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Reviewed work(s):

Source: *Evolution*, Vol. 39, No. 3 (May, 1985), pp. 505-522

Published by: [Society for the Study of Evolution](#)

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GENOTYPE-ENVIRONMENT INTERACTION AND THE EVOLUTION OF PHENOTYPIC PLASTICITY

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Summary.—Studies of spatial variation in the environment have primarily focused on how genetic variation can be maintained. Many one-locus genetic models have addressed this issue, but, for several reasons, these models are not directly applicable to quantitative (polygenic) traits. One reason is that for continuously varying characters, the evolution of the mean phenotype expressed in different environments (the norm of reaction) is also of interest. Our quantitative genetic models describe the evolution of phenotypic response to the environment, also known as phenotypic plasticity (Gause, 1947), and illustrate how the norm of reaction (Schmalhausen, 1949) can be shaped by selection. These models utilize the statistical relationship which exists between genotype-environment interaction and genetic correlation to describe evolution of the mean phenotype under soft and hard selection in coarse-grained environments. Just as genetic correlations among characters within a single environment can constrain the response to simultaneous selection, so can a genetic correlation between states of a character which are expressed in two environments. Unless the genetic correlation across environments is ± 1 , polygenic variation is exhausted, or there is a cost to plasticity, panmictic populations under a bivariate fitness function will eventually attain the optimum mean phenotype for a given character in each environment. However, very high positive or negative correlations can substantially slow the rate of evolution and may produce temporary maladaptation in one environment before the optimum joint phenotype is finally attained.

Evolutionary trajectories under hard and soft selection can differ: in hard selection, the environments with the highest initial mean fitness contribute most individuals to the mating pool. In both hard and soft selection, evolution toward the optimum in a rare environment is much slower than it is in a common one.

A subdivided population model reveals that migration restriction can facilitate local adaptation. However, unless there is no migration or one of the special cases discussed for panmictic populations holds, no geographical variation in the norm of reaction will be maintained at equilibrium. Implications of these results for the interpretation of spatial patterns of phenotypic variation in natural populations are discussed.

Received April 9, 1984. Accepted December 11, 1984

Environmental modification of the phenotype is common in the quantitative (polygenic) characters of organisms that inhabit heterogeneous environments. The profile of phenotypes produced by a genotype across environments is the "norm of reaction" (Schmalhausen, 1949); the extent to which the environment modifies the phenotype is termed "phenotypic plasticity" (Gause, 1947; Bradshaw, 1965). Because phenotypic response to environmental change may facilitate the exploitation of some environments and provide protection from others, the level of plasticity in a given trait is thought to be molded by selection (Gause, 1947;

Schmalhausen, 1949; Bradshaw, 1965). The models presented here concern the evolution of quantitative traits in spatially variable environments. Within this general context, they explore how an advantageous level of phenotypic plasticity might evolve.

Schmalhausen (1949) recognized that mutations are likely to be expressed differently in various environments. Mutation can thus act to disrupt the most advantageous norm of reaction by creating genetic variation in phenotypic plasticity. Such variation in response to the environment is also known as genotype-environment interaction (Falconer, 1981). Schmalhausen's view was that natural selection molds the norm of reaction from the variants produced by

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mutation. In other words, genotype-environment interaction is the type of genetic variation required for the evolution of a selectively advantageous level of phenotypic plasticity.

Although Schmalhausen argued that the optimal norm of reaction will eventually evolve from the variation among genotypes in reaction norms generated by mutation, agriculturalists find that genotype-environment interaction can act as a constraint in the selection of a genotype with broad adaptability (Robertson, 1959; James, 1961; Dickerson, 1962). Genotype-environment interaction may thus have different long- and short-term effects on the process of evolution.

Many classical population genetic models of spatial variation in the environment have been made since Levene's original (1953) "multiple-niche" model (reviewed in Hedrick et al., 1976). These models share a similar intent: to determine the conditions under which polymorphism at a single locus can be maintained. The multiple-niche model has substantially influenced the course of experimental work, motivating many attempts to document the effects of environmental variation on the maintenance of genetic variation in both electrophoretic and polygenic traits (Beardmore and Levine, 1963; Powell, 1971; McDonald and Ayala, 1974; Powell and Wistrand, 1978; Mitter et al., 1979; MacKay, 1981; Lacy, 1982; Jaenike and Grimaldi, 1983). However, for several reasons, existing one-locus models do not provide an adequate description of evolution in the quantitative traits often studied with respect to adaptation to different environments. 1) In the simplest models of one locus with two alleles, the mean and the genetic variance are always statistically dependent, while in polygenic traits, they can often evolve independently (Slatkin, 1978). 2) The multiple-niche models derive criteria for the maintenance of polymorphism in terms of the mean fitnesses of alleles in different environments; these fitnesses cannot be measured for quan-

titative traits in which the influence of individual loci cannot be identified. 3) The dynamics of the mean phenotype and the norm of reaction are of considerable interest in polygenic characters; these are not described by existing models. 4) In two-niche models with only two alleles, the additive genetic correlation between the expression of the genotypes in the two environments is always -1 , even with dominance, because the breeding value of the heterozygote is always intermediate between the two homozygotes.

Quantitative genetic models are used here to investigate the effects of genetic variation in phenotypic plasticity (genotype-environment interaction) on both the trajectories and rates of evolution of the average phenotype under simultaneous selection in two discrete environments. Although these models do not consider continuous environmental variation such as temperature or photoperiod, they may be useful in the interpretation of experimental data in which tests are performed at discrete points along an environmental continuum.

Genotype-Environment Interaction as Genetic Correlation.—Falconer (1952) first noted that a character expressed in two environments can be viewed as two characters which are genetically correlated. This view is an essential feature of the present models: a separate variable is defined for the expression of a given trait in each environment. We will call the expression of a character in a given environment a *character state*. For example, body weight in one environment and body weight in another environment can be thought of as two genetically correlated character states (Falconer, 1952).

In this context, the additive genetic correlation estimates the degree to which the phenotypes expressed in two environments have the same genetic basis, attributable either to pleiotropic effects of genes or to linkage disequilibrium between alleles at different loci. A high genetic correlation across environments implies that the same alleles or sets of alleles influence the character states in

the same way in two environments. If the genetic correlation between two character states is ± 1 , they should be considered to be exactly the same character; the correlation indicates that they have an identical genetic basis. In contrast, a cross-environment genetic correlation between $+1$ and -1 indicates that the phenotypes in each environment are influenced either by some different alleles or differently by the same alleles, and thus can have some degree of independent evolution. Previous polygenic models of spatial variation have assumed that the character states in the two environments are identical, that is, that the additive genetic correlation across environments is $+1$ (e.g., Bulmer, 1971; Slatkin, 1978).

Although a well-defined statistical relationship exists between genotype-environment interaction and genetic covariance (Robertson, 1959; Dickerson, 1962; Yamada, 1962; Fernando et al., 1984), estimation of the genetic correlation across environments is the more precise way of the two to evaluate genetic variance in response to the environment. Any genetic correlation between characters expressed in different environments which is less than $+1$ will translate into a significant genotype-environment interaction (Robertson, 1959). The correlation format is also more useful mathematically, because estimates of genotype-environment interaction cannot be incorporated into any current theory of evolution. In contrast, genetic correlations between polygenic characters in a single environment are known to affect both the direction and rate of joint evolution (Hazel, 1943; Dickerson, 1955; Lande, 1979, 1980*b*, 1982). The models presented here explore how genetic correlations between character states expressed in different environmental niches may similarly constrain evolution in variable environments. In particular, the models investigate the effects of these correlations on the evolution of phenotypic plasticity.

In the present models, any individual experiences only one environment. To

estimate the genetic correlation between character states, replicated genotypes or family members are allowed to develop in the different environments. Because measurements of different character states must be made on separate individuals, the usual statistical methods for calculating the genetic correlation (e.g., Falconer, 1981 Ch. 19) are not applicable. In this case alternatives may be employed, such as the correlation of family means or the re-expression of genotype-environment interaction as a genetic covariance between character states expressed in different environments (reviewed in Via, 1984).

Both "soft" and "hard" selection are examined (following the terminology of Christiansen, 1975), and, as will be shown, the evolutionary dynamics of the mean phenotype in heterogeneous environments differ for these modes of selection. In all but a few circumstances, optimal levels of phenotypic plasticity are eventually attained at equilibrium. Population subdivision and reduced migration will be seen to permit more direct and rapid local adaptation than is possible with high levels of migration. However, the equilibrium mean phenotype expressed by the population in each environment generally reaches the optimum, where the population as a whole is under stabilizing, not disruptive selection. Stabilizing selection depletes additive genetic variance in polygenic characters (Scharloo, 1964; Wright, 1969 Ch. 4); observed levels of additive genetic variance at equilibrium are thus presumed to be maintained by mutation-selection balance (Lande, 1976, 1980*a*; Turelli, 1984). Spatial variation in selection pressures will persist and augment genetic variance at equilibrium only when there is no migration or when the genetic correlation across environments is ± 1 .

Genetic Models of Panmictic Populations

Assumptions and Limitations of the Models.—Using standard quantitative genetics techniques (e.g., Falconer, 1981 Ch. 9), variation in the phenotypic value

of the character in the i th environment, z_i , can be partitioned into additive genetic and within- or micro-environmental portions, with non-additive genetic variance pooled into the within-environmental variance. The phenotypic variance of the character state in the i th environment is $P_{ii} = G_{ii} + E_{ii}$, where E_{ii} is the within-environmental variance and is assumed to follow a normal (Gaussian) distribution. When character states in different environments cannot be measured on the same individual, the phenotypic covariance, P_{ij} with $i \neq j$, is undefined (Falconer, 1981 p. 284). It is assumed throughout that scales of measurement are used such that the phenotypic distribution is normal in each environment, with the variance independent of the mean. A logarithmic transformation will often improve the fit of the data to the normal distribution (Wright, 1968 Chs. 10 and 11).

For polygenic characters in which several loci of small effect are assumed to contribute to the phenotype, the distribution of additive genetic effects on each character can also be assumed to be approximately Gaussian. The matrix of additive genetic variances and covariances of character states can be written as G , where the element G_{ii} is the additive genetic variance of the character state in the i th environment and G_{ij} is the additive genetic covariance of character states expressed in the i th and j th environments.

Selection is assumed to be weak and populations to be large, allowing genetic variation depleted by selection to be replenished by mutation (Lande, 1976, 1980a). The matrix of genetic variances and covariances can thus be assumed to remain roughly constant as evolution of the mean phenotype proceeds. This assumption has been examined in iterations of equations approximating the evolution of the covariance structure under selection in two environments, and was found to be robust (Via and Lande, unpubl.).

The models described here are pri-

marily concerned with evolution of phenotypic traits which have an intermediate optimum. Many morphological, physiological, and behavioral traits, and minor components of fitness like growth rate, development time, or body size are typically under such stabilizing selection (e.g., Rendel, 1943); these traits may be selected in the same or different directions across environments. In contrast, major components of fitness like fecundity or survival can be presumed to be under continual directional selection to increase in all environments. The portion of the analysis of the present models which assumes a Gaussian form for the fitness function is not applicable to such characters.

In the first two models, we assume that the population is panmictic and that mated adults disperse into the available habitats at random each generation. Selection in each environment acts on individuals before dispersal and mating. Under weak or moderate selection and panmixis, the means of the groups selected in each environment will not diverge enough in one generation to cause appreciable non-normality in the phenotypic distribution before selection.

Hard and soft selection, as defined by Christiansen (1975), are distinguished by the form of population regulation which is presumed to occur. In soft selection, populations in each environment are regulated independently, so that each environmental niche contributes a constant fraction of the total population. In hard selection, the contribution of each niche to the total population is weighted by its mean fitness; the population is regulated globally. Soft selection may apply when populations in different niches are held at constant numbers by resource limitation. If populations are limited by evolving traits, such as the ability to utilize the available resources effectively, then hard selection may apply. As evolution occurs under hard selection to increase adaptation in a given environment, that niche's contribution to the total population will increase.

Soft Selection.—With q_i defined as the proportion of individuals entering the i th habitat ($\sum q_i = 1$), \bar{z}_i as the mean value of the character state expressed in the i th environment, P_{ii}^{-1} as the reciprocal of the phenotypic variance in the i th environment, and s_i as the difference between the mean phenotype before and after selection in the i th environment, the dynamical equation for soft selection in two environments is:

$$\begin{pmatrix} \Delta\bar{z}_1 \\ \Delta\bar{z}_2 \end{pmatrix} = \begin{pmatrix} G_{11} & G_{12} \\ G_{21} & G_{22} \end{pmatrix} \begin{pmatrix} q_1 P_{11}^{-1} s_1 \\ q_2 P_{22}^{-1} s_2 \end{pmatrix}. \quad (1)$$

Thus,

$$\begin{aligned} \Delta\bar{z}_1 &= qG_{11}P_{11}^{-1}s_1 \\ &\quad + (1 - q)G_{12}P_{22}^{-1}s_2 \\ \Delta\bar{z}_2 &= qG_{21}P_{11}^{-1}s_1 \\ &\quad + (1 - q)G_{22}P_{22}^{-1}s_2, \end{aligned} \quad (2)$$

where $q = q_1$. Eqs. 2 illustrate that the evolution of each of the character states includes both a *direct response* to selection in the environment in which the character state of interest is expressed and a *correlated response* to selection on the state expressed in the other environment. Thus, if two character states are simultaneously selected to increase in equally frequent environments ($s_1 > 0$ and $s_2 > 0$, $q = 0.5$), a low or negative genetic covariance in the phenotype across environments (G_{12}) will slow the rate of evolution. Similarly, evolution under disruptive selection ($s_1 > 0$ and $s_2 < 0$ or conversely) will be retarded by positive genetic covariance. If multiple traits in each environment are included, then selection on other characters in the same environment can also cause correlated changes in the mean phenotype. All the models described here can be generalized to include multiple environments with many characters expressed in each environment by expanding the dimensionality of the matrices in (1).

The fitness of an individual of phenotype z in environment i is defined as $W_i(z)$. With a normal distribution of phenotypes, $p(z)$, and mean fitness \bar{W}_i , the selection differential in the i th environment is

$$s_i = [\int z_i p_i(z) W_i(z) dz_i] / \bar{W}_i - \bar{z}_i. \quad (3)$$

Expressing the change in mean fitness with an incremental change in \bar{z}_i and using (3), the observed selection differential can be rewritten in terms of the gradient of the logarithm of mean fitness in the i th environment (Lande, 1979):

$$P_{ii}^{-1}s_i = \nabla_i \ln \bar{W}_i \quad (4)$$

where the gradient operator $\nabla_i = \delta/\delta\bar{z}_i$ acting on $\ln \bar{W}_i$ represents the direct effect of selection in the i th environment on the character state expressed there, with the states expressed in other environments held constant. This selective force, $\nabla_i \ln \bar{W}_i$, is also equal to the partial regression coefficient of individual relative fitness in the i th environment (W_i/\bar{W}_i) on z_i (Lande and Arnold, 1983). By substituting (4) into (1), the dynamic equations for soft selection in two environments can be rewritten as

$$\begin{pmatrix} \Delta\bar{z}_1 \\ \Delta\bar{z}_2 \end{pmatrix} = \begin{pmatrix} G_{11} & G_{12} \\ G_{21} & G_{22} \end{pmatrix} \cdot \begin{pmatrix} \nabla_1 \\ \nabla_2 \end{pmatrix} \ln[\bar{W}_1^q \bar{W}_2^{(1-q)}]. \quad (5)$$

The function $\bar{W} = \bar{W}_1^q \bar{W}_2^{(1-q)}$ gives the joint mean fitness under soft selection as the weighted geometric mean of the mean fitnesses in the two environments, defining an adaptive topography for evolution in two environments. Assuming a Gaussian fitness function in each environment, this topography is plotted in Figure 1A. The height of this adaptive landscape for phenotypes is the joint mean fitness at each value of the vector of mean phenotypes in the two environments; the peak defines an equilibrium at which the phenotype is at the joint optimum and the geometric mean fitness is maximized (Wright, 1969 Ch. 4; Lande, 1979). Together with the genetic covariance matrix, the adaptive topography determines the rate and direction of multivariate evolution. The form of the joint fitness function is thus an important element in

the dynamics of phenotypic evolution in variable environments.

The evolutionary dynamics of mean fitness can be determined by expanding \bar{W} in a Taylor series around an arbitrary point. Assuming weak selection, higher order terms can be ignored to yield

$$\begin{aligned} \Delta \ln[\bar{W}_1^q \bar{W}_2^{(1-q)}] &= (\Delta \bar{z}_1, \Delta \bar{z}_2) \\ &\quad \cdot \nabla \ln[\bar{W}_1^q \bar{W}_2^{(1-q)}] \\ &= (\nabla \ln \bar{W})^T \mathbf{G} \nabla \ln \bar{W} \\ &\geq 0, \end{aligned} \quad (6)$$

where $\nabla^T = (\nabla_1, \nabla_2)$, and T indicates matrix transposition. The quadratic form in (6) ensures that the evolution of the mean phenotypes selected in different environments always occurs in a direction which increases the joint mean fitness in the population. However, correlated responses to selection caused by genetic covariance of character states in different environments can cause mean fitness to decrease temporarily in one of the environments during the course of evolution. Even so, unless the genetic correlation across environments is ± 1 , an optimal level of phenotypic plasticity will eventually be attained at equilibrium. The mean fitness in each environment will then be at a local maximum. For example, when the fitness function in the i th environment is of a Gaussian form with width ω_i and optimum θ_i , $W_i(z_i) = \exp\{- (z_i - \theta_i)^2 / 2\omega_i^2\}$. The mean fitness of phenotype z_i is then

$$\begin{aligned} \bar{W}_i &= \int W_i(z_i) p_i(z_i) dz_i \\ &= \sqrt{\omega_i^2 / (\omega_i^2 + P_{ii})} \\ &\quad \cdot \exp\{- (\bar{z}_i - \theta_i)^2 / 2(\omega_i^2 + P_{ii})\}. \end{aligned} \quad (7)$$

At equilibrium, unless \mathbf{G} is singular, $\nabla_i \ln \bar{W}_i = -(\bar{z}_i - \theta_i) / (\omega_i^2 + P_{ii}) = 0$, so that $\bar{z}_i = \theta_i$.

Rates of Evolution under Soft Selection. — The dynamics of phenotypic evolution under soft selection are described by (5). With Gaussian fitness functions as in (7), the dynamical system is linear. Analysis of the eigenstructure of this sys-

tem produces a set of axes (the eigenvectors) with the rate of evolution in each direction determined by the corresponding eigenvalues. If the eigenvalue for a given direction is small, $\lambda \ll 1$, then the rate of approach to the equilibrium from that direction is $(1 + \lambda)^t \simeq e^{\lambda t}$, where t is the number of generations. This rate corresponds to a time scale of $-1/\lambda$ generations, where the time scale is the number of generations required to move $1/e$ of the distance from the initial position in phenotype space to the optimum in a direction which is parallel to the corresponding eigenvector.

The effect of the genetic correlation on the eigenvalues, and thus on the evolutionary rate, can be most simply illustrated for the symmetrical case in which $q = 0.5$, $G_{11} = G_{22} = G$, $G_{12} = G_{21} = \gamma G$, $P_{11} = P_{22} = P$, and $\omega_1 = \omega_2 = \omega$. The dynamical equation in (5) can then be rewritten as

$$\begin{pmatrix} \Delta \bar{z}_1 \\ \Delta \bar{z}_2 \end{pmatrix} = \frac{-G}{2(\omega^2 + P)} \begin{pmatrix} 1 & \gamma \\ \gamma & 1 \end{pmatrix} \begin{pmatrix} \bar{z}_1 - \theta_1 \\ \bar{z}_2 - \theta_2 \end{pmatrix}. \quad (8)$$

The eigenvalues of this system are $\lambda_1 = -G(1 + \gamma) / 2(\omega^2 + P)$ and $\lambda_2 = -G(1 - \gamma) / 2(\omega^2 + P)$. These are associated respectively with the eigenvectors corresponding to evolution of the character states in the same direction [$\mathbf{x}_1^T = (1/\sqrt{2})(1, 1)$] and evolution of the character states in opposite directions [$\mathbf{x}_2^T = (1/\sqrt{2})(1, -1)$].

High or low values of γ lead to increasing discrepancy of the time scales for evolution in the directions of the eigenvectors. Negative genetic correlations across environments will slow evolution along the eigenvector associated with parallel change, \mathbf{x}_1 . In contrast, positive genetic correlations across environments will retard movement along \mathbf{x}_2 , which corresponds to the evolution of geographical variation under selection in different directions in the two environments. Any evolutionary trajectory can be considered as a combination of movement in the directions of the two eigenvectors, and evolution will proceed at a rate determined by the appropriate combination of the eigenvalues.

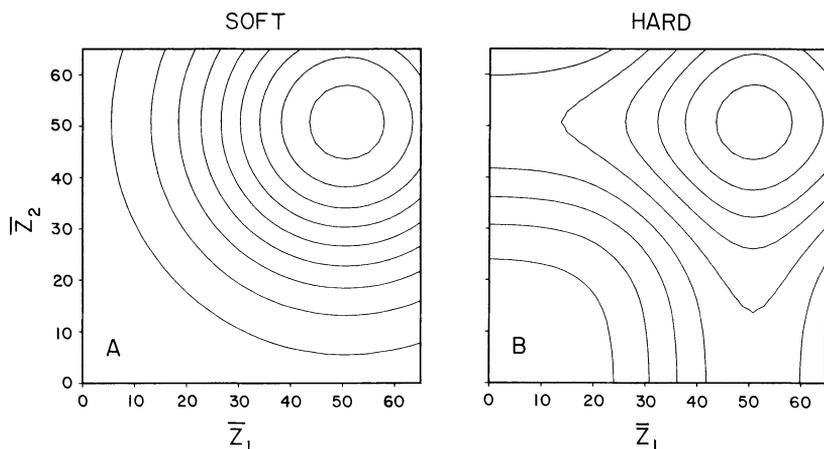


FIG. 1. Adaptive topographies for a character selected in two environments under either soft selection (A) or hard selection (B). The phenotypes of the trait in the two environments are considered to be two separate, but genetically correlated, character states with mean phenotypes \bar{z}_1 and \bar{z}_2 . Contours represent levels of joint mean fitness at different combinations of mean phenotypes in the two environments. Contours are 0.1 units apart. Under soft selection, joint mean fitness is $\bar{W}_1^q \bar{W}_2^{(1-q)}$, while under hard selection, the joint mean fitness is $q\bar{W}_1 + (1-q)\bar{W}_2$, where \bar{W}_i is the mean fitness in the i th environment, given by Equation (7). Parameters for both plots are $G_{11} = G_{22} = 10$, $P_{11} = P_{22} = 20$, $\omega_1^2 = \omega_2^2 = 200$, $q = 0.5$, and $\theta_1 = \theta_2 = 50$.

If the environments are not equally frequent ($q \neq 0.5$), the eigenvalues are $\lambda = -G[1 \pm \sqrt{1 - 4q(1-q)(1-\gamma^2)}]/2(\omega^2 + P)$. When one environment is very rare ($q \ll 1$), then the smallest eigenvalue can be approximated by $\lambda = -qG(1 - \gamma^2)/(\omega^2 + P)$. Thus, the rate of approach of the mean phenotype to the joint optimum when one environment is rare will be extremely slow.

To aid in interpretation of the equations, several numerical examples of evolution of one trait under soft selection in two environments are presented in Figures 2 and 3. All examples concern populations which have been perturbed from the joint optimum by various amounts. The effect of the genetic correlation between the character states on the course of evolution back toward the joint optimum is then examined.

In the first examples, individuals are initially poorly adapted to both habitats. An example of such a case might be an herbivore which invades a geographical area containing a new constellation of host plants to which it is uniformly poorly

adapted. It can be seen that, when only a slight asymmetry exists in the initial conditions (Fig. 2A), the genetic covariance across environments has little effect on the evolutionary trajectories under soft selection regardless of whether selection on the two character states is in the same or different directions (compare Fig. 2A, C). However, the genetic correlation between character states in the two environments will affect the rate of evolution as discussed above: the rate of approach to equilibrium under soft selection is slowest for extremely negative correlations. Under disruptive selection (Fig. 2C), the slowest evolution will occur with a high positive correlation between states.

When one of the habitats comprises a larger fraction of the total environment than the other and both character states are selected to increase, the effects of negative genetic covariance across environments on the joint trajectory are more striking. In Figure 3A, 70% of the individuals are selected in environment 1: evolution thus occurs more rapidly there, and much of the change in the average

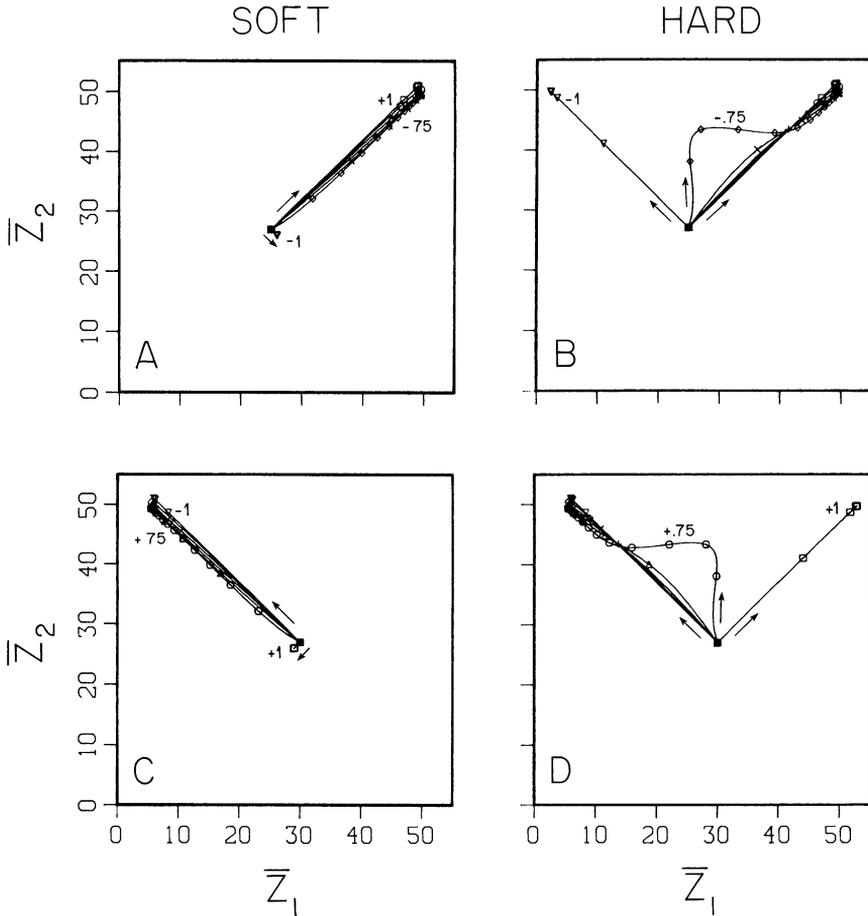


FIG. 2. Effect of the genetic correlation in the expression of a character in two environments on the evolutionary trajectories of the mean phenotype under soft selection (A, C) and hard selection (B, D). The values of the genetic correlations across environments are: +1 (\square), 0.75 (\circ), 0.375 (\triangle), 0 (+), -0.375 (\times), -0.75 (\diamond), -1 (∇). Selected trajectories are labelled with the corresponding value of the genetic correlation. Markers on the plots are at 50 generation intervals. Parameters for all plots are as in Figure 1 except that in A and B, the initial values are $z_1 = 25$, $z_2 = 27$, and in C and D, the initial conditions are $z_1 = 30$, $z_2 = 27$ and the optimum is at (5, 50). Arrows indicate the direction of evolution.

phenotype in the rare environment is due to a correlated response (see Eqs. 2). When the phenotypes in the two environments are negatively genetically correlated, adaptation to the rare environment cannot proceed until the population approaches the local optimum in the more common environment and the intensity of selection diminishes there. When the environments occur in unequal frequencies, an unfavorable correlation structure can

thus produce temporary maladaptation to the rare environment and cause the approach to the joint optimum to be greatly slowed.

As a final example, consider the case in which the population is perturbed from the joint optimum much more in one environment than in the other. For example, if a new host plant were introduced into the range of an herbivore species which was already well adapted

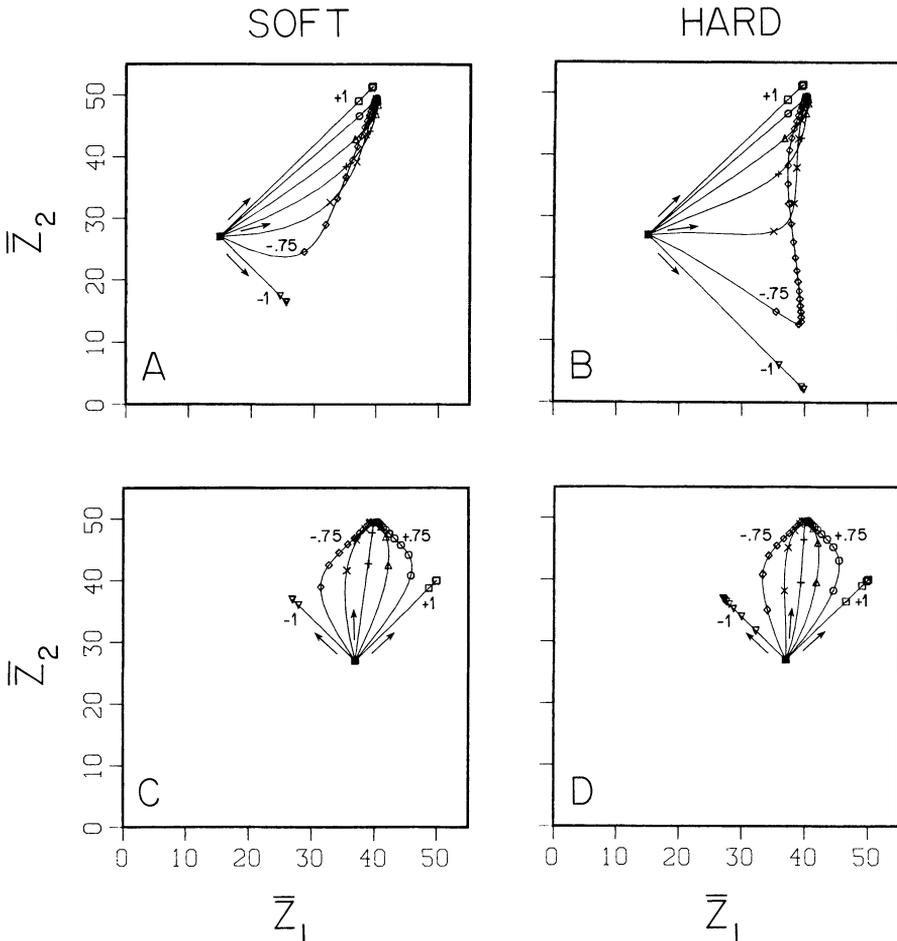


FIG. 3. Effects of genetic correlation across environments on the trajectory of the mean phenotype when environments are represented in unequal frequencies or when the population is initially well adapted to only one environment. Except as noted, parameters are the same as Figure 1; symbols are as in Figure 2. Optima are $\theta_1 = 40$ and $\theta_2 = 50$. In A and B, the initial values are $\bar{z}_1 = 15$, $\bar{z}_2 = 27$, $q = 0.7$; in C and D, the initial values are $\bar{z}_1 = 37$, $\bar{z}_2 = 27$ and $q = 0.5$.

to another plant species, the population might be expected to be close to the optimum phenotype on the old plant, but poorly adapted to the new host plant. The numerical example shown in Figure 3C illustrates that the most direct evolution in this situation occurs when the character of interest is genetically uncorrelated across environments. High positive genetic correlations between character states in different environments cause an overshoot of the optimum in the envi-

ronment where the initial mean phenotype was well adapted, while negative genetic correlations lead to similar maladaptive evolution in the opposite direction. As expected from the eigenvalues, high genetic correlations of either sign also substantially decrease the rate of approach to the joint optimum; in both cases, some evolution must occur in a direction with a very small eigenvalue.

In these examples, the population may experience selection in different direc-

tions in the two environments when it is far from the joint optimum. This can increase the genetic variation. However, numerical examples in which (1) is coupled with an equation for the evolution of genetic variance under soft selection reveal that the qualitative patterns presented in the figures are not greatly affected by evolutionary change in the genetic covariance matrix, G (Via and Lande, unpubl.).

Hard Selection.—The dynamical equation for phenotypic evolution under hard selection can be expressed in a form which differs from (1) only by the weighting function: the contribution of each environment to the total population is now the product of its frequency, q , and the relative mean fitness (\bar{W}_i/\bar{W}) of individuals selected there, where, as shown below, $\bar{W} = q\bar{W}_1 + (1 - q)\bar{W}_2$. For the two environment case,

$$\begin{aligned} & \begin{pmatrix} \Delta \bar{z}_1 \\ \Delta \bar{z}_2 \end{pmatrix} \\ &= \begin{pmatrix} G_{11} & G_{12} \\ G_{21} & G_{22} \end{pmatrix} \begin{pmatrix} [q\bar{W}_1/\bar{W}]P_{11}^{-1}s_1 \\ [(1 - q)\bar{W}_2/\bar{W}]P_{22}^{-1}s_2 \end{pmatrix} \\ &= \begin{pmatrix} G_{11} & G_{12} \\ G_{21} & G_{22} \end{pmatrix} \begin{pmatrix} [q\bar{W}_1/\bar{W}]\nabla_1 \ln \bar{W}_1 \\ [(1 - q)\bar{W}_2/\bar{W}]\nabla_2 \ln \bar{W}_2 \end{pmatrix} \end{aligned} \quad (9)$$

Noting that \bar{W}_2 is not a function of \bar{z}_1 , so that $\delta \bar{W}_2/\delta \bar{z}_1 = 0$,

$$\begin{aligned} & (q\bar{W}_1/\bar{W})\nabla_1 \ln \bar{W}_1 \\ &= (q/\bar{W})(\delta \bar{W}_1/\delta \bar{z}_1) \\ &= (1/\bar{W})[q\delta \bar{W}_1/\delta \bar{z}_1 \\ &\quad + (1 - q)\delta \bar{W}_2/\delta \bar{z}_1] \\ &= \nabla_1 \ln \bar{W} \end{aligned} \quad (10)$$

and similarly for the second term in the selection vector on the right side of (10). Hence,

$$\begin{aligned} \begin{pmatrix} \Delta \bar{z}_1 \\ \Delta \bar{z}_2 \end{pmatrix} &= \begin{pmatrix} G_{11} & G_{12} \\ G_{21} & G_{22} \end{pmatrix} \\ &\quad \cdot \begin{pmatrix} \nabla_1 \\ \nabla_2 \end{pmatrix} \ln [q\bar{W}_1 + (1 - q)\bar{W}_2]. \end{aligned} \quad (11)$$

The gradient vector in (11) reveals that the joint mean fitness (\bar{W}) in hard selection is the arithmetic average of the mean fitnesses in the separate environments. Thus, the adaptive topographies for soft and hard selection differ (Fig. 1); in hard selection, the joint fitness function is no longer bivariate normal. It is of interest to note that both of the adaptive topographies in these polygenic models are the same as derived in the corresponding single locus treatments (e.g., Li, 1955; Dempster, 1955).

The difference in the adaptive landscapes for the two modes of selection is reflected in the evolutionary trajectories which are expected following a perturbation. Under hard selection, even a small asymmetry in the initial location of the phenotype in the two niches relative to the joint optimum (Fig. 2B, D) causes evolution of the character state expressed in the environment with the lowest initial mean fitness (here, \bar{z}_1) to be dominated by the correlated response to selection on the character state in the other environment. When that character state (\bar{z}_2) approaches its optimum, the intensity of selection on it will diminish and the characters in other environments will begin to proceed more directly toward their optima. Only if no asymmetries exist in the variances, the selection parameters, or the initial distance from the phenotypic optimum in the two environments, will the evolutionary trajectories of the mean phenotypes proceed directly toward the optimum regardless of the cross-environment genetic correlation. This degree of symmetry is unlikely in natural populations. Note that maladaptive correlated responses can occur whether the characters are selected in the same or in different directions (compare Fig. 2B, D).

As in soft selection, adaptation will occur first in the most abundant environment, and only later in rare ones (Fig. 3B). When individuals are initially much better adapted to one environment than the other, Figure 3D illustrates that high genetic correlations between character states can cause evolution away from the

optimum for the character in the environment to which individuals were initially better adapted.

Because the equations for hard selection (9, 11) are non-linear, eigenvalues of a linearized version describe the rates of evolution only when the joint mean phenotype is near the optimum. In that case, the weightings are roughly constant and the eigenvalues can be approximated by those already presented for soft selection. Numerical iterations of the hard selection models show that the rates are indeed close to those under soft selection. The evolutionary rates in the examples can also be roughly compared by using the generation markers on the figures.

Using a proof analogous to (6), it can be shown that the joint mean fitness under hard selection will also increase until an equilibrium is reached in each environment with the mean phenotype at the optimum. However, as in soft selection, mean fitness in one of the environments can temporarily decrease under hard selection during the course of evolution. This decrease can be pronounced, tending to occur in the rare environment or the one in which mean fitness is initially lowest.

Genetic Models of Subdivided Populations

Most theoretical treatments of subdivided populations have noted that population divergence is increasingly likely with reduced migration (Maynard Smith, 1966; Dickinson and Antonovics, 1973; Felsenstein, 1981). Subdivided population models of evolution in two environments were made to determine whether restricted migration can decrease the constraining effects of high genetic correlations across environments and thus facilitate local adaptation.

When the population is subdivided, the distributions of genotypes may differ in the two environments. As before, each character state is expressed in only one environment. However, the unexpressed states must be followed in each environ-

ment because the genes which determine them will be carried by migrants to the alternate environment where they will be expressed. For the two environment case, four variables are defined for each trait of interest: z_{ij} is the character state which is expressed in the i th environment but carried by individuals located in the j th environment. When $i \neq j$, the character state is not expressed and will evolve only by correlated responses to selection on the expressed state. Thus, z_{11} is the character state which is both expressed in environment 1 and carried by individuals located there, while z_{21} is the value of the character which is expressed in environment 2, but which is carried by individuals located in environment 1. Therefore, only z_{11} and z_{22} are exposed to direct selection, while z_{12} and z_{21} are unexpressed. Note that in a subdivided population, unexpressed characters may temporarily diverge from the versions expressed in the other environment (i.e., $\bar{z}_{21} \neq \bar{z}_{22}$ and $\bar{z}_{12} \neq \bar{z}_{11}$). As before, the gradients of mean fitness, $\nabla_1 \ln \bar{W}_1$ and $\nabla_2 \ln \bar{W}_2$, are functions only of \bar{z}_{11} and \bar{z}_{22} respectively.

Individuals migrate before selection with equal propensity and enter the two environments randomly in proportion to their representation in the migrant pool. Mating, reproduction and selection then occur in each environment. Under soft selection, niches contribute to the pool in constant proportions. Under hard selection, the contribution of each niche to the migrant pool varies through time, weighted both by niche frequency (q) and by local relative mean fitness (\bar{W}_i/\bar{W}). Thus, the hard selection model is equivalent to a form of group selection mediated by differential migration. If selection is assumed to be weak and the means in the two populations remain similar, then the matrix of genetic variances and covariances can be assumed to remain nearly constant throughout the course of evolution. If the means of the subpopulations do become appreciably different, these approximations will not be very accurate because they are based on a nor-

mal distribution of phenotypes before selection.

From the derivations in the Appendix, the dynamic equation for phenotypic change under soft selection in a subdivided population is

$$\begin{pmatrix} \Delta \bar{z}_{11} \\ \Delta \bar{z}_{21} \\ \Delta \bar{z}_{12} \\ \Delta \bar{z}_{22} \end{pmatrix} = \begin{pmatrix} G_{11} & G_{12} & 0 & 0 \\ G_{21} & G_{22} & 0 & 0 \\ 0 & 0 & G_{11} & G_{12} \\ 0 & 0 & G_{21} & G_{22} \end{pmatrix} \cdot \begin{pmatrix} [1 - m(1 - q)]\nabla_1 \ln \bar{W}_1 \\ m(1 - q)\nabla_2 \ln \bar{W}_2 \\ mq\nabla_1 \ln \bar{W}_1 \\ (1 - mq)\nabla_2 \ln \bar{W}_2 \end{pmatrix} - m \begin{pmatrix} (1 - q)(\bar{z}_{11} - \bar{z}_{12}) \\ (1 - q)(\bar{z}_{21} - \bar{z}_{22}) \\ q(\bar{z}_{12} - \bar{z}_{11}) \\ q(\bar{z}_{22} - \bar{z}_{21}) \end{pmatrix} \quad (12)$$

where m is the proportion of each population which is composed of migrants each generation and selection is assumed to act independently in each environment. This independence allows the combination of Equations A6 into this single equation, with zeros in the off-diagonal submatrices of G . With panmixis, $m = 1$ and $\Delta \bar{z}_i = q\Delta \bar{z}_{i1} + (1 - q)\Delta \bar{z}_{i2}$. Then (12) reduces to (5), the basic equation for soft selection in a single panmictic population.

At equilibrium, the populations under selection in different environments will generally converge, not necessarily to the same optimum, but to the same vector of mean breeding values, so that indirectly selected characters attain the same value as their directly selected counterparts ($\bar{z}_{11} = \bar{z}_{12}$ and $\bar{z}_{21} = \bar{z}_{22}$, see Appendix for details). Thus, a reciprocal transplant or its laboratory analog in which samples from several populations at equilibrium were raised in each environment would reveal no geographical variation in the vector of mean phenotypes (\bar{z}), even though the mean phenotype ex-

pressed in each environment might differ.

If any of three well defined conditions pertain, however, the vectors of mean phenotypes in the subpopulations will not be equal at equilibrium: 1) if there is no migration among environments; 2) if genetic variance in one of the character states is exhausted; or 3) if the genetic correlation across environments is ± 1 . Moreover, if there is a cost to phenotypic plasticity, the population may also equilibrate away from the optimum. These cases are discussed below. Finally, if there is very low migration, low genetic variation, or a very high genetic correlation, it may take so long to reach equilibrium that the joint optimum may move before it is attained. Thus, geographical variation in the vector of mean breeding values could be visible for a very long period of time if the genetic correlation structure is unfavorable.

To determine the rate of approach to the joint optimum under population subdivision, a stability analysis of a symmetrized version of this model with $q = 0.5$ and the same pattern of variation and selection in each niche was performed (see the Appendix). From the eigenvalues given in the Appendix, it can be shown that if migration is a much stronger force than selection [$m \gg G/(\omega^2 + P)$], geographical variation in the vector of mean breeding values is reduced on the time scale of $1/m$ generations; as migration increases, the time required to homogenize the populations genetically is reduced. In this case, as in the panmictic model, the time scale for the approach of the mean phenotype to the joint optimum is roughly the larger of $2(\omega^2 + P)/G(1 \pm \gamma)$ generations. In contrast, if selection is the stronger force ($G/(\omega^2 + P) \gg m$), then geographical variation in the vector of mean breeding values decreases on a time scale which is approximately the larger of $2/(1 \pm \gamma)m$ generations, and the mean phenotype in each environment evolves toward its optimum on a time scale of $(\omega^2 + P)/G$ generations.

The dynamical equations for hard selection in a subdivided population are derived in the Appendix.

DISCUSSION

Using the observation that a trait expressed in two environments can be considered to be two genetically correlated characters (Falconer, 1952; Robertson, 1959; Yamada, 1962; Fernando et al., 1984), the models derived here link evolution in heterogeneous environments to existing theory describing the evolutionary effects of genetic correlations on evolution in single environments (Hazel, 1943; Dickerson, 1955; Lande, 1979). If, as we assume, the covariance between the character states expressed in different environments is primarily due to pleiotropy (Lande, 1980*a*), then the genetic correlation across environments estimates the extent to which the phenotype in different habitats is determined by the same alleles acting in the same way (Falconer, 1981; Pirchner, 1983). A significant genotype-environment interaction reveals only that the genetic correlation across environments is less than +1; the resolution of genotype-environment interaction is thus too poor for a quantitative understanding of its evolutionary effects (Robertson, 1959).

Two types of selection have been considered in coarse-grained environments where individuals experience only one selection regime. Under soft selection, the fraction of the total population contributed from each environment is constant, while under hard selection, the contribution of each niche depends on the mean fitness of individuals in it relative to that in other environments. Under hard selection, even slight asymmetry in the distance of the characters from their optima, in the genetic parameters, or in the intensity of selection in the two environments leads to an asymmetry in the contribution of the environments to the mating pool (9): the environment with the highest initial mean fitness will contribute increasing numbers of individuals to the total population until its individual

phenotypic optimum is nearly attained. During this phase, genetic correlations between the phenotypes expressed in two different niches can cause the evolutionary trajectory of the mean bivariate phenotype to deviate far from a direct course toward the joint optimum (e.g., Fig. 2B, D). With an unfavorable correlation structure, populations under either soft or hard selection will evolve to the optimum most rapidly in common or favorable environments; adaptation to rare or marginal habitats will occur later (Fig. 3C, D). Unless the genetic correlation is ± 1 , however, the maladaptation which may occur will be temporary. Because conditions in natural populations will rarely be perfectly symmetrical, it is possible that the sort of asymmetrical evolution illustrated in the examples may often occur. The addition of more characters or environments may further retard the course of evolution.

The differences between the evolutionary patterns shown in the figures are primarily determined by the relative positions of the initial mean phenotype and the joint optimum, not by whether the optima in the two environments are the same or different. If the phenotypic optima differ across environments, then these models describe the evolution of phenotypic plasticity. The case in which the optima in the two environments are the same is a special case of this more general evolutionary problem.

These models illustrate that when conditions are such that the joint optimum is attained by the population at equilibrium, genetic variation will not be maintained in quantitative characters by environmental heterogeneity. At the optimum, the population will be under bivariate stabilizing selection, which cannot maintain genetic variation. Variance around the equilibrium norm of reaction will, however, be generated by mutation. The genotype-environment interaction in fitness which this mutation produces will equilibrate in a mutation-selection balance (Lande, 1976, 1980*a*; Turelli, 1984).

Several circumstances exist which can prevent the joint optimum from being attained at equilibrium, precluding the evolution of a selectively advantageous level of phenotypic plasticity. 1) If the genetic correlation of character states in two environments is ± 1 , then \mathbf{G} is singular and no genetic variation exists for evolution in one of the principle directions in phenotype space (one of the eigenvalues will be zero). Almost any perturbation from the joint optimum will then result in a permanent displacement of the population from the optimum. In this case, there will be spatial variation in the direction of selection and a corresponding increase in the genetic variance (Slatkin, 1978; Via and Lande, unpubl.). In an analogous way, if n characters are simultaneously selected to increase in a range of environments, then an average correlation of $-1/(n-1)$ can halt the response to selection (Dickerson, 1955). Thus, even small negative correlations among a large suite of characters simultaneously selected in several environments can virtually preclude evolutionary change. Genetic correlations may thus place an upper limit on the number of environments to which a population can simultaneously adapt. 2) If genetic variation in either character state is exhausted, evolution toward the joint optimum will cease. Thus, some optima may never be attained simply because there is no genetic variation in that direction. This is another way of describing a "developmental constraint." 3) If no gene flow occurs between subdivided populations ($m = 0$ in Eq. 12), populations in different environments will never converge to the joint optimum because the states which are not expressed in a given environment are not subjected to selection there. In this case, if individuals from each environment were allowed to develop both in the home and in the alternate environment, geographical variation in the vectors of breeding values would be expected at equilibrium. 4) If individuals can select their habitat, or tend to return to their home environ-

ment, migration among subpopulations may be greatly decreased, speeding local adaptation and population divergence. In extreme cases, this could lead to such low migration that the subpopulations could become reproductively isolated before the joint optimum is attained. 5) If there is a "cost" to plasticity, then selection will act to make the character states expressed in different environments more similar. Eventually, this force is expected to oppose the force of selection for plasticity, resulting in an equilibrium with the mean phenotype located somewhere between the joint optimum and a point at which the mean phenotypes expressed in each environment are the same (Via, unpubl.). The frequency of any of these cases relative to the situation in which the optimum is reached at equilibrium remains as an empirical question.

The possibility that many field populations may not yet be at equilibrium due to an unfavorable correlation structure complicates the interpretation of experimental data: differences observed between the mean phenotypes in different environments may reflect a deflection of the evolutionary trajectory due to genetic correlations among homologous traits rather than indicating variation in phenotypic optima in different habitats. This problem can be particularly important when the environments under consideration are the product of relatively recent man-made disturbance (e.g., Snaydon, 1970; Antonovics, 1971). In such situations, non-equilibrium phenotypic states may be more the rule than the exception.

A theory of evolution in heterogeneous environments based on genetic correlation may allow some long-standing ecological hypotheses to be tested. For example, host plants often form discrete patches which act as different selective environments for herbivores (e.g., Gilbert, 1978). Genetically based "trade-offs" in the expression of traits like growth or feeding behavior on different host plants (estimable as genetic correlations across hosts) have been thought to be important in the evolution of herbivore spe-

cialization (Rausher, 1984; Futuyma, 1985). By formalizing ecological hypotheses like the "tradeoff" concept, these models suggest the experimental data which should be taken to test their role in the evolution of populations in variable environments.

Estimates of the genetic covariance structure will, of course, be most useful in the interpretation of field data when accompanied by estimates of the shape of the selective surface and the intensity of selection (cf. Lande and Arnold, 1983), as well as by information on the extent of migration and the relative niche proportions. For example, if one observes phenotypic differentiation among populations inhabiting different environments, the estimation of a directional component to selection in the various environments will reveal that the phenotypes observed are not at the individual optima and can also provide an estimate of the location of the joint optimum. Then, estimates of non-zero genetic variation, a genetic correlation between -1 and $+1$, and non-zero migration can be used to eliminate the possibility that the population is at an equilibrium away from the joint optimum. In this case, one could infer that evolution of the norm of reaction is still in progress.

The subdivided population model suggests that the vectors of breeding values of expressed and unexpressed traits estimated from samples of populations in different environments are generally expected to be equal at equilibrium, even though the mean character states expressed may differ across environments. Thus, genetic variation among populations, manifest in variation in the vector of mean breeding values, cannot be used as a criterion for adaptation to special environmental circumstances. However, because some phenotypic variance about the mean will usually exist in each environment at equilibrium, techniques for estimating the existence and intensity of stabilizing selection (Lande and Arnold, 1983) can be employed to determine whether the phenotypic mean is actually

at a selective optimum in each environment. The expected equivalence of the phenotypic mean vector between subdivided populations provides an experimental criterion for equilibrium: if samples from several environments which are tested in all environments have significantly different mean vectors, then it can be hypothesized that further evolution should be expected unless there is no gene flow or the genetic covariance matrix is singular.

ACKNOWLEDGMENTS

We thank J. Cheverud, D. Futuyma, M. Kirkpatrick, T. Price, M. Slatkin, and M. Wade for comments on the manuscript and discussions of this topic. Support was provided by National Research Service Award GM-09597 to S. Via and U.S. Public Health Service grant GM-27120 to R. Lande.

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Corresponding Editor: C. Strobeck

APPENDIX

Subdivided Population Models: Soft Selection.—As described in the text, a single character which is expressed in two environments is considered. Assume that mating occurs within environments and that production of offspring is followed by selection which proceeds separately in each environment. Then in the first environment, the change in the mean phenotype after selection is

$$\begin{pmatrix} \Delta \bar{z}_{11} \\ \Delta \bar{z}_{21} \end{pmatrix} = \begin{pmatrix} G_{11} & G_{12} \\ G_{21} & G_{22} \end{pmatrix} \begin{pmatrix} \nabla_1 \ln \bar{W}_1 \\ 0 \end{pmatrix} \quad (\text{A1})$$

so that the mean breeding values, \bar{x}^* , after selection are

$$\begin{pmatrix} \bar{x}^*_{11} \\ \bar{x}^*_{21} \end{pmatrix} = \begin{pmatrix} G_{11} & G_{12} \\ G_{21} & G_{22} \end{pmatrix} \begin{pmatrix} \nabla_1 \ln \bar{W}_1 \\ 0 \end{pmatrix} + \begin{pmatrix} \bar{z}_{11} \\ \bar{z}_{21} \end{pmatrix}. \quad (\text{A2})$$

Similarly, the breeding values after selection in environment 2 are

$$\begin{pmatrix} \bar{x}^*_{12} \\ \bar{x}^*_{22} \end{pmatrix} = \begin{pmatrix} G_{11} & G_{12} \\ G_{21} & G_{22} \end{pmatrix} \begin{pmatrix} 0 \\ \nabla_2 \ln \bar{W}_2 \end{pmatrix} + \begin{pmatrix} \bar{z}_{12} \\ \bar{z}_{22} \end{pmatrix}. \quad (\text{A3})$$

In soft selection, each environment contributes migrants to a migrant pool according to its representation in the total environment. Thus, the mean breeding values in the migrant pool are

$$\begin{pmatrix} \bar{x}_{1m} \\ \bar{x}_{2m} \end{pmatrix} = q \begin{pmatrix} \bar{x}^*_{11} \\ \bar{x}^*_{21} \end{pmatrix} + (1 - q) \begin{pmatrix} \bar{x}^*_{12} \\ \bar{x}^*_{22} \end{pmatrix}. \quad (\text{A4})$$

After migration, migrants compose the same fraction, m , of the population in each environment, so that after migration, the breeding values in environment 1 are

$$\begin{aligned} \begin{pmatrix} \bar{x}'_{11} \\ \bar{x}'_{21} \end{pmatrix} &= (1 - m) \begin{pmatrix} \bar{x}^*_{11} \\ \bar{x}^*_{21} \end{pmatrix} + m \begin{pmatrix} \bar{x}_{1m} \\ \bar{x}_{2m} \end{pmatrix} \\ &= [1 - m(1 - q)] \begin{pmatrix} \bar{x}^*_{11} \\ \bar{x}^*_{21} \end{pmatrix} + m(1 - q) \begin{pmatrix} \bar{x}^*_{12} \\ \bar{x}^*_{22} \end{pmatrix} \end{aligned} \quad (\text{A5})$$

and similarly for \bar{x}'_{12} and \bar{x}'_{22} . Using (A2) and (A3), the changes in the mean phenotypes in the two environments are

$$\begin{pmatrix} \Delta \bar{z}_{11} \\ \Delta \bar{z}_{21} \end{pmatrix} = [1 - m(1 - q)] \begin{pmatrix} G_{11} \nabla_1 \ln \bar{W}_1 \\ G_{21} \nabla_1 \ln \bar{W}_1 \end{pmatrix} + m(1 - q) \begin{pmatrix} G_{12} \nabla_2 \ln \bar{W}_2 \\ G_{22} \nabla_2 \ln \bar{W}_2 \end{pmatrix} - m(1 - q) \begin{pmatrix} \bar{z}_{11} - \bar{z}_{12} \\ \bar{z}_{21} - \bar{z}_{22} \end{pmatrix} \quad (\text{A6})$$

and

$$\begin{pmatrix} \Delta \bar{z}_{12} \\ \Delta \bar{z}_{22} \end{pmatrix} = (1 - mq) \begin{pmatrix} G_{12} \nabla_2 \ln \bar{W}_2 \\ G_{22} \nabla_2 \ln \bar{W}_2 \end{pmatrix} + mq \begin{pmatrix} G_{11} \nabla_1 \ln \bar{W}_1 \\ G_{21} \nabla_1 \ln \bar{W}_1 \end{pmatrix} - mq \begin{pmatrix} \bar{z}_{12} - \bar{z}_{11} \\ \bar{z}_{22} - \bar{z}_{21} \end{pmatrix}.$$

Rearrangement leads to (12) in the text.

Equilibria.—At an equilibrium, there is no change in the mean breeding values. Hence,

$$\begin{pmatrix} G_{11} & G_{12} \\ G_{21} & G_{22} \end{pmatrix} \begin{pmatrix} [1 - m(1 - q)] \nabla_1 \ln \bar{W}_1 \\ m(1 - q) \nabla_2 \ln \bar{W}_2 \end{pmatrix} = m(1 - q) \begin{pmatrix} \bar{z}_{11} - \bar{z}_{12} \\ \bar{z}_{21} - \bar{z}_{22} \end{pmatrix},$$

and

$$\begin{pmatrix} G_{11} & G_{12} \\ G_{21} & G_{22} \end{pmatrix} \begin{pmatrix} mq \nabla_1 \ln \bar{W}_1 \\ (1 - mq) \nabla_2 \ln \bar{W}_2 \end{pmatrix} = mq \begin{pmatrix} \bar{z}_{12} - \bar{z}_{11} \\ \bar{z}_{22} - \bar{z}_{21} \end{pmatrix}. \quad (\text{A7})$$

Thus, if $0 < q < 1$, $|G| \neq 0$ and $m \neq 0$, at equilibrium:

$$\begin{pmatrix} \nabla_1 \ln \bar{W}_1 \\ \nabla_2 \ln \bar{W}_2 \end{pmatrix} = \mathbf{0} \quad \text{and} \quad \begin{pmatrix} \bar{z}_{11} \\ \bar{z}_{21} \end{pmatrix} = \begin{pmatrix} \bar{z}_{12} \\ \bar{z}_{22} \end{pmatrix}. \quad (\text{A8})$$

This result means that the mean phenotype is at a local maximum of \bar{W} in each environment and there is no geographic variation in the vector of mean breeding values (\bar{z}) when samples of individuals derived from different environments are raised in each of the environmental alternatives.

Stability.—With Gaussian fitness functions, stability properties can be determined for the symmetrical

case with $G_{11} = G_{22} = G$, $G_{12} = G_{21} = \gamma G$, $\omega_1 = \omega_2 = \omega$, $P_{11} = P_{22} = P$, $q = 0.5$, and arbitrarily setting $\theta_1 = \theta_2 = 0$. Then, (12) is

$$\begin{pmatrix} \Delta \bar{z}_{11} \\ \Delta \bar{z}_{12} \\ \Delta \bar{z}_{22} \\ \Delta \bar{z}_{21} \end{pmatrix} = \begin{pmatrix} \beta - (1 + \beta)m/2 & m/2 & \gamma\beta m/2 & 0 \\ (1 + \beta)m/2 & -m/2 & \gamma\beta(1 - m/2) & 0 \\ \gamma\beta m/2 & 0 & \beta - (1 + \beta)m/2 & m/2 \\ \gamma\beta(1 - m/2) & 0 & (1 + \beta)m/2 & -m/2 \end{pmatrix} \begin{pmatrix} \bar{z}_{11} \\ \bar{z}_{12} \\ \bar{z}_{22} \\ \bar{z}_{21} \end{pmatrix}, \quad (\text{A9})$$

where $\beta = -G/(\omega^2 + P)$. The four eigenvalues of the matrix are always real and negative, with a magnitude less than or equal to unity:

$$\begin{aligned} \lambda &= \frac{1}{2}\{[1 - (1 - \gamma)m/2]\beta - m \pm \sqrt{([1 - (1 - \gamma)m/2]\beta - m)^2 + 2(1 + \gamma)m\beta}\} \\ \lambda &= \frac{1}{2}\{[1 - (1 + \gamma)m/2]\beta - m \pm \sqrt{([1 - (1 + \gamma)m/2]\beta - m)^2 + 2(1 - \gamma)m\beta}\}. \end{aligned} \quad (\text{A10})$$

Thus, the equilibrium with the mean phenotypes at the optimum in each environment is asymptotically stable, and no geographical variation is maintained in the vector of mean breeding values unless $\gamma = \pm 1$ or $m = 0$.

Hard Selection.—The hard selection model is constructed similarly to the soft selection one, except that the contribution of each niche to the migrant pool is weighted both by its proportional representation and by its mean fitness:

$$\begin{pmatrix} \bar{x}_{1m} \\ \bar{x}_{2m} \end{pmatrix} = [q\bar{W}_1/\bar{W}] \begin{pmatrix} \bar{x}_{11}^* \\ \bar{x}_{21}^* \end{pmatrix} + [(1 - q)\bar{W}_2/\bar{W}] \begin{pmatrix} \bar{x}_{12}^* \\ \bar{x}_{22}^* \end{pmatrix}, \quad (\text{A11})$$

where $\bar{W} = q\bar{W}_1 + (1 - q)\bar{W}_2$. The selection in each environment before migration is the same as in soft selection (Eqs. A2 and A3), and the rest of the model proceeds in the same way as in Eqs. A5 and A6 to produce the dynamic equations for hard selection.