotypes are normally distributed (dashed line) with standard deviation σ_p . We illustrate their results with an example from Table 1 in Taper and Case (1992) where $\sigma_k = 1.6 \times \sigma_p$. Competition is asymmetric, with larger individuals having a greater impact on the growth rate of smaller individuals than the reverse. In this example, the competitive interaction between two individuals one standard deviation apart causes a 50% greater decrement to the growth rate of the smaller individual than to the growth rate of the large individual. The equilibrium mean body size is indicated by the arrow.

discussions, and theory has largely been confined to the frequency-independent case. While it is important that the theoretical implications of frequency dependence be investigated, it is likely that the mechanisms of peak shift which have been proposed are applicable whether or not there is frequency dependence (Coyne et al. 1997).

Peak shifts in continuously varying traits

Several mechanisms have been proposed by which a population's mean phenotype may shift from one adaptive peak to another. These mechanisms fall into three categories: 1) A change in the selective pressures causes a change in the shape of both the individual and the mean fitness surfaces. The population shifts deterministically to a new peak without crossing an adaptive valley. 2) A change in the phenotypic distribution of a population causes a change in the mean fitness surface (Fig. 2). If the valley between two peaks disappears, the population may shift from one peak to the other with no decrease in mean fitness, even though the individual fitness function remains bimodal. 3) A peak shift occurs which does not involve a change in either the mean fitness or individual fitness surfaces. Such a mechanism requires that the population moves against selection (e.g. by genetic drift) across a valley of reduced mean fitness in order to reach the new peak. Below, we discuss in more detail specific mechanisms underlying peak shifts.

1) Changing selection pressures

Changing selection pressure in response to a changing environment is widely viewed as the most common means of transition between alternative phenotypic states (Grant 1986, Milligan 1986, Price et al. 1993b). The change in selection pressures may be brought about through both temporal fluctuations and spatial variation, as when a population invades a new environment. As the selective pressures which a population faces change, so does the adaptive surface. Populations deterministically move under the force of natural selection to a peak in the new adaptive surface. This mechanism is one way by which species can evolve on so-called 'holey landscapes' (Gavrilets 1997). Here, transitions between two adaptive peaks in one location can be achieved in three steps: 1) invasion to a separate location, where there is an intermediate peak, 2) evolution to lie under that peak, and 3) subsequent reinvasion back into the original location, followed by capture by the peak.

2) Genetic drift

The most widely discussed mechanism of peak shifts is that of genetic drift. Random drift of the mean pheno-

type can result in the crossing of a shallow valley (Lande 1985), followed by deterministic evolution to a new peak. This mechanism forms a component of Wright's (1932) famous shifting balance theory of evolution, although he applied it primarily to genotypes. Wright viewed a species as being composed of many small, partially isolated demes, which increases the probability of a peak shift occurring somewhere within the species range. Once a peak shift has occurred in a deme, migration from that deme could lead to the same peak shift occurring throughout the species.

Genetic drift in small populations affects the phenotypic variance of a population as well as the mean phenotype. Sometimes the variance increases, which can cause a peak shift (Whitlock 1995). Increased phenotypic variation results in many individuals having high fitness by virtue of them lying under the second higher peak in the individual fitness function. Because the shape of the adaptive surface depends on the phenotype distribution in the population, increased phenotypic variation can obliterate the valley in the adaptive surface, causing deterministic evolution to the higher peak (Kirkpatrick 1982, Whitlock 1995) (Fig. 2). Whitlock (1995) argues that genetic drift is much more likely to result in a peak shift through an increase in the phenotypic variance of a population than through a change in the mean.

While peak shifts by genetic drift are possible, recent quantitative analyses indicate that for genetic drift to have an appreciable chance of producing a peak shift (by any mechanism), the strength of selection opposing the shift must be so weak that very small changes in the environment can easily produce the same peak shift (Lande 1985, Milligan 1986, Whitlock 1997). Since environmental fluctuation is inevitable, a role for genetic drift is largely ruled out. This conclusion is supported by a review of the empirical evidence by Coyne et al. (1997).

3) Environmental induction

Both the mean phenotype and its variance in a population can be affected by direct influences of the environment on development, again resulting in peak shifts. We first present an example of how a peak shift may be facilitated by an environmentally induced change in the mean phenotype. Waddington (1959) showed that exposure to high levels of salt increased the surface area of the anal papillae in *Drosophila melanogaster* as a phenotypically plastic response. Individuals with greater surface area are better able to deal with high concentrations of salt (te Velde et al. 1988) and are favoured in the high salinity environment. After 21 generations of exposure to salt, Waddington (1959) found that the area of the anal papillae had increased beyond the original plastic response, indicating an evolutionary response to high salt concentration (for a similar example of genetic change preceded by environmental induction in

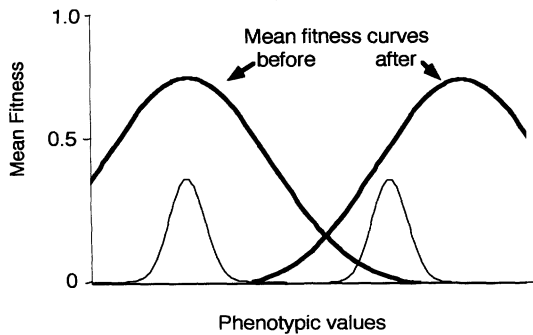


Fig. 6. A change in the environment can induce a change in the mean phenotype, through its effects on development, as well as altering the adaptive surface (thick curves). The phenotypic distributions before and immediately after the environmental change are illustrated by the thin curves. In the example illustrated, without the environmental induction, the population would go extinct. Instead, adaptation to the new peak will occur.

Drosophila see Partridge et al. 1994). In this case, an environmental change is having the dual effect of inducing the expression of a new phenotype, thereby changing the phenotypic mean of a population, and altering the selective pressures to which the population responds (Fig. 6). The peak shift itself is caused by changing selection pressures. However, in the absence of a phenotypically plastic shift in the mean, the fitness of all individuals in the population may be so low following the environmental change that the population goes extinct rather than evolving to the new peak (Fig. 6).

Environmental influences on development can also induce peak shifts when there is no change in the adaptive surface. An example was investigated by Waddington (1953). In one experiment, when pupae of *Drosophila melanogaster* were exposed to heat shock, some individuals expressed a phenotype known as cross-veinless (*cvl*). Waddington applied artificial selection favouring the *cvl* phenotype and found that after 14 generations, the phenotype appeared in some individuals even in the absence of heat shock, indicating that the *cvl* phenotype had been genetically assimilated. This example differs from the previous example in that the environmental change (heat shock) which induced the expression of the new phenotype did not impose the selective pressure which favoured the new phenotype. Thus, the selective advantage of the *cvl* phenotype could have been present even before the appearance of the phenotype itself. In general, environmental induction can cause both a shift in the mean phenotype, which can bring a population into the domain of attraction of a new peak, and a change in the phenotypic variance of the population, which may result in the loss of an adaptive valley on the mean fitness surface (Fig. 2).

4) Macromutation

A final way by which peak shifts can be brought about is through mutation. Petry (1982) has shown that large mutations, or macromutations, can induce peak shifts by allowing populations to evolve in directions on the adaptive surface which were previously unavailable to them. For example, in the evolution of mimicry, a large mutation which causes a mimic to roughly resemble the model creates the conditions under which modifier loci can refine the phenotype to perfect the mimicry (Turner 1988).

Empirical studies of adaptive surfaces

It is clearly important to obtain more measures of adaptive surfaces in nature in order to understand how peak shifts may be brought about. There are various methods for estimating adaptive surfaces (Lande and Arnold 1983, Schluter and Grant 1984, Kingsolver 1988, Schluter 1988, Armbruster 1990). No method measures the adaptive surface as we have defined it, but some come close. The most common method is to directly measure individual fitnesses in nature, and to estimate the individual fitness surface using various curve-fitting techniques (Lande and Arnold 1983, Schluter 1988, Armbruster 1990, Smith 1990, Brodie et al. 1995). A shortcoming of this method is that if there is frequency dependence, the individual surface will change if the distribution of phenotypes changes (Creswell and Galen 1991). A measure of the individual fitness surface can also be obtained by investigating the functional utility of a trait through experiments on individuals with different phenotypes (Kingsolver 1988, Benkman 1993). Here there is no interaction among individuals, and frequency dependence is ignored (though not corrected for).

These methods estimate an individual fitness surface, which will agree with the mean fitness surface only if population variation is small relative to variation in the environment. Therefore, lack of agreement between the observed and predicted positions of mean phenotypes may reflect a failure of the peak in the individual fitness surface to reflect itself as a peak in the mean fitness surface (Fig. 1), or unaccounted for frequency dependence. However, the experimental methods do have the advantage of estimating fitness for portions of the phenotypic space not currently occupied by a population. The idea that the individual and mean fitness surfaces exist independent of organisms was first formalized by Burger (1986). When extrapolated to phenotypes not present in the population, the fitness surface provides a complete description of the selection pressures affecting a trait (Schluter 1988), and can be used to test hypotheses regarding optimality and the functional utility of a trait (Kingsolver 1988, Schluter 1988,

Armbruster 1990). This approach is particularly powerful when the predicted adaptive surface is tested using data independent of those used to generate the surface. Large disagreements can be used to refine adaptive hypotheses. For example, Armbruster (1990) suggests that the large difference between observed mean and predicted optimal flower structure for a component of fitness associated with pollination efficiency reflects trade-offs with other components of fitness.

An alternative way to estimate adaptive surfaces is to measure population size as a function of resource base and mean phenotype, an approach which has been used in Darwin's finches (Schluter and Grant 1984). While population size is often not clearly related to mean fitness, in this particular example it is thought that population size is highly correlated with probability of survival, and thus provides an adequate measure of mean survival as a function of mean phenotype. This study represents the closest measure yet obtained of a true adaptive surface in nature.

Conclusions

The concept of the adaptive surface has been used widely as a heuristic tool in many studies in evolution, behaviour, and ecology. Species occupy discrete areas of phenotypic space. Consideration of these discrete positions as adaptive peaks focuses discussion on the evolutionary mechanisms maintaining stasis and promoting transitions. We are now in a position to be able to partition the relative roles of different processes. Both theory and empirical results imply that perhaps too much attention has been paid to genetic drift, and too little to environmental induction.

We suggest that the relationship among 1) the position of peaks in the adaptive surface, 2) the position of peaks in the individual fitness function, 3) peaks in maximum population size, and 4) positions of equilibria should be carefully considered in future studies. Associations among these four variables will help us to understand potential roles of frequency and density dependence in affecting evolution. It should be possible to assess the extent to which at least some of these values coincide, based on measurements frequently collected in empirical studies. The empirical estimation of fitness surfaces in nature will also help determine the extent to which adaptive topographies are rugged or smooth, and will allow more rigorous tests of optimality, although the role of frequency dependence and the relationship of the estimated surface to the 'adaptive surface' needs elaboration. Provided attention is paid to such details we suggest that the adaptive surface diagrams will continue to be valuable in evolution, behaviour and ecology.

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