

Intra- and Interspecific Relationships between Morphology, Performance, and Fitness

S.B. Emerson¹ and S.J. Arnold^{2,3}

¹*Department of Biology
University of Utah
Salt Lake City, UT 84112, U.S.A.*

²*Department of Ecology and Evolution
University of Chicago
Chicago, IL 60637, U.S.A*

Abstract. Intra- and interspecific studies of morphology and performance provide different information about selection. In combination, the two kinds of studies can be used to address an additional set of issues. Intraspecific study of the association between morphology and performance can help characterize the selection that acts within populations. Interspecific studies of morphology and performance could be used to resolve components of species selection. Theoretical studies indicate that traits experiencing correlational selection within populations will tend to show interspecific correlation. This prediction could be tested by combining intra- and interspecific studies of morphology and performance. By combining such studies with phylogenetic and genetic analyses, one would test for an additional determinant of interspecific correlation, namely interspecific covariance in directional selection.

INTRODUCTION

Integration, as a fundamental property of complex systems, has many meanings. For Riedl (1978) it signifies the degree of tolerance which must not be exceeded in a particular functional connection or the direction and importance of functional connections. For Olson and Miller (1958) morphological integration "refers to the summation of the totality of characters which, in their interdependency of form, produce an organism." The basic evolutionary prediction arising from these perspectives is that selection for interdependence may cause the pattern of connections to evolve so that it comes to resemble the functional interdependencies (Olson and

³Order of authorship is arbitrary.

Miller 1958; Riedl 1978; Cheverud 1982). Thus, phenotypic and, especially, genetic correlation between two traits may reflect a history of selection for functional interaction. Several workers have measured the degree of morphological integration by assessing phenotypic and genetic correlations. For example, are functionally interacting parts of the vertebrate cranium or mandible more highly correlated than parts that are not so functionally interdependent (Bailey 1956; Leamy 1977; Atchley et al. 1981; Cheverud 1982)? We also take a biometrical approach to integration, but we propose directly to measure the consequences of integration by assessing whole organism performance. By measuring performance one could directly test the proposition that functional interdependencies have promoted the evolution of integration.

By performance we mean measures of whole organism capacity at specific tasks (e.g., jumping ability in frogs, maximum swimming speed in fish, running stamina in lizards). In the most insightful studies of performance, tasks are chosen that represent actual challenges faced by the organism in its natural world (e.g., Wainwright 1987). Thus speed in the one-meter dash is an ecologically relevant performance task for garter snakes (*Thamnophis*) because these animals commonly bask within one meter of a retreat site (e.g., bramble thicket, rock pile) in order to elude such predators as raptorial birds (Arnold and Bennett 1988). Perhaps the primary goal in studying performance is to understand how particular traits interact with each other and with the environment to affect fitness. The toe pads of arboreal frogs, for example, are likely to influence fitness via effects on clinging ability. Clinging ability will determine where a frog may rest during the day and where it may deposit its eggs. Consequently, the capacity of cling to smooth objects (such as leaves) represents a natural currency for evaluating the consequences of differences in size and configuration of toe pads (Emerson and Diehl 1980).

What would be the potential benefits of studying morphology and performance at both the intra- and interspecific levels? While some progress has been made in relating the study of variation in intraspecific performance to microevolutionary theory (Arnold 1983; Bennett 1987), the theoretical significance of species differences in performance is less clear. Despite this estrangement from microevolutionary theory, interspecific studies of covariation in morphology have a long history (e.g., large literatures on allometry and functional morphology) and interspecific studies of performance are beginning to expand. The identification of the need for a theoretical grounding for morphology-performance studies is perhaps the main contribution of this paper. We believe that we have also made some progress in sketching connections to formal evolutionary theory, but more work needs to be done.

In the sections that follow we give examples of various studies of morphology, performance, and fitness and discuss the evolutionary insights that they provide. We begin with the simplest study of performance, conducted in a single population, and work up to more complicated studies that examine morphology, performance, and fitness in numerous populations and species, perhaps including genetical analyses. We do not claim that only these more complicated research endeavors have legitimacy or that they should be the goal of every researcher, for clearly such studies will be impractical with most taxa. Nevertheless, by carefully considering what information and inferences may be gained at each step in our research continuum, the potentials and limitations of each kind of study become more obvious. By contemplating the impossible, we can put our current endeavors in perspective.

We use "morphology" as a shorthand for behavioral, physiological, and structural attributes. By "fitness" within populations we mean the number of progeny (zygotes) produced by an individual during its lifetime in a population of constant size (or a progeny number corrected for the rate of population growth in a nonstationary population). This definition of fitness is the one that has proved to be of greatest utility in population genetics (Crow and Kimura 1970; Charlesworth 1980; Lande 1982). One could define fitness as "the number of surviving offspring" in the discussions that follow. Most of the topographic arguments would still apply but connections to formal theory for genetic change would be more difficult. We consider only two levels of analysis (intrapopulation and interspecific), but obviously our discussion could be extended to multiple levels. To keep the discussion simple we have skipped over the issues of interdemic and geographic variation within species. Accordingly, we will use "population" and "species" interchangeably.

PERFORMANCE

A main idea in devising a measure of performance is to choose a variable that represents a major pathway between the traits of interest and fitness (Arnold 1983). A successful measure of performance is one that accounts for much of the correlation between the traits and fitness. Clinging ability might represent such a critical performance variable for toe pad size in treefrogs. By phrasing the problem in statistical terms, we can test the validity of our proposition using the variation in morphology and performance that prevails within a natural population. Our proposition has two parts: the hypothesis that morphology affects performance and the hypothesis that performance affects fitness. Using standard statistical theory, we can show that the two effects can be conveniently evaluated by computing partial

regression coefficients. Thus the *performance gradient* is the effect of a particular morphological trait on performance (holding other traits constant), while the *fitness gradient* for a particular performance is the effect of that performance variable on fitness (holding other performances and morphologies constant). We can view natural selection on a trait as the partial regression of fitness on that trait holding other traits constant (Lande and Arnold 1983). From this perspective, selection on a trait is the product of a set of performance gradients and a set of fitness gradients. These two sets of gradients represent two parts of the path from the trait to fitness. By adding performance as an intervening step, we can test specific hypotheses about how morphology affects fitness.

The investigator need not pretend that performance is fitness, for clearly it is not. The performance gradient cannot measure and is not intended to measure the total selection that acts on a trait. To accomplish that goal one must measure the effects of performance on fitness or the effects of the trait on fitness. Nevertheless, the performance gradient does measure a part of selection and consequently its estimation is a legitimate undertaking for the student of selection.

The study of performance is an adjunct to other approaches to understanding adaptation. Biomechanical analysis (Alexander 1972; Gans 1974), optimal design models (Dullemeijer 1974) and morphology-environment correlation (e.g., Mares 1976) can provide insights about adaptation complementary to those deduced by studying performance (see Arnold 1988a). Furthermore, biomechanical or physical models can be used to identify traits that are likely to influence a particular kind of performance and to make a priori predictions about the relative magnitude of effects.

Performance has most commonly been studied within populations or among species but not simultaneously at both levels. Yet, the notion that the interspecific relationship between morphology and performance is the same as the intraspecific relationship is implicit in most higher level studies (e.g., 1980 American Society of Zoologist symposium on Adaptation). In the next few sections we critically examine this proposition.

INTRASPECIFIC STUDIES OF MORPHOLOGY AND PERFORMANCE

Two kinds of studies have been undertaken. In *cross-sectional studies*, measurements are made on animals of diverse size and unknown age. In *cohort studies*, measurements are made on animals of the same age. Cohort studies have the advantage that the results can be related to microevolutionary theory with fewer assumptions. Cross-sectional studies have the advantage that the scaling of performance with size may be easier to detect and measure because a greater size range of animals is tested.

In cross-sectional studies the relationship between morphology and performance can be estimated using residual values from the statistical regression of the trait on body size. For example, Garland (1985) studied the effect of relative limb proportions on locomotion performance in the agamid lizard *Amphibolurus nuchalis*. Using a sample of 68 lizards, ranging from small juveniles to large adults, Garland measured limb and body proportions and scored running performance. Not surprisingly, larger lizards ran faster, so Garland computed the statistical relation (regression slope and intercept) of morphology and performance to size. Using residual values from those regressions, Garland then computed performance gradients for the various limb dimensions. The key assumptions in equating such results to performance gradients for like-aged animals are: (a) that the performance gradient is the same at all ages and (b) that viability selection does not change the relationship between morphology and performance. Neither of these assumptions must be made in cohort studies.

The results of a cohort study can be directly related to the selection that acts on individuals at a particular age. For example, Arnold and Bennett (1988) studied the effects of vertebral numbers on locomotion performance using a sample of 174 newborn garter snakes (*Thamnophis radix*). They found that the numbers of vertebrae in the body and tail had an interactive effect on speed in the one-meter dash. The optimal number of tail vertebrae was an increasing function of the number of body vertebrae. This interactive effect constitutes part of the selection that acts on newborn garter snakes. To evaluate how important that selection is, we would need to estimate the effect of burst speed on the survivorship of newborn snakes. B. Jayne and A. Bennett currently are conducting such a study using a related species, *T. sirtalis*. Jayne and Bennett (personal communication) measured the burst speeds of two cohorts of newborn snakes, individually marked all the animals and then released them in their natal population. By repeatedly sampling this population for recaptures, they hope to relate burst speed to survivorship and growth rate in the field.

The performance gradients can be visualized as a surface (Fig. 1). With data on both morphology and performance for a series of animals, we can compute a multiple regression equation that relates morphology to performance. In the garter snake example, Arnold and Bennett (1988) computed the relationship of burst speed to five morphological variables: number of body vertebrae, number of tail vertebrae, squared number of body vertebrae, squared number of tail vertebrae, and the product of numbers of body and tail vertebrae. The multiple regression procedure estimates a coefficient (slope) for each of these five variables. The variables were chosen so that their coefficients would describe different aspects of the surface that relates performance to morphology. The coefficients for the numbers of body and tail vertebrae (the linear coefficients or so-called *directional performance gradients*) measure the overall effect of vertebral

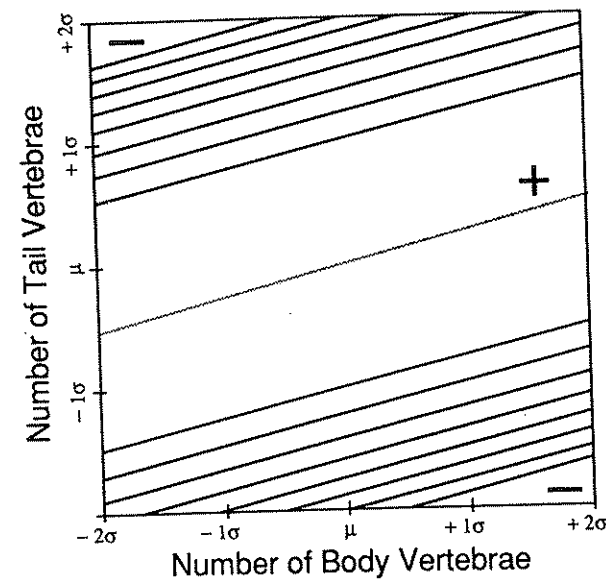


Fig. 1—A locomotion performance surface for the garter snake *Thamnophis radix*. Contours of burst speed are shown as a function of the numbers of body and tail vertebrae (Arnold and Bennett 1988).

directional performance gradients) measure the overall effect of vertebral counts on speed. These coefficients test for a linear effect of morphology on performance and therefore tell us whether the performance surface has an overall upward or downward inclination. The directional performance gradients were not demonstrably different from zero in the garter snake case. The coefficients for the squared and product variables (the quadratic coefficients or so-called *stabilizing and correlational performance gradients*) tell us about the curvature of the performance surface and its orientation. Negative stabilizing gradients (i.e., coefficients for squared variables) indicate downward curvature; positive coefficients are indicators of upward curvature. Correlational selection gradients test for interactive character effects on performance. A positive correlational performance gradient (i.e., the coefficient for the product term) indicates an upward inclination of the main axis of the surface (e.g., Fig. 1), while a negative coefficient indicates a downward inclination of the main axis. Phillips and Arnold (1988) discuss other aspects of graphical interpretation of the gradients. Thus, the visualization of the performance gradients as a surface gives a compact summary of the numerous coefficients that describe the relationship between morphology and performance.

In the same way as there is a performance surface, we can also construct a "selection surface." Under some circumstances the performance surface for a set of morphologies may closely resemble the selection surface for those traits. The selection surface is a graph of relative lifetime fitness (standardized to a mean of one) as a function of morphology. The selection surface summarizes the selective forces that affect the evolution of the traits. If the relationship between performance and fitness is linear (i.e., no curvature of fitness gradient) then the performance surface will generally be shaped like the selection surface but with more exaggerated curvature. If the relationship between performance and fitness is curvilinear, however, there may be little resemblance between the performance and selection surfaces. Thus, elucidation of modes of selection on performance is crucial to making evolutionary predictions from the performance surface.

The selection surface is closely related to, but not identical with, the adaptive landscape for a set of traits. The selection surface relates individual lifetime fitness to individual values of phenotypic traits. The adaptive landscape graphs mean fitness in the population as a function of gene frequencies (Wright 1932) or as a function of mean phenotypic values for a set of traits (Lande 1979). The selection surface and corresponding adaptive landscape for a set of phenotypic traits will be roughly similar in shape but their curvatures may differ (Phillips and Arnold 1989). The main use of the adaptive landscape (in conjunction with genetic parameters) is to predict evolutionary trajectories. Populations tend to evolve uphill on the adaptive landscape (Wright 1932; Lande 1979). The main use of the selection surface is to depict the forces of directional, stabilizing, and correlational selection that act on the population.

INTERSPECIFIC STUDIES OF MORPHOLOGY AND PERFORMANCE

Interspecific studies of morphology are much more common than studies of performance, partly because the former includes a large literature on allometry. Interspecific studies that combine measurements of morphology and performance are rarer still and fall into three general categories: (a) those that measure performance as a reproductive variable such as egg or clutch size (e.g., Dunham et al. 1988; Wilbur and Morin 1988), (b) those that measure performance as a qualitative variable such as microhabitat choice or food preference (e.g., Alberch 1981; Jaksic et al. 1980; Liem 1980), (c) those that study the scaling relationship between performance and body size (e.g., Wainwright 1987; Garland 1983; Hespeneide 1971; Toft 1980). Of most interest to us is a fourth, more specialized group—those studies that quantitatively compare performance with morphology independent of the confounding effects of body size scaling (e.g., Andrews

et al. 1987; Huey and Bennett 1987; Miles 1987; Emerson 1978, 1985; Emerson and Diehl 1980). In such studies, problems of allometry are circumvented by using residuals from a regression of performance on body size or by restricting comparisons to similar-sized species.

So far such interspecific studies are uncommon; however, since we wish to consider the implications of interspecific data, let us suppose that morphology and performance have been measured in an extremely large sample of species so that the surface relating average performance to average morphology can be accurately estimated. What issues could be addressed with such extensive data? They could be used to make inferences about the selection that acts within populations if there was a close resemblance between the intra- and interspecific performance or selection surfaces. Although this resemblance is sometimes implicitly assumed, of course it cannot be evaluated unless one has both intra- and interspecific data (see next section). Such resemblance might be expected when the same biomechanical principles dictate the form of the performance surface at both levels. Currently, however, there are no strong theoretical grounds for expecting similar performance topographies at the intra- and interspecific levels and there has been virtually no empirical exploration. Another significance of interspecific data relates to selection occurring above the species level.

Interspecific data on morphology and performance can provide tests for species selection. To see two possible connections, we return to the prospect of having morphology and performance data for many species. For each species we have evaluated both the morphology and the performance of each individual in a reasonably large sample. For the first connection, we could compute performance surfaces (using formulas given by Arnold 1983; Lande and Arnold 1983) for each species and determine whether the different species lie on the same surface. If they do lie on the same surface, there is no basis for invoking species selection (Arnold and Fristrup 1982; Heisler and Damuth 1987). For the second connection to species selection, we imagine that we also have data on species-level fitness (e.g., evolutionary persistence or number of descendant species) for each species. Those data might be extremely difficult to obtain for the same set of species that yielded data on morphology and performance. Let us ignore such difficulty and imagine that we have all three kinds of data so that we can see the conceptual consequences. Using the species fitness and average performance data, we could compute a species fitness gradient (analogous to the within population fitness gradient) that would describe the relationship between average performance and species fitness. Those coefficients would tell us whether our measures of performance have any relevance to the persistence or proliferation of species. With species fitness data in hand, we could also bypass performance and compute species selection gradients for our average

morphologies. Those gradients could be used to test hypotheses about species selection on morphology (i.e., to test whether morphological differences between species are associated with differences in persistence and speciation, etc.).

The gradients just described do not satisfy everyone's concept of species selection (see Arnold et al., this volume, for a brief review of some of the controversies). In particular, some authors would require that species performance and morphology be emergent properties rather than simple averages (e.g., Vrba 1984).

COMBINED INTRA- AND INTERSPECIFIC STUDIES OF MORPHOLOGY AND PERFORMANCE

Nearly all studies that have examined covariation at two or more levels have focused only on morphology and not on performance. The available studies are of two kinds: comparisons of trait variances within and among populations and allometric studies conducted at different taxonomic levels. Variance studies have been aimed at evaluating the generality of Kluge and Kerfoot's (1973) observation that traits that are variable within populations are also prone to interpopulation differentiation. The proposition remains controversial because the intra-interpopulation association may arise as a scaling artifact (Sokal 1976, 1978; Johnson and Mickevich 1977; Pierce and Mitton 1979; Baker 1980; Atchley et al. 1982; Rohlf et al. 1983). As Zeng (1988) points out, such problems do not plague the observation that high intrapopulation correlations are associated with high interpopulation correlations in data sets for aphids and ticks (Sokal 1962; Thomas 1968; Sokal et al. 1980; Sokal and Riska 1981). However, in those data sets there is no intra-interpopulation association for traits with low or moderate intrapopulation correlations. In the literature devoted to size-scaling, interspecific allometric slopes are generally higher than intraspecific slopes (reviewed by Lande 1979).

Until recently there was little theoretical impetus to compare variation and covariation at different taxonomic levels. In the last ten years, however, evolutionary models based on quantitative genetics (the inheritance of traits affected by many genes) have provided a series of predictions (e.g., Lande 1979, 1986; Burger 1986; Felsenstein 1979, 1988; Kirkpatrick 1982; Wagner 1988; Zeng 1988). These models focus attention on crucial elements of selection and inheritance that have not been addressed in the literature devoted to allometry and the Kluge-Kerfoot phenomenon. At least some of the key new issues can be approached by combining intra- and interspecific studies of performance. One general point is that interspecific correlation can arise in many ways. Thus an observation of allometry or interspecific correlation provides very little information about underlying processes.

Theoretical investigations may be roughly grouped into three kinds according to whether they assume (a) selectively neutral traits, (b) selection acting on only one of two traits, or (c) selection acting on each of two or more traits. Models of the first two types give similar results. When two traits differentiate because they are selectively neutral and are buffeted by random genetic drift (Fig. 2) or because a selectively neutral trait evolves in response to directional selection acting on another, genetically correlated trait (Fig. 3), differentiated populations will be arrayed with a slope determined by the genetic covariance that prevails within populations (Reeve 1950; Lande 1979). The third case, in which selection acts on both traits is examined in detail below. It is potentially more interesting but also less susceptible to simple generalizations. The main point arising from such bivariate selection models is that correlational selection within populations and among-population correlations in directional selection play crucial roles in predicting the pattern of intra-interspecific association. Because these selection patterns have analogues in performance relations, elements in these models can be partially assayed by morphology-performance studies.

Zeng (1988) models a case in which populations evolve toward a dome-shaped adaptive peak. He investigates the differentiation that will arise among populations that have the same inheritance system (identical genetic variances and covariances) and experience the same pattern of stabilizing (nonlinear) selection but are exposed to different patterns of directional selection. The crucial variables that predict the magnitude of interspecific

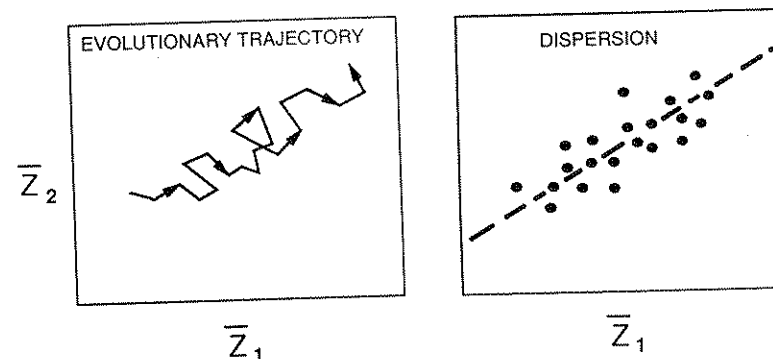


Fig. 2—Differentiation of selectively neutral traits that are genetically coupled. The two axes are the population means of the two traits, \bar{z}_1 and \bar{z}_2 . Left: The path of a population evolving by random genetic drift. The path tends to show a nonrandom upward orientation because of a positive genetic correlation between the two traits. Right: Bivariate dispersion of populations or species descended from a single common ancestor. The populations are arrayed along a genetic regression (dashed line) which could be estimated by computing the best fit line for a plot of offspring averages for trait \bar{z}_2 against their parent's average for trait \bar{z}_1 within a representative population.

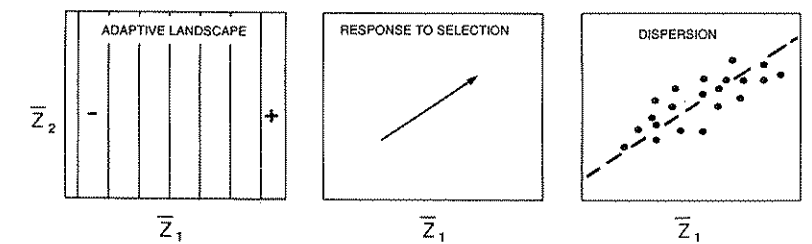


Fig. 3—Differentiation of a trait, \bar{z}_1 , under directional selection and of a selectively neutral but genetically correlated trait, \bar{z}_2 . Left: The adaptive landscape for the two traits. Mean relative population fitness is plotted as a function of the population means for the two traits. The landscape is a plane that rises with increasing value of the average of the trait \bar{z}_1 . Middle: The expected evolutionary path or trajectory of a population evolving on the landscape shown in Fig. 3 left. The population evolves upward, rather than simply to the right, because of a positive genetic correlation between the two traits. Right: Bivariate dispersion of descendant populations. The genetic regression (ratio of genetic covariance to genetic standard deviation of trait \bar{z}_1) is shown as a dashed line.

correlation are: (a) the strengths of stabilizing and correlational selection within populations and (b) the magnitudes of interspecific variance and covariance in directional selection. Correlational selection is selection on character combinations that has the effect of changing trait covariance, Arnold (1986b). Thus, the set of characteristics most conducive to the evolution of a high interspecific correlation between two traits are weak stabilizing selection on each of the traits but strong correlational selection, as well as large interspecific variance and covariance in directional selection. Furthermore, interspecific correlation is promoted if correlational and interspecific covariance in directional selection have the same sign (Fig. 4, top). Conversely, strong stabilizing selection with no correlational selection inhibits interspecific correlation, as does a random pattern of interspecific differences in directional selection (Fig. 4, bottom). Felsenstein (1988) discusses two related models in which covariance in directional selection also plays an important role.

A slightly different cast of variables affects the evolution of interspecific correlation when directional but no stabilizing selection prevails (Zeng 1988). This case might correspond to the selection that acts on certain performance traits (e.g., overall athletic ability) for which there is no intermediate optimum. In this case, as before, large interspecific variance and covariance in directional selection promote interspecific correlation. The other facilitating factors are large genetic variance for each trait and a high genetic covariance between them which has the same sign as the interspecific covariance in directional selection. These genetic factors also promote divergence in the

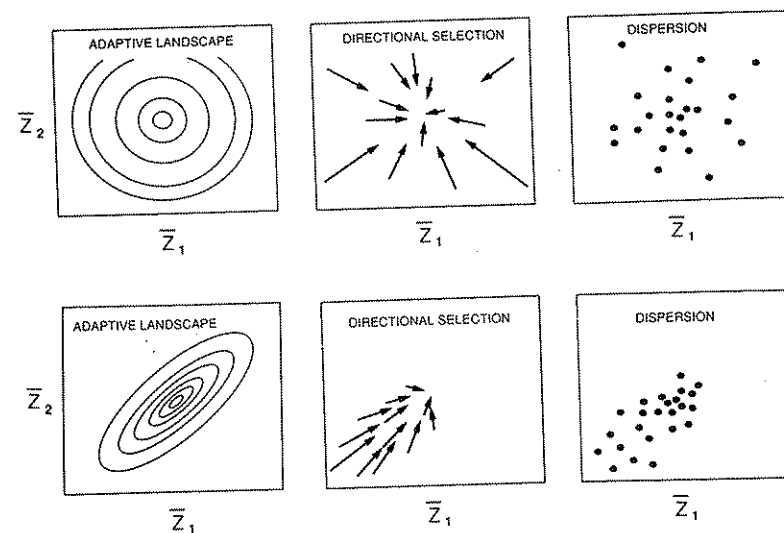


Fig. 4—Differentiation in response to stabilizing and directional selection, using simplified versions of Zeng's (1988) arguments. Adaptive landscapes are shown on the left and patterns of interspecific dispersion are shown on the right. The arrows in the middle panels denote the direction and magnitude of directional selection acting on the two traits in each population. Above: In the worse case for interspecific correlation (right), populations experience bivariate stabilizing selection with no correlational selection (left), and there is no interpopulation covariance in directional selection (middle). Below: In the best case for interspecific correlation (e.g., positive correlation among population means, shown at right), populations experience strong correlational selection (shown as the inclined ridge-like shape of the adaptive landscape). Directional selection (indicated by the arrows in the middle panel) has the same interpopulation pattern as the correlational selection acting within populations.

model with stabilizing selection, but their contributions last only in the short term and do not affect the final evolutionary outcome.

Ridge-shaped adaptive landscapes (Fig. 5) can also produce interspecific correlation. Burger (1986) and Wagner (1988) have investigated corridor models of phenotypic evolution in which there is a ridge on the adaptive landscape. Such ridges are a manifestation of correlational selection. Populations or species tend to evolve upward towards the ridgecrest, resulting in interspecific dispersion along the ridge and hence in interspecific correlation. If the ridge is level (Fig. 5, left), there is no selective force to move populations along the ridge, but they might move along it by random drift or by an interaction of drift and selection (e.g., see Lande 1981 for an analogous case). Ascending ridges are of two main types. If the flanks of the ridge have the same steepness everywhere along the ridge (Fig. 5, middle), populations will tend to move up the ridge at a constant rate

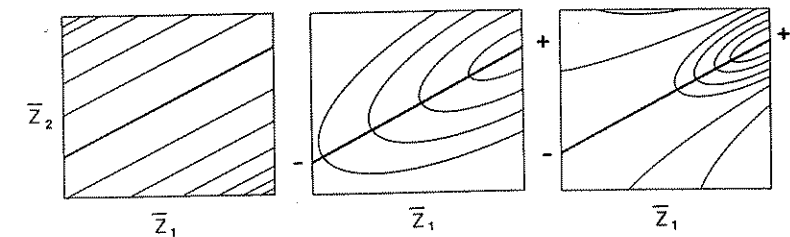


Fig. 5—Corridor models for differentiation. Three alternative adaptive landscapes. Left: a level ridge; middle: an ascending ridge; right: an ascending ridge that has progressively steeper flanks towards the upper right.

determined by the genetic variances of the traits and the inclination of the ridgecrest. However, a ridge whose flanks steepen as the ridge ascends (Fig. 5, right) can cause populations to equilibrate along the ridgecrest (Wagner 1988).

Interspecific correlation will also arise on more complicated adaptive landscapes that have multiple peaks. Lande (1986) reviewed "peak shift" models of phenotypic evolution in which evolving populations move from one peak on the adaptive landscape to another. These models yield an evolutionary tempo in which long-term stasis (residence on a peak) is punctuated by rapid transition between peaks (Lande 1985; Newman et al. 1985), as well as a static pattern of interspecific correlation (Fig. 6). A temporal pattern of intermittent evolution is the empirical foundation of Eldredge and Gould's (1972) theory of punctuated equilibrium, but they attribute the tempo to other processes.

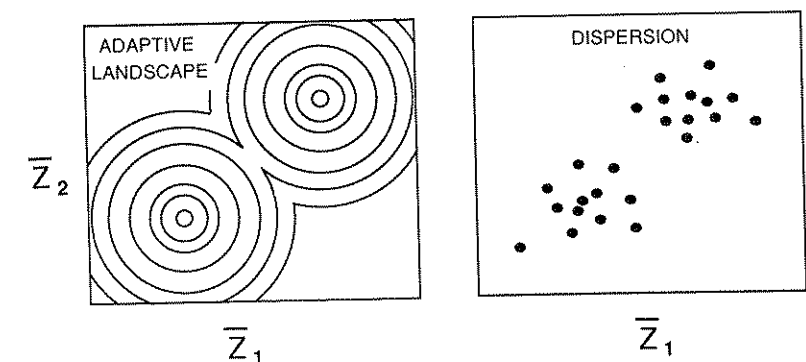


Fig. 6—Differentiation on an adaptive landscape with two peaks. Left: Populations situated on either of the two peaks have the highest mean fitness. Right: Descendant populations will tend to evolve uphill on the landscape, towards one of the two peaks. Because of the relative position of the two peaks, descendant populations in evolutionary equilibrium or quasi-equilibrium will yield a pattern of interpopulation correlation.

Because populations tend to evolve uphill on the adaptive landscape, the fundamental problem in models with multiple peaks is the movement downslope—against the force of selection—which must precede a shift from one peak to another. Wright (1932, 1977), working with genotypic models, and investigators using quantitative genetic models have invoked random genetic drift as an essential process in initiating a peak shift. Thus small effective population size and a shallow valley between adaptive peaks facilitate downslope movement during the initial stage of peak shift. Surprisingly, the expected time until a population experiences a peak shift is more sensitive to the depth of the adaptive valley (relative to the peak of residence) than to the distance between peaks (Barton and Charlesworth 1984; Lande 1985). A valley may become shallow because of a change in environment or because of an increase in the phenotypic variance of the traits of interest (Kirkpatrick 1982). Large genetic variance has no effect on the statistical probability of residing on or between peaks, because its effect in promoting uphill response to selection is canceled by its positive effect on random drift (e.g., Lande 1985). However, genetic variance or covariance that is aligned with the main axis of multiple ascending peaks (as in Fig. 7) will increase the rate of transition between peaks.

These results are directly relevant to the question of how evolutionary novelties arise. Thus, a great morphological distance from a non-flying ancestor to a winged descendant may be traversed relatively quickly if intermediate morphologies are only slightly disadvantageous.

These theoretical results and possibilities suggest two main phenotypic issues that can be addressed with combined intra- and interspecific studies of morphology and performance. Many of the issues that spring from the

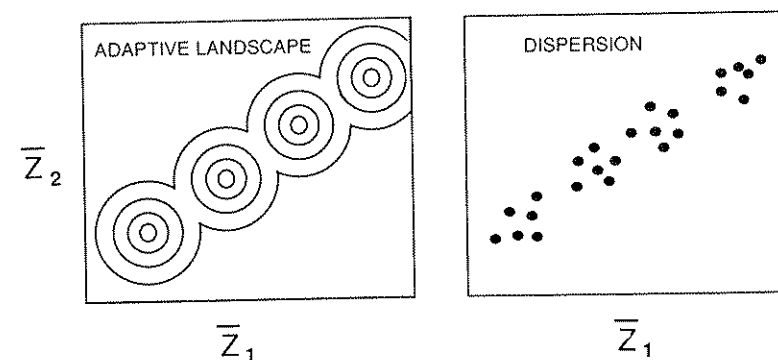


Fig. 7—Differentiation on an adaptive landscape with an ascending series of peaks. Left: Adaptive peaks are higher towards the upper right. Right: Descendant populations will show a pattern of positive correlation.

theoretical work are couched in terms of adaptive landscapes and selection surfaces, but all of those issues have analogues in terms of performance surfaces. In order for the performance and selection issues to be congruent, the selection surface for performance itself must be linear, as discussed in the preceding section. On the assumption of linear selection gradients for performance, we may list the following issues: (1) Do different populations experience different performance surfaces? Using the methods outlined in preceding sections we could estimate the performance surfaces for each of a series of populations. We can compare the coefficients that describe the average slopes and curvatures of those surfaces using the standard errors of the estimates (assuming multivariate normality of the morphological traits). This exercise could tell us whether the surfaces have the same shape. Phillips and Arnold (1989) describe the use of response surface analysis to locate the peak of the performance surface, should it exist. Applying that methodology to each population, we could locate the peaks of each population's (or species's) performance surface and determine whether they coincide.

(2) Are the intra- and interspecific performance surfaces isomorphic? This question is of interest in the event that all (or most) of the populations have performance surfaces of similar shape. If intra- and interspecific surfaces are isomorphic, then theoretical work would be vastly simplified. If they are not, then extensive empirical work may be required to establish generalities.

THE ROLE OF GENETICAL STUDIES

The theoretical studies surveyed in the last section stressed the importance of two key genetical issues: genetic variance and covariance. Genetical covariances (or correlations) between traits are of particular interest because they can have important short-term deflecting effects on evolutionary trajectories (e.g., Lande 1980a; Arnold 1987; Slatkin and Kirkpatrick 1986). These within-population genetical parameters can be estimated using systematic breeding plans that produce sets of individuals of known relationship, such as sets of parents and offspring or sets of full siblings (Falconer 1981). Many studies of linear dimensions (conformation) have been made by applied animal breeders and these have usually demonstrated high heritabilities (standardized genetic variances). Relatively few genetical studies of performance have been made, but there are some encouraging recent developments (van Berkum and Tsuji 1987; Garland 1988; Curtsinger and Laurie-Ahlberg 1981). Functionally related traits often show genetic correlations (Cheverud 1982), as might be expected on theoretical grounds (Lande 1980b), but there is a great need for additional empirical work (Arnold 1986a).

COMBINING PHYLOGENETIC ANALYSIS WITH INTRA- AND INTERSPECIFIC STUDIES OF MORPHOLOGY AND PERFORMANCE

If we know the phylogeny of our taxa, a host of additional issues opens before us. (1) As Lauder (1981) has stressed, phylogenetic information is crucial for determining the actual polarity of evolution (see also Lauder and Liem, this volume). Without it, transformational analysis is replaced by morphoclines that may have no historical basis. (2) The reality of interspecific correlation is difficult to assess without phylogenetic information (Felsenstein 1985). Standard statistical tests assume independent observations, but this assumption is violated when some taxa are more closely related than others. Ways of circumventing the problem are discussed by Felsenstein (1988), Huey (1987), and Huey and Bennett (1987). (3) With a phylogeny in hand we could determine, in principle, whether populations are evolving uphill on the interspecific surface. In other words, we could test for a phylogenetic response to species selection. (4) Using a phylogeny we could extract independent contrasts (Felsenstein 1985) and estimate the net forces of directional selection responsible for the divergence in each contrast (Lande 1979; Grant 1986; Arnold 1988b). With those data we could assess the interspecific covariance in directional selection that figures so importantly in Zeng's (1988) and Felsenstein's (1988) models of interspecific divergence. (5) With multiple clades and a known phylogeny, we could determine whether the uncoupling of intraspecific or interspecific relationships between morphology and performance is related to macroevolutionary patterns (Lauder and Liem, this volume).

Acknowledgements. We are grateful to A. Bennett, V. Csányi, R. Dawkins, C. Gans, R. Lande, D. Schluter, J. Maynard Smith, E. Vrba, M. Wade, D.B. Wake, and M.H. Wake for helpful discussions and comments on the manuscript.

REFERENCES

- Alberch, P. 1981. Convergence and parallelism in foot morphology in the neotropical salamander genus *Bolitoglossa*. I. Function. *Evolution* 35: 84-100.
- Alexander, McN. 1972. *Animal Mechanics*. Seattle: Univ. Washington Press.
- Andrews, R.; Pough, F.H.; Collazo, A.; and de Queiroz, A. 1987. The ecological cost of morphological specialization: feeding by a fossorial lizard. *Oecologia* 73: 139-145.
- Arnold, A.J., and Fristrup, K. 1982. The theory of evolution by natural selection: a hierarchical expansion. *Paleobiol.* 8: 113-129.
- Arnold, S.J. 1983. Morphology, performance and fitness. *Am. Zool.* 23: 347-361.
- Arnold, S.J. 1986a. Laboratory and field approaches to the study of adaptation. In: *Predator-prey Relationships: Perspectives and Approaches from the Study of*

- Lower Vertebrates*, eds. M.E. Feder and G.V. Lauder, pp. 157-179. Chicago: Univ. Chicago Press.
- Arnold, S.J. 1986b. Limits on stabilizing, disruptive, and correlational selection set by the opportunity for selection. *Am. Nat.* 128: 143-146.
- Arnold, S.J. 1987. Genetic correlation and the evolution of physiology. In: *New Directions in Ecological Physiology*, eds. M.E. Feder, A.F. Bennett, W. Burggren, and R.B. Huey, pp. 189-212. Cambridge: Cambridge Univ. Press.
- Arnold, S.J. 1988a. Behavior, energy and fitness. *Am. Zool.* 28: 815-827.
- Arnold, S.J. 1988b. Quantitative genetics and selection in natural populations: microevolution of vertebral numbers in the garter snake *Thamnophis elegans*. In: *Proc. Second International Conference on Quantitative Genetics*, eds. B. Weir, G. Eisen, M. Goodman, and G. Namkoong, pp. 619-636. Sunderland, MA: Sinauer.
- Arnold, S.J., and Bennett, A.F. 1988. Behavioural variation in natural populations. V. Morphological correlates of locomotion in the garter snake *Thamnophis radix*. *Biol. J. Linn. Soc.* 34: 175-190.
- Atchley, W.R.; Rutledge, J.J.; and Cowley, D.E. 1981. Genetic components of size and shape. II. Multivariate covariance patterns in the rat and mouse skull. *Evolution* 35: 1037-1055.
- Atchley, W.R.; Rutledge, J.J.; and Cowley, D.E. 1982. A multivariate statistical analysis of direct and correlated response to selection in the rat. *Evolution* 36: 677-698.
- Bailey, D. 1956. A comparison of genetic and environmental principal components of morphogenesis in mice. *Growth* 20: 63-74.
- Baker, A.J. 1980. Morphometric differentiation in New Zealand populations of the house sparrow (*Passer domesticus*). *Evolution* 34: 638-653.
- Barton, N.H., and Charlesworth, B. 1984. Genetic revolutions, founder effects, and speciation. *Ann. Rev. Ecol. Syst.* 15: 133-164.
- Bennett, A.F. 1987. Interindividual variability: an underutilized resource. In: *New Directions in Ecological Physiology*, eds. M.E. Feder, A.F. Bennett, W. Burggren, and R.B. Huey, pp. 147-166. Cambridge: Cambridge Univ. Press.
- Burger, R. 1986. Constraints for the evolution of functionally coupled characters: a nonlinear analysis of a phenotypic model. *Evolution* 40: 182-193.
- Charlesworth, B. 1980. *Evolution in Age-structured Populations*. Cambridge: Cambridge Univ. Press.
- Cheverud, J.M. 1982. Phenotypic, genetic, and environmental morphological integration in the cranium. *Evolution* 36: 499-516.
- Crow, J.F., and Kimura, M. 1970. *An Introduction to Population Genetics Theory*. New York: Harper and Row.
- Curtsinger, J.W., and Laurie-Ahlberg, C.C. 1981. Genetic variability of flight metabolism in *Drosophila melanogaster*. I. Characterization of power output during tethered flight. *Genetics* 98: 549-564.
- Dullemeijer, P. 1974. *Concepts and Approaches in Animal Morphology*. Assen, The Netherlands: Van Gorcum.
- Dunham, A.E.; Miles, D.B.; and Reznick, D.N. 1988. Life history patterns in squamate reptiles. In: *Biology of the Reptilia*, eds. C. Gans and R.B. Huey, vol. 16, pp. 441-522. New York: Alan R. Liss.
- Emerson, S. 1978. Allometry and jumping in frogs: helping the twain to meet. *Evolution* 12: 551-564.
- Emerson, S. 1985. Skull shape in frogs—correlations with diet. *Herpetol.* 41: 177-188.
- Emerson, S., and Diehl, D. 1980. Toe pad morphology and mechanisms of sticking in frogs. *Biol. J. Linn. Soc.* 13: 199-216.

- Falconer, D.S. 1981. Introduction to Quantitative Genetics, 2nd ed. London: Longman.
- Felsenstein, J. 1979. Excursions along the interface between disruptive and stabilizing selection. *Genetics* **93**: 773-795.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *Am. Nat.* **125**: 1-15.
- Felsenstein, J. 1988. Phylogenies and quantitative characters. *Ann. Rev. Ecol. Syst.* **19**: 445-471.
- Gans, C. 1974. Biomechanics: An Approach to Vertebrate Biology. Philadelphia: J.P. Lippincott.
- Garland, T., Jr. 1983. The relationship between maximal running speed and body mass in terrestrial mammals. *J. Zool. (Lon.)* **199**: 157-170.
- Garland, T., Jr. 1985. Ontogenetic and individual variation in size, shape and speed in the Australian agamid lizard, *Amphibolurus nuchalis*. *J. Zool. (Lon.) A* **207**: 425-439.
- Garland, T., Jr. 1988. Genetic basis of metabolism. I. Inheritance of speed, stamina, and antipredator displays in the garter snake, *Thamnophis sirtalis*. *Evolution* **42**: 335-350.
- Grant, P. 1986. Ecology and Evolution of Darwin's Finches. Princeton: Princeton Univ. Press.
- Heisler, I.L., and Damuth, J. 1987. A method for analyzing selection in hierarchically structured populations. *Am. Nat.* **130**: 582-602.
- Hespenheide, H. 1971. Food preference and the extent of overlap in some insectivorous birds, with special reference to the Tyrannidae. *Ibis* **113**: 59-72.
- Huey, R.B. 1987. Phylogeny, history and the comparative method. In: New Directions in Ecological Physiology, eds. M.E. Feder, A.F. Bennett, W. Burggren, and R.B. Huey, pp. 76-101. Cambridge: Cambridge Univ. Press.
- Huey, R.B., and Bennett, A.F. 1987. Phylogenetic studies of coadaptation: preferred versus optimal performance temperatures of lizards. *Evolution* **41**: 1098-1115.
- Jaksic, F.; Nunez, H.; and Ojeda, F. 1980. Body proportions, microhabitat selection and adaptive radiation of *Liolaemus* lizards in Chile. *Oecologia* **45**: 178-181.
- Johnson, N.S., and Micevich, M.F. 1977. Variability and evolutionary rates of characters. *Evolution* **31**: 642-648.
- Kirkpatrick, M. 1982. Quantum evolution and punctuated equilibria in continuous genetic characters. *Am. Nat.* **119**: 833-848.
- Kluge, A.G., and Kerfoot, W.C. 1973. The predictability of regularity of character divergence. *Am. Nat.* **107**: 426-442.
- Lande, R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain:body size allometry. *Evolution* **33**: 402-416.
- Lande, R. 1980a. Sexual dimorphism, sexual selection and adaptation in polygenic characters. *Evolution* **34**: 292-305.
- Lande, R. 1980b. The genetic covariance between characters maintained by selection, linkage and inbreeding. *Genet. Res. Camb.* **44**: 309-320.
- Lande, R. 1981. Models of speciation by sexual selection on polygenic traits. *Proc. Natl. Acad. Sci. USA* **78**: 3721-3725.
- Lande, R. 1982. A quantitative genetic theory of life history evolution. *Ecology* **63**: 607-615.
- Lande, R. 1985. Expected time for random genetic drift of a population between stable phenotypic states. *Proc. Natl. Acad. Sci. USA* **82**: 7641-7645.
- Lande, R. 1986. The dynamics of peak shifts and the pattern of morphological evolution. *Paleobiol.* **12**: 343-354.
- Lande, R., and Arnold, S.J. 1983. The measurement of selection on correlated characters. *Evolution* **37**: 1210-1226.

- Lauder, G.V. 1981. Form and function: structural analysis in evolutionary morphology. *Paleobiol.* **7**: 430-442.
- Leamy, L. 1977. Genetic and environmental correlations of morphometric traits in random bred housemice. *Evolution* **31**: 357-369.
- Liem, K. 1980. Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. *Am. Zool.* **20**: 295-314.
- Mares, M. 1976. Convergent evolution of desert rodents: multivariate analysis and zoogeographic implications. *Paleobiol.* **2**: 39-63.
- Miles, D.B. 1987. Habitat related differences in locomotion and morphology in two populations of *Urosaurus ornatus*. *Am. Zool.* **44A**.
- Newman, C.M.; Cohen, J.E.; and Kipnis, C. 1985. Neo-Darwinian evolution implies punctuated equilibria. *Nature* **315**: 400-401.
- Olson, E., and Miller, R. 1958. Morphological Integration. Chicago: Univ. Chicago Press.
- Phillips, P.C., and Arnold, S.J. 1989. Visualizing multivariate selection. *Evolution*, in press.
- Pierce, B.A., and Mitton, J.B. 1979. A relationship of genetic variation within and among populations: an extension of the Kluge-Kerfoot phenomenon. *Syst. Zool.* **28**: 63-70.
- Reeve, E.C.D. 1950. Genetical aspects of size allometry. *Proc. R. Soc. Lon. B* **137**: 515-518.
- * Riedl, R. 1978. Order in Living Organisms. New York: Wiley.
- Rohlf, F.J.; Gimartin, A.J.; and Hart, G. 1983. The Kluge-Kerfoot phenomenon—a statistical artifact. *Evolution* **37**: 180-202.
- Slatkin, M., and Kirkpatrick, M. 1986. Extrapolating quantitative genetic theory to evolutionary problems. In: Evolutionary Genetics of Invertebrate Behavior, ed. M. Huettel, pp. 283-294. New York: Plenum.
- Sokal, R.R. 1962. Variation and covariation of characters of alate *Pemphigus populitransversus* in eastern North America. *Evolution* **16**: 227-245.
- Sokal, R.R. 1976. The Kluge-Kerfoot phenomenon re-examined. *Am. Nat.* **110**: 1077-1091.
- Sokal, R.R. 1978. Population differentiation: something new or more of the same? In: Ecological Genetics: The Interface, ed. P.F. Brussard, pp. 215-239. New York: Springer.
- Sokal, R.R.; Bird, J.; and Riska, B. 1980. Geographic variation in *Pemphigus populicaulic* (Insecta: Aphididae) in eastern North America. *Biol. J. Linn. Soc.* **14**: 163-200.
- Sokal, R.R., and Riska, B. 1981. Geographic variation in *Pemphigus populitransversus* (Insecta: Aphididae). *Biol. J. Linn. Soc.* **15**: 201-233.
- Thomas, P.A. 1968. Variation and covariation in characters of the rabbit tick, *Haemaphysalis leporispalustris*. *Univ. Kans. Sci. Bull.* **47**: 829-862.
- Toft, C. 1980. Feeding ecology of thirteen syntopic species of anurans in a seasonal tropical environment. *Oecologia* **45**: 131-141.
- van Berkum, F.H., and Tsuji, J.S. 1987. Interfamilial differences in sprint speed of hatchling *Sceloporus occidentalis*. *J. Zool. (Lon.)* **212**: 511-519.
- Vrba, E.S. 1984. What is species selection? *Syst. Zool.* **33**: 318-328.
- Wagner, G.P. 1988. The influence of variation and of developmental constraints on the rate of multivariate phenotypic evolution. *J. Evol. Biol.* **1**: 45-66.
- Wainwright, P.C. 1987. Biomechanical limits to ecological performance: mollusc-crushing by the Caribbean hogfish, *Lachnolaimus maximus* (Labridae). *J. Zool. (Lon.)* **213**: 283-297.
- Wilbur, H.M., and Morin, P.J. 1988. Life history evolution in turtles. In: Biology

- of the Reptilia, eds. C. Gans and R.B. Huey, vol. 16, pp. 387-440. New York: Alan R. Liss.
- Wright, S. 1932. The roles of mutation, inbreeding, crossbreeding and selection in evolution. *Proc. 6th Int. Cong. Genet.* 1: 356-366.
- Wright, S. 1977. *Evolution and the Genetics of Populations*, vol. 3. Experimental Results and Evolutionary Deductions. Chicago: Univ. Chicago Press.
- Zeng, Z.-B. 1988. Long-term correlated response, interpopulation covariation, and interspecific allometry. *Evolution* 42: 363-374.

Syllabus for an Embryological Synthesis

T.J. Horder

*Department of Human Anatomy
 University of Oxford
 Oxford OX1 3QX, U.K.*

Abstract. It is argued that the "modern evolutionary synthesis" has failed fully to bridge the genetic and phylogenetic levels of explanation of organisms due to a neglect of causal mechanisms most directly relevant to the realistic interpretation of adult morphological form and that the processes of embryogenesis should occupy a pivotal position in such considerations. Elucidation of the rules of embryogenesis and their consequences for evolutionary transitions provides a new conceptual framework in which to understand anatomical organizational complexity and integration, the relation of structure to function, programing of form by the genome, homology, and the reconstruction of evolutionary sequences.

INTRODUCTION

A scientific theory not only reflects available knowledge and techniques, it also bears the imprint of its conceptual history. Modern evolution theory stems from two distinct traditions: the tradition dealing with the actual products of evolution built up over the "phylogenetic" time scale, i.e., based on the principally morphological material of palaeontologists and taxonomists, and that dealing with mechanisms mediating evolutionary change accessible in living forms, which has increasingly become identified with a "genetic" tradition. Despite the success of the "modern synthesis" in bridging these traditions (Mayr and Provine 1980), the historical background may still polarize priorities and obscure alternative possible viewpoints.

The first aim of this paper is to define the differences between the two traditions, particularly the nature of the restrictions they impose on implied evolutionary "explanations" of animal forms. I then consider how these have limited the completeness of the modern synthesis and suggest a more coherent view. In concentrating on the clear setting out of the most general