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Measuring Multivariate Selection

Building on the machinery introduced in Chapter 31, these next two chapters extend the concepts for univariate selection (Chapters 25-30) to multivariate selection. This chapter considers the measurement of multivariate selection and hence focuses on **phenotypic selection** (the **within-generation** effects of selection on the multivariate distribution of phenotypes), while Chapter 33 is concerned with the **response to selection** (how these within-generation changes are passed onto the next generation). The complication introduced by multiple characters is the potential presence of phenotypic and/or genetic associations between characters. This chapter examines the consequence of **phenotypic** correlations, while the next examines the role of **genetic** correlations. Essentially all the measures of phenotypic selection discussed here are multivariate extensions of measures introduced in Chapter 30. We also rely rather heavily in places on the matrix machinery developed in Chapter 31 (especially extracting the canonical axis of a quadratic form and taking derivatives of vector-valued functions), so that the reader may wish to review these before proceeding.

SELECTION ON MULTIVARIATE PHENOTYPES: DIFFERENTIALS AND GRADIENTS

Chapter 30 described a variety of measures of univariate selection, with an emphasis on approximating the individual fitness function. In extending these methods to multiple characters, our main concern besides those discussed in Chapter 30 is the effect of phenotypic correlations. Our development is based on the multiple regression approach of Lande and Arnold (1983). Similar approaches based on path analysis (Appendix 2) have also been suggested e.g., (Maddox and Antonovics 1983, Mitchell-Olds 1987, Crespi and Bookstein 1988). These offer a complementary method of analysis as is discussed below.

The phenotype of an individual is now a vector $\mathbf{z} = (z_1, z_2, \dots, z_n)^T$ of n character values. Denote the mean vector and covariance matrix of \mathbf{z} before selection by $\boldsymbol{\mu}$ and \mathbf{P} , and by $\boldsymbol{\mu}^*$ and \mathbf{P}^* after selection (but before reproduction). To avoid additional complications, we examine only a single episode of selection. Partitions over multiple episodes follow as simple and obvious extensions of the univariate partitions discussed in Chapter 30.

Changes in the Mean Vector: The Directional Selection Differential s

The multivariate extension of the **directional selection differential** is the vector

$$s = \mu^* - \mu$$

whose i th element is s_i , the differential for character z_i . As with the univariate case, the Robertson-Price identity (Equation 3.21) holds, so that the elements of s represent the covariance between character value and relative fitness, $s_i = \sigma(z_i, w)$. This immediately implies (Equation 29.5) that the opportunity for selection I (the population variance in **relative** fitness) bounds the range of s_i ,

$$\frac{|s_i|}{\sigma_{z_i}} \leq \sqrt{I} \tag{20.1}$$

As is illustrated in Figure 20.1, s confounds the direct effects of selection on a character with the indirect effects due to selection on phenotypically correlated characters. Suppose character 1 is under direct selection to increase in value while character 2 is not directly selected. As Figure 20.1 shows, if z_1 and z_2 are uncorrelated, there is no within-generation change in μ_2 (the mean of z_2). However, if z_1 and z_2 are positively correlated, individuals with large values of z_1 also tend to have large values of z_2 , resulting in a within-generation increase in μ_2 . Conversely, if z_1 and z_2 are negatively correlated, selection to increase z_1 results in a within-generation decrease in μ_2 . Hence, a character not under selection can still experience a within-generation change in its phenotypic distribution due to selection on a phenotypically correlated character (indirect selection). Fortunately, the **directional selection gradient** $\beta = P^{-1}s$ accounts for indirect selection due to phenotypic correlations, providing a less biased picture of the nature of directional selection acting on z .

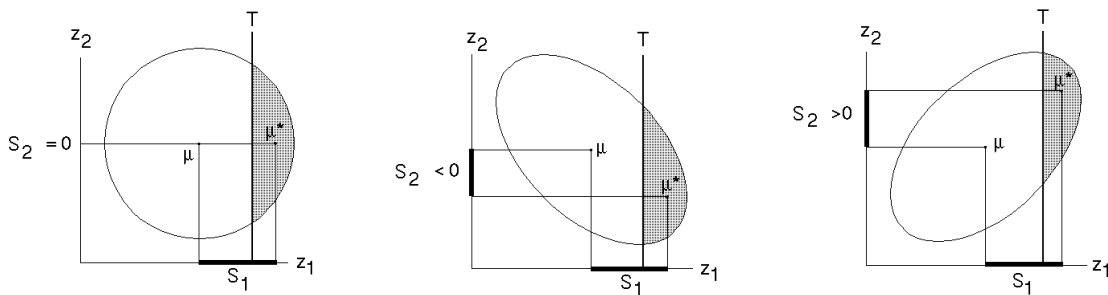


Figure 20.1. Selection on a character can result in a within-generation change in the mean of other phenotypically correlated characters not themselves under direct selection. Assume that character 1 is under simple truncation selection so that only individuals with $z_1 > T$ reproduce. **Left:** When z_1 and z_2 are

uncorrelated, $s_2 = 0$. **Center:** When z_1 and z_2 are negatively correlated, $s_2 < 0$.

Right: When z_1 and z_2 are positively correlated, $s_2 > 0$.

The Directional Selection Gradient β

As was discussed in Chapter 7, β removes the effects of phenotypic correlations because it is a vector of partial regression coefficients. From multiple regression theory (Chapter 7), the vector of partial regression coefficients for predicting the value of y given a vector of observations \mathbf{z} is $\mathbf{P}^{-1} \boldsymbol{\sigma}(\mathbf{z}, y)$ where \mathbf{P} is the covariance matrix of \mathbf{z} , and $\boldsymbol{\sigma}(\mathbf{z}, y)$ is the vector of covariances between the elements of \mathbf{z} and the variable y . Since $\mathbf{s} = \boldsymbol{\sigma}(\mathbf{z}, w)$, it immediately follows that

$$\mathbf{P}^{-1} \boldsymbol{\sigma}(\mathbf{z}, w) = \mathbf{P}^{-1} \mathbf{s} = \boldsymbol{\beta} \quad (20.2)$$

is the vector of partial regression for the best linear regression of **relative** fitness w on phenotypic value \mathbf{z} , viz.,

$$w(\mathbf{z}) = 1 + \sum_{j=1}^n \beta_j (z_j - \mu_j) = 1 + \boldsymbol{\beta}^T (\mathbf{z} - \boldsymbol{\mu}) \quad (20.3)$$

Since β_j is a partial regression coefficient, it represents the change generated in relative fitness by changing z_j while holding all other character values in \mathbf{z} constant — a one unit increase in z_j (holding all other characters constant) increases the expected relative fitness by β_j . Provided all characters under selection are measured (i.e., we can exclude the possibility of unmeasured characters influencing fitness that are phenotypically correlated with \mathbf{z}), a character under no directional selection has $\beta_j = 0$ — when all other characters are held constant, the best linear regression predicts no change in expected fitness as we change the value of z_j . Thus, $\boldsymbol{\beta}$ accounts for the effects of phenotypic correlations only among the **measured** characters. Provided we measure all characters under selection and there are no confounding environmental or genetic effects, $\boldsymbol{\beta}$ provides an unbiased measure of the amount of directional selection acting on each character. Some partial solutions when these complications arise are discussed later in this chapter.

Since $\mathbf{s} = \mathbf{P}\boldsymbol{\beta}$, we have

$$s_i = \sum_{j=1}^n \beta_j P_{ij} = \beta_i P_{ii} + \sum_{j \neq i}^n \beta_j P_{ij} \quad (20.4)$$

illustrating that the directional selection differential confounds direct selection on that character with indirect contributions due to selection on phenotypically correlated characters. Equation 20.4 implies that if two characters are phenotypically

uncorrelated ($P_{ij} = 0$), selection on one has no within-generation effect on the phenotypic mean of the other.

Directional Gradients, Fitness Surface Geometry and Selection Response

When phenotypes are multivariate normal, β provides a convenient descriptor of the geometry of both the individual and mean population fitness surfaces. As we have seen (Example 11 of Chapter 31),

$$\beta = \nabla_{\boldsymbol{\mu}}[\ln \bar{W}(\boldsymbol{\mu})] = \bar{W}^{-1} \cdot \nabla_{\boldsymbol{\mu}}[\bar{W}(\boldsymbol{\mu})] \quad (20.5a)$$

which holds provided fitnesses are frequency-independent (Lande 1976, 1979). In this case β is the gradient of **mean population** fitness with respect to the mean vector $\boldsymbol{\mu}$. Since β gives the direction of steepest increase in the mean population fitness surface, mean population fitness increases most rapidly when $\Delta\boldsymbol{\mu} = \beta$. If fitnesses are frequency-dependent (individual fitnesses change as the population mean changes), then for $\mathbf{z} \sim \text{MVN}$,

$$\beta = \nabla_{\boldsymbol{\mu}}[\ln \bar{W}(\boldsymbol{\mu})] + \int \nabla_{\boldsymbol{\mu}}[w(\mathbf{z})] \phi(\mathbf{z}) \, d\mathbf{z} \quad (20.5b)$$

where the second term accounts for the effects of frequency-dependence and ϕ is the MVN density function (Lande 1976). Here β does not point in the direction of steepest increase in \bar{W} unless the second integral is zero.

If we instead consider the **individual fitness** surface, we can alternatively consider β as the gradient of **individual fitnesses** averaged over the population distribution of phenotypes,

$$\beta = \int \nabla_{\mathbf{z}}[w(\mathbf{z})] \phi(\mathbf{z}) \, d\mathbf{z} \quad (20.6)$$

which holds provided $\mathbf{z} \sim \text{MVN}$ (Lande and Arnold 1983). To see this, using integration by parts gives

$$\int_{\mathbf{a}}^{\mathbf{b}} \nabla_{\mathbf{z}}[w(\mathbf{z})] \phi(\mathbf{z}) \, d\mathbf{z} = w(\mathbf{z}) \phi(\mathbf{z}) \Big|_{\mathbf{a}}^{\mathbf{b}} - \int_{\mathbf{a}}^{\mathbf{b}} \nabla_{\mathbf{z}}[\phi(\mathbf{z})] w(\mathbf{z}) \, d\mathbf{z}$$

Taking the limit as $\mathbf{a} \rightarrow -\infty$ and $\mathbf{b} \rightarrow \infty$, the first term on the right-hand side vanishes as $\phi(\mathbf{z}) \rightarrow 0$ when $\mathbf{z} \rightarrow \pm\infty$ (as the phenotypic distribution is assumed to be bounded). If $\mathbf{z} \sim \text{MVN}$, then Equation 31.49a gives

$$\begin{aligned} \int \nabla_{\mathbf{z}}[w(\mathbf{z})] \phi(\mathbf{z}) \, d\mathbf{z} &= - \int \nabla_{\mathbf{z}}[\phi(\mathbf{z})] w(\mathbf{z}) \, d\mathbf{z} = \int w(\mathbf{z}) \phi(\mathbf{z}) \mathbf{P}^{-1} (\mathbf{z} - \boldsymbol{\mu}) \, d\mathbf{z} \\ &= \mathbf{P}^{-1} \left(\int \mathbf{z} w(\mathbf{z}) \phi(\mathbf{z}) \, d\mathbf{z} - \boldsymbol{\mu} \int w(\mathbf{z}) \phi(\mathbf{z}) \, d\mathbf{z} \right) \\ &= \mathbf{P}^{-1} (\boldsymbol{\mu}^* - \boldsymbol{\mu}) = \mathbf{P}^{-1} \mathbf{s} = \beta \end{aligned}$$

Note from this derivation that Equation 20.6 holds regardless of whether fitness is frequency dependent or frequency independent.

Finally, while our focus has been on the role β plays in measuring phenotypic selection, it also plays an important role in the response to selection. If we can assume the breeders' equation holds, β is the only measure of phenotypic selection required to predict the response in mean as $\Delta\boldsymbol{\mu} = \mathbf{G}\beta$. Cheverud (1984) makes the important point that although it is often assumed a set of phenotypically correlated traits responds to selection in a coordinated fashion, this is not necessarily the case. Since β removes the effects of phenotypic correlations, phenotypic characters will only respond as a group if they are all under direct selection or if they are **genetically** correlated, a point we discuss in detail in the next chapter.

Changes in the Covariance Matrix: The Quadratic Selection Differential \mathbf{C}

Motivated by the univariate case wherein $C = \sigma[w, (z - \mu)(z - \mu)]$, we define the multivariate **quadratic selection differential** to be a square ($n \times n$) matrix \mathbf{C} whose elements are the covariances between all pairs of quadratic deviations $(z_i - \mu_{z_i})(z_j - \mu_{z_j})$ and relative fitness w , viz.,

$$C_{ij} = \sigma[w, (z_i - \mu_{z_i})(z_j - \mu_{z_j})] \quad (20.7a)$$

As is derived in Example 1, Lande and Arnold (1983) showed that

$$\mathbf{C} = \sigma[w, (\mathbf{z} - \boldsymbol{\mu})(\mathbf{z} - \boldsymbol{\mu})^T] = \mathbf{P}^* - \mathbf{P} + \mathbf{s}\mathbf{s}^T \quad (20.7b)$$

If no quadratic selection is acting, the covariance between each quadratic deviation and fitness is zero and $\mathbf{C} = \mathbf{0}$. In this case Equation 20.7b gives

$$P_{ij}^* - P_{ij} = -s_i s_j \quad (20.8)$$

demonstrating that the $s_i s_j$ term corrects C_{ij} for the change in covariance caused by directional selection alone.

Example 1. We wish to show $\mathbf{P}^* - \mathbf{P} = \sigma[w, (\mathbf{z} - \boldsymbol{\mu})(\mathbf{z} - \boldsymbol{\mu})^T] - \mathbf{s}\mathbf{s}^T$, which implies Equation 20.7b. From the definition of the variance-covariance matrix,

$$\mathbf{P} = E[(\mathbf{z} - \boldsymbol{\mu})(\mathbf{z} - \boldsymbol{\mu})^T] = \int (\mathbf{z} - \boldsymbol{\mu})(\mathbf{z} - \boldsymbol{\mu})^T p(\mathbf{z}) d\mathbf{z}$$

$$\mathbf{P}^* = E[(\mathbf{z}^* - \boldsymbol{\mu}^*)(\mathbf{z}^* - \boldsymbol{\mu}^*)^T] = \int (\mathbf{z} - \boldsymbol{\mu}^*)(\mathbf{z} - \boldsymbol{\mu}^*)^T p^*(\mathbf{z}) d\mathbf{z}$$

where $p^*(\mathbf{z}) = w(\mathbf{z})p(\mathbf{z})$ is the distribution of \mathbf{z} after selection (but before reproduction). Noting that $\boldsymbol{\mu}^* = \boldsymbol{\mu} + \mathbf{s}$,

$$\begin{aligned} (\mathbf{z} - \boldsymbol{\mu}^*)(\mathbf{z} - \boldsymbol{\mu}^*)^T &= (\mathbf{z} - \boldsymbol{\mu} - \mathbf{s})(\mathbf{z} - \boldsymbol{\mu} - \mathbf{s})^T \\ &= (\mathbf{z} - \boldsymbol{\mu} - \mathbf{s})(\mathbf{z} - \boldsymbol{\mu})^T - \mathbf{s}^T \\ &= (\mathbf{z} - \boldsymbol{\mu})(\mathbf{z} - \boldsymbol{\mu})^T - (\mathbf{z} - \boldsymbol{\mu})\mathbf{s}^T - \mathbf{s}(\mathbf{z} - \boldsymbol{\mu})^T + \mathbf{s}\mathbf{s}^T \end{aligned}$$

Since $\int \mathbf{z} p^*(\mathbf{z}) d\mathbf{z} = \boldsymbol{\mu}^*$ and $\int p^*(\mathbf{z}) d\mathbf{z} = 1$, we have that $\int \mathbf{s} \mathbf{s}^T p^*(\mathbf{z}) d\mathbf{z} = \mathbf{s} \mathbf{s}^T$,

$$\begin{aligned} \int (\mathbf{z} - \boldsymbol{\mu}) \mathbf{s}^T p^*(\mathbf{z}) d\mathbf{z} &= (\boldsymbol{\mu}^* - \boldsymbol{\mu}) \mathbf{s}^T = \mathbf{s} \mathbf{s}^T, \quad \text{and} \\ \int \mathbf{s} (\mathbf{z} - \boldsymbol{\mu})^T p^*(\mathbf{z}) d\mathbf{z} &= \mathbf{s} (\boldsymbol{\mu}^*)^T - \mathbf{s} \boldsymbol{\mu}^T = \mathbf{s} (\boldsymbol{\mu}^* - \boldsymbol{\mu})^T = \mathbf{s} \mathbf{s}^T \end{aligned}$$

Combining these results,

$$\begin{aligned} \mathbf{P}^* &= \int (\mathbf{z} - \boldsymbol{\mu}) (\mathbf{z} - \boldsymbol{\mu})^T w(\mathbf{z}) p(\mathbf{z}) d\mathbf{z} - \mathbf{s} \mathbf{s}^T - \mathbf{s} \mathbf{s}^T + \mathbf{s} \mathbf{s}^T \\ &= E [w(\mathbf{z}) \cdot (\mathbf{z} - \boldsymbol{\mu}) (\mathbf{z} - \boldsymbol{\mu})^T] - \mathbf{s} \mathbf{s}^T \end{aligned}$$

Since $E[w(\mathbf{z})] = 1$, we can write $\mathbf{P} = E[w(\mathbf{z})] \cdot \mathbf{P}$. Using the definition of \mathbf{P} then gives

$$\begin{aligned} \mathbf{P}^* - \mathbf{P} &= E [w(\mathbf{z}) \cdot (\mathbf{z} - \boldsymbol{\mu}) (\mathbf{z} - \boldsymbol{\mu})^T] - \mathbf{s} \mathbf{s}^T - E[w(\mathbf{z})] \cdot E[(\mathbf{z} - \boldsymbol{\mu}) (\mathbf{z} - \boldsymbol{\mu})^T] \\ &= \boldsymbol{\sigma} [w(\mathbf{z}), (\mathbf{z} - \boldsymbol{\mu}) (\mathbf{z} - \boldsymbol{\mu})^T] - \mathbf{s} \mathbf{s}^T \end{aligned}$$

with the last equality following from $\sigma(x, y) = E(x \cdot y) - E(x) E(y)$.

As was the case for \mathbf{s} , the fact that C_{ij} is a covariance immediately allows us to bound its range using the opportunity for selection. Since $\sigma^2(x, y) \leq \sigma^2(x) \sigma^2(y)$,

$$C_{ij}^2 \leq I \sigma^2[(z_i - \mu_{z_i})(z_j - \mu_{z_j})] \quad (20.9a)$$

When z_i and z_j are bivariate normal, then (Kendall and Stuart 1983),

$$\sigma^2[(z_i - \mu_{z_i})(z_j - \mu_{z_j})] = P_{ij}^2 + P_{ii} P_{jj} = P_{ij}^2 (1 + \rho_{ij}^{-2}) \quad (20.9b)$$

where ρ_{ij} is the phenotypic covariance between z_i and z_j . Hence, for Gaussian-distributed phenotypes,

$$\left| \frac{C_{ij}}{P_{ij}} \right| \leq \sqrt{I} \sqrt{1 + \rho_{ij}^{-2}} \quad (20.10)$$

which is a variant of the original bound based on I suggested by Arnold (1986).

The Quadratic Selection Gradient γ

Like \mathbf{s} , \mathbf{C} confounds the effects of direct selection with selection on phenotypically correlated characters. However, as was true for \mathbf{s} , these indirect effects

can also be removed by a regression. Consider the best **quadratic** regression of relative fitness as a function of phenotypic value,

$$w(\mathbf{z}) = a + \sum_{j=1}^n b_j z_j + \frac{1}{2} \sum_{j=1}^n \sum_{k=1}^n \gamma_{jk} (z_j - \mu_j)(z_k - \mu_k) \quad (20.11a)$$

$$= a + \mathbf{b}^T \mathbf{z} + \frac{1}{2} (\mathbf{z} - \boldsymbol{\mu})^T \boldsymbol{\gamma} (\mathbf{z} - \boldsymbol{\mu}) \quad (20.11b)$$

Using multiple regression theory (Lande and Arnold 1983) the matrix $\boldsymbol{\gamma}$ of quadratic partial regression coefficients is given by

$$\boldsymbol{\gamma} = \mathbf{P}^{-1} \boldsymbol{\sigma} [w, (\mathbf{z} - \boldsymbol{\mu})(\mathbf{z} - \boldsymbol{\mu})^T] \mathbf{P}^{-1} = \mathbf{P}^{-1} \mathbf{C} \mathbf{P}^{-1} \quad (20.12)$$

This is the **quadratic selection gradient** and (like $\boldsymbol{\beta}$) removes the effects of phenotypic correlations, providing a more accurate picture of how selection is operating on the multivariate phenotype.

The vector of linear coefficients \mathbf{b} for the quadratic regression need not equal the vector of partial regression coefficients $\boldsymbol{\beta}$ obtained by assuming only a **linear** regression. Equation 29.24 shows (for the univariate case) that if the phenotypic distribution is skewed, b is a function of both s and C , while β is only a function of s . When phenotypes are multivariate normal skew is absent and Lande and Arnold (1983) show that $\mathbf{b} = \boldsymbol{\beta}$, recovering the multivariate version of the Pearson-Lande-Arnold regression,

$$w(\mathbf{z}) = a + \boldsymbol{\beta}^T \mathbf{z} + \frac{1}{2} (\mathbf{z} - \boldsymbol{\mu})^T \boldsymbol{\gamma} (\mathbf{z} - \boldsymbol{\mu}) \quad (20.13)$$

Since the γ_{ij} are partial regression coefficients, they predict the change in expected fitness caused by changing the associated quadratic deviation while holding all other variables constant. Increasing $(z_j - \mu_j)(z_k - \mu_k)$ by one unit in such a way as to hold all other variables and pairwise combinations of characters constant, relative fitness is expected to increase by γ_{jk} for $j \neq k$ and by $\gamma_{jj}/2$ if $j = k$ (the difference arises because $\gamma_{jk} = \gamma_{kj}$, so that γ_{jk} appears twice in the regression unless $j = k$). The coefficients of $\boldsymbol{\gamma}$ thus describe the nature of selection on quadratic deviations from the mean for both single characters and pairwise combinations of characters. $\gamma_{ii} < 0$ implies fitness is expected to decrease as z_i moves away (in either direction) from its mean. As was discussed in Chapter 30, this is a necessary, *but not sufficient*, condition for stabilizing selection on character i . Similarly, $\gamma_{ii} > 0$ implies fitness is expected to increase as i moves away from its mean, again a necessary, but not sufficient conditional for disruptive selection. Turning to combinations of characters, non-zero values of γ_{jk} ($j \neq k$) suggests the presence of **correlation selection** — $\gamma_{jk} > 0$ suggests selection for a positive correlation between characters j and k , while $\gamma_{jk} < 0$ suggests selection for a negative correlation.

Example 2. Brodie (1992) examined one-year survivorship in the garter snake *Thamnophis ordinoides* in a population in Oregon. Over a three year period, 646 snakes were marked, 101 of which were eventually recaptured. Four morphological and behavior characters were measured — overall stripedness of the body color pattern (stripes), sprint speed, distance moved until an antipredator display performed, and number of reversals of direction during flight from predators (reversals). None of the β_i or γ_{ii} were significant. However, there was a significant quadratic association between striping pattern and number of reversals, with $\gamma_{ij} = -0.268 \pm 0.097$ (confidence intervals were generated using the delete-one jackknife program of Mitchell-Olds 1989). As is shown in Figure 20.2, the best-fitting quadratic regression of individual fitness has a saddle point. Brodie suggests a biological explanation for selection favoring a negative correlation between these two characters. The presence of body stripes makes it difficult for predators to judge the speed of the snake, so frequent reversals would be disadvantageous. Conversely, when the body pattern is banded, blotched or spotted, detection of movement by visual predators is enhanced. In such individuals, frequent reversals can disrupt a visual search.

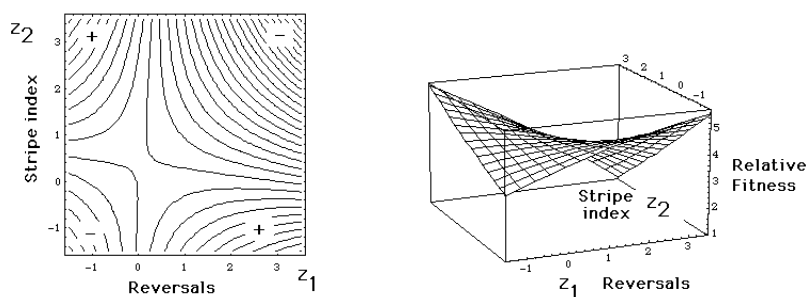


Figure 20.2. The fitness surface (measured as one-year survivorship) for z_1 (number of reversals) and z_2 (body stripe index) in the garter snake *Thamnophis ordinoides*. There is a significant correlational gradient between these two characters, with all other directional and quadratic gradients being nonsignificant. **Left:** Plotting lines of equal fitness, with peaks represented by a + and valleys by a - shows the best-fitting quadratic fitness surface has a saddle point. **Right:** Three-dimensional representation of the best-fitting quadratic fitness surface. The eigenvalues of γ are 0.256 and -0.290 , indicating roughly equal amounts of directional selection along one canonical axis (given by the index $0.77 \cdot z_1 - 0.64 \cdot z_2$) and stabilizing selection along the other ($0.64 \cdot z_1 + 0.77 \cdot z_2$). Data from Brodie (1992).

Although it seems straightforward to infer the overall nature of selection by looking at these various pairwise combinations, this can give a very misleading picture about the geometry of the fitness surface (e.g., Figure 20.3). We discuss this problem and its solution shortly.

Finally, we can see the effects of phenotypic correlations in the quadratic selection differential. Solving for \mathbf{C} by post- and pre-multiplying γ by \mathbf{P} gives $\mathbf{C} = \mathbf{P} \gamma \mathbf{P}$, or

$$C_{ij} = \sum_{k=1}^n \sum_{\ell=1}^n \gamma_{k\ell} P_{ik} P_{\ell j} \quad (20.14)$$

showing that within-generation changes in phenotypic covariance, as measured by \mathbf{C} , are influenced by quadratic selection on phenotypically-correlated characters.

Quadratic Gradients, Fitness Surface Geometry and Selection Response

When phenotypes are multivariate-normally distributed, γ provides a measure of the average curvature of the **individual** fitness surface, as

$$\gamma = \int \mathbf{H}_{\mathbf{z}}[w(\mathbf{z})] \phi(\mathbf{z}) d\mathbf{z} \quad (20.15a)$$

where $\mathbf{H}_{\mathbf{z}}[f]$ denotes the hessian with respect to \mathbf{z} and is a multivariate measure of the quadratic curvature of a function (see Chapter 31). This result, due to Lande and Arnold (1983) can be obtained by an integration by parts argument similar to that used to obtain Equation 20.6, and holds for both frequency-dependent and frequency-independent fitnesses. When fitnesses are frequency-independent (again provided $\mathbf{z} \sim \text{MVN}$), γ provides a description of the curvature of the **log mean population** fitness surface, with

$$\mathbf{H}_{\boldsymbol{\mu}}[\ln \bar{W}(\boldsymbol{\mu})] = \gamma - \boldsymbol{\beta} \boldsymbol{\beta}^T \quad (20.15b)$$

This result is due to Lande (cited in Phillips and Arnold 1989) and points out that there are two sources for curvature in the mean fitness surface: $-\boldsymbol{\beta} \boldsymbol{\beta}^T$ from directional selection and γ from quadratic selection.

Finally, when the breeders' equation holds, γ and $\boldsymbol{\beta}$ are sufficient to describe phenotypic selection on the additive-genetic covariance matrix. From Equation 31.41,

$$\begin{aligned} \mathbf{G}^* - \mathbf{G} &= \mathbf{G} \mathbf{P}^{-1} (\mathbf{P}^* - \mathbf{P}) \mathbf{P}^{-1} \mathbf{G} \\ &= \mathbf{G} \mathbf{P}^{-1} (\mathbf{C} - \mathbf{s} \mathbf{s}^T) \mathbf{P}^{-1} \mathbf{G} \\ &= \mathbf{G} (\mathbf{P}^{-1} \mathbf{C} \mathbf{P}^{-1} - (\mathbf{P}^{-1} \mathbf{s})(\mathbf{P}^{-1} \mathbf{s})^T) \mathbf{G} \\ &= \mathbf{G} (\gamma - \boldsymbol{\beta} \boldsymbol{\beta}^T) \mathbf{G} \end{aligned} \quad (20.16a)$$

Hence, the within-generation change in \mathbf{G} has a component from directional selection and a second due from quadratic selection,

$$\begin{aligned} \mathbf{G}^* - \mathbf{G} &= -\mathbf{G}\boldsymbol{\beta}\boldsymbol{\beta}^T\mathbf{G} + \mathbf{G}\boldsymbol{\gamma}\mathbf{G} \\ &= -\Delta\boldsymbol{\mu}\Delta\boldsymbol{\mu}^T + \mathbf{G}\boldsymbol{\gamma}\mathbf{G} \end{aligned} \tag{20.16b}$$

In terms of the change in covariance for two particular characters, this can be factored as

$$\begin{aligned} G_{ij}^* - G_{ij} &= -\left(\sum_{k=1}^n \beta_k G_{ik}\right)\left(\sum_{k=1}^n \beta_k G_{jk}\right) + \sum_{k=1}^n \sum_{\ell=1}^n \gamma_{k\ell} G_{ik} G_{\ell j} \\ &= -\Delta\mu_i \cdot \Delta\mu_j + \sum_{k=1}^n \sum_{\ell=1}^n \gamma_{k\ell} G_{ik} G_{\ell j} \end{aligned} \tag{20.16c}$$

Thus the within-generation change in the additive genetic variance of character i is given by

$$G_{ii}^* - G_{ii} = -(\Delta\mu_i)^2 + \sum_{k=1}^n \sum_{\ell=1}^n \gamma_{k\ell} G_{ik} G_{i\ell} \tag{20.16d}$$

Summary. Table 20.1 summarizes the main features of differentials and gradients.

Table 20.1. Analogous features of directional and quadratic differentials and gradients.

Changes in Means (Directional Selection)	Changes in Covariances (Quadratic Selection)
Differentials measure the covariance between relative fitness and phenotype	
$s_i = \sigma [w, z_i]$	$C_{ij} = \sigma [w, (z_i - \mu_i)(z_j - \mu_j)]$
The opportunity for selection bounds the differential	
$\frac{ s_i }{\sigma(z_i)} \leq \sqrt{I}$ for any distribution of \mathbf{z}	$\left \frac{C_{ij}}{P_{ij}} \right \leq \sqrt{I} \sqrt{1 + \rho_{ij}^{-2}}$ provided $\mathbf{z} \sim \text{MVN}$
Differentials confound direct and indirect selection	
$\mathbf{s} = \boldsymbol{\mu}^* - \boldsymbol{\mu} = \mathbf{P}\boldsymbol{\beta}$	$\mathbf{C} = \mathbf{P}^* - \mathbf{P} + \mathbf{s}\mathbf{s}^T = \mathbf{P}\boldsymbol{\gamma}\mathbf{P}$
Gradients measure the amount of direct selection	
$\boldsymbol{\beta} = \mathbf{P}^{-1}\mathbf{s}$	$\boldsymbol{\gamma} = \mathbf{P}^{-1}\mathbf{C}\mathbf{P}^{-1}$

Gradients describe the slope and curvature of the mean population fitness surface, provided $z \sim \text{MVN}$ and fitnesses are frequency-independent

$$\beta_i = \frac{\partial \ln \bar{W}(\boldsymbol{\mu})}{\partial \mu_i} \qquad \gamma_{ij} = \frac{\partial^2 \ln \bar{W}(\boldsymbol{\mu})}{\partial \mu_i \partial \mu_j} + \beta_i \beta_j$$

Gradients describe the average slope and average curvature of the individual fitness surface, provided $\mathbf{z} \sim \text{MVN}$

$$\beta_i = \int \frac{\partial w(\mathbf{z})}{\partial z_i} \phi(\mathbf{z}) d\mathbf{z} \qquad \gamma_{ij} = \int \frac{\partial^2 w(\mathbf{z})}{\partial z_i \partial z_j} \phi(\mathbf{z}) d\mathbf{z}$$

Gradients appear as coefficients in fitness regressions

$$w(\mathbf{z}) = a + \boldsymbol{\beta}^T (\mathbf{z} - \boldsymbol{\mu}) \qquad w(\mathbf{z}) = a + \mathbf{b}^T (\mathbf{z} - \boldsymbol{\mu}) + \frac{1}{2} (\mathbf{z} - \boldsymbol{\mu})^T \boldsymbol{\gamma} (\mathbf{z} - \boldsymbol{\mu})$$

$\boldsymbol{\beta}$ = slope of best linear fit $\boldsymbol{\gamma}$ = the quadratic coefficient of the best quadratic fit. $\mathbf{b} = \boldsymbol{\beta}$ when $\mathbf{z} \sim \text{MVN}$

Gradients appear as coefficients in evolutionary equations when $(\mathbf{z}, \mathbf{g}) \sim \text{MVN}$

$$\Delta \boldsymbol{\mu} = \mathbf{G} \boldsymbol{\beta} \qquad \mathbf{G}^* - \mathbf{G} = \mathbf{G} (\boldsymbol{\gamma} - \boldsymbol{\beta} \boldsymbol{\beta}^T) \mathbf{G}$$

MULTIDIMENSIONAL QUADRATIC FITNESS REGRESSIONS

As noted in Chapter 30, in many cases approximating the individual fitness function by a quadratic may give a very distorted view of the true fitness surface (e.g., when multiple fitness peaks are present). With this caveat in mind, quadratic fitness surfaces are still quite useful. One advantage is that a quadratic is the simplest surface allowing for curvature. Further, when phenotypes are gaussian distributed, the coefficients in the quadratic regression also appear as the coefficients of equations for predicting evolutionary change (Table 20.1). We briefly review some statistical issues of fitting such regressions before examining the geometry of multivariate quadratic regressions, which can get rather involved.

Estimation, Hypothesis Testing and Confidence Intervals

Even if we can assume that a best-fit quadratic is a reasonable approximation of the individual fitness surface, we are still faced with a number of statistical problems. Unless we test for, and confirm, multivariate normality (Chapter 31), $\boldsymbol{\beta}$ and $\boldsymbol{\gamma}$ must be estimated from separate regressions — $\boldsymbol{\beta}$ from the best linear regression, $\boldsymbol{\gamma}$ from the best quadratic regression. In either case, there are a large number of parameters to estimate — $\boldsymbol{\gamma}$ has $n(n+1)/2$ terms and $\boldsymbol{\beta}$ has n terms, for a total $n(n+3)/2$. With 5, 10, and 25 characters, this corresponds to 20, 65 and

350 parameters. The number of observations should greatly exceed $n(n+3)/2$ in order estimate these parameters with any precision.

A second problem is **multicollinearity** — if many of the characters being measured are highly correlated with each other, the phenotypic covariance matrix \mathbf{P} can be nearly singular, so that small errors in estimating \mathbf{P} result in large differences in \mathbf{P}^{-1} , which in turn gives a very large sampling variance for the estimate of β and γ . One possibility is to use principal components (Chapter 31) to extract a subset of the characters (measured as PCs, linear combinations of the characters) that explains most of the phenotypic variance of \mathbf{P} , and fitness regressions using the first few PCs as the characters can then be computed (Lande and Arnold 1983). This approach also reduces the problem of the number of parameters to estimate, but risks the real possibility of removing the most important characters. Further, PCs are often difficult to interpret biologically. While the first PC for morphological characters generally corresponds to a general measure of size, the others are typically much more problematic. Finally, using PCs can spread the effects of selection on one character over several PCs, further complicating interpretation.

A variety of additional concerns were discussed in Chapter 30. Briefly, residuals of fitness regressions are expected by their nature to be poorly-behaved so that standard methods of confidence intervals on regression coefficients are not appropriate. Mitchell-Olds and Shaw (1987) suggest using the delete-one jackknife method for approximating confidence intervals in this case, and Mitchell-Olds (1989) has developed a program to jackknife multivariate quadratic regressions. Likewise, the discussions of randomization tests and cross-validation procedures in Chapter 30 extend to multivariate regressions in a straightforward manner. Multivariate tests of the presence of a single mode in the fitness surface are discussed by Mitchell-Olds and Shaw (1987).

Geometric Aspects

In spite of their apparent simplicity, multivariate quadratic fitness regressions have a rather rich geometric structure. Scaling characters so that they have mean zero, the general quadratic fitness regression can be written as

$$w(\mathbf{z}) = a + \sum_{i=1}^n b_i z_i + \frac{1}{2} \sum_{i=1}^n \sum_{j=1}^n \gamma_{ij} z_i z_j = a + \mathbf{b}^T \mathbf{z} + \frac{1}{2} \mathbf{z}^T \boldsymbol{\gamma} \mathbf{z} \quad (20.17)$$

If $\mathbf{z} \sim \text{MVN}$, then $\mathbf{b} = \beta$ (the vector of coefficients of the best *linear* fit). Note by comparison to Equation 31.53 that if we regard Equation 20.17 as a second-order Taylor series approximation of $w(z)$, \mathbf{b} and $\boldsymbol{\gamma}$ can be interpreted as the gradient and hessian of individual fitness evaluated at the population mean (here $\boldsymbol{\mu} = \mathbf{0}$ by construction). The nature of curvature of Equation 20.17 is determined by the matrix $\boldsymbol{\gamma}$. Even though a quadratic is the simplest curved surface, its geometry can still be very difficult to visualize.

We start our exploration of this geometry by considering the gradient of this

best-fit quadratic fitness surface. Applying Equations 31.48a and 48c gives

$$\nabla_{\mathbf{z}}[w(\mathbf{z})] = \mathbf{b} + \gamma \mathbf{z} \quad (20.18a)$$

Thus, at the point \mathbf{z} the direction of steepest ascent on the fitness surface (the direction in which to move in phenotype space to maximally increase individual fitness) is given by the vector $\mathbf{b} + \gamma \mathbf{z}$ (when $\boldsymbol{\mu} = \mathbf{0}$). If the true individual fitness surface is indeed a quadratic, then the average gradient of individual fitness taken over the distribution of phenotypes is

$$\int \nabla_{\mathbf{z}}[w(\mathbf{z})] p(\mathbf{z}) d\mathbf{z} = \mathbf{b} \int p(\mathbf{z}) d\mathbf{z} + \gamma \int \mathbf{z} p(\mathbf{z}) d\mathbf{z} = \mathbf{b} \quad (20.18b)$$

as the last integral is $\boldsymbol{\mu}$ (which is zero by construction). Hence, if the true fitness function is quadratic, the average gradient of individual fitness is given by \mathbf{b} , independent of the distribution of \mathbf{z} .

Solving $\nabla_{\mathbf{z}}[w(\mathbf{z})] = \mathbf{0}$, a point \mathbf{z}_o is a candidate for a local extremum (stationary point) if $\gamma \mathbf{z}_o = -\mathbf{b}$. When γ is nonsingular,

$$\mathbf{z}_o = -\gamma^{-1} \mathbf{b} \quad (20.19a)$$

is the unique stationary point of this quadratic surface. Substituting into Equation 20.17, the expected individual fitness at this point is

$$w_o = a + \frac{1}{2} \mathbf{b}^T \mathbf{z}_o \quad (20.19b)$$

as obtained by Phillips and Arnold (1989). Since $\partial^2 w(\mathbf{z}) / \partial z_i \partial z_j = \gamma_{ij}$, the hessian of $w(\mathbf{z})$ is just γ . Thus \mathbf{z}_o is a local minimum if γ is positive-definite (all eigenvalues are positive), a local maximum if γ is negative-definite (all eigenvalues are negative), or a saddle point if the eigenvalues differ in sign (see Chapter 31). If γ is singular (has at least one zero eigenvalue) then there is no unique stationary point. An example of this is seen in Figure 20.3 where there is a ridge (rather than a single point) of phenotypic values having the highest fitness value. The consequence of a zero eigenvalue is that the fitness surface has no curvature along the axis defined by the associated eigenvector. If γ has k zero eigenvalues, then the fitness surface has no curvature along k dimensions. Ignoring fitness change along these dimensions, the remaining fitness space has only a single stationary point, which is given by Equation 20.19a for γ and \mathbf{b} reduced to the $n - k$ dimensions showing curvature.

While the curvature is completely determined by γ , it is easy to be misled about the actual nature of the fitness surface if one simply tries to infer it by inspection of γ , as the following example illustrates.

Example 3. Consider selection acting on two characters z_1 and z_2 . Suppose we find that $\gamma_{11} = -2$ and $\gamma_{22} = -1$, suggesting that the individual fitness surface has negative curvature in both z_1 and z_2 . At first glance the picture this evokes is stabilizing selection on both z_1 and z_2 , with the stabilizing selection surface perhaps rotated due to selection for correlations between z_1 and z_2 . The first caveat, as mentioned in Chapter 30, is that negative curvature, by itself, does not imply a local maximum. Even if γ is negative definite, the equilibrium point \mathbf{z}_0 may be *outside* of the observed range of population values and hence not currently applicable to the population being studied. A much more subtle point is that, as Figure 20.3 shows, the nature of the fitness surface is very dependent on the amount of selection for correlations between z_1 and z_2 . Figure 20.3 considers the surfaces associated with three different values of γ_{12} under the assumption that $\mathbf{b} = 0$. Note that although in all three cases $\gamma_{12} > 0$ (i.e., selection favors increased correlations between the phenotypic values of z_1 and z_2), the fitness surfaces are qualitatively very different. When $\gamma_{12} = 0.25$, the individual fitness surface indeed shows stabilizing selection in both characters. However, when $\gamma_{12} = \sqrt{2} \simeq 1.42$, the fitness surface has a ridge in one direction, with stabilizing selection in the other. When $\gamma_{12} = 4$, the fitness surface is a saddle, with stabilizing selection along one axis and disruptive selection along the other. An especially troubling point is that if the standard error of γ_{12} is sufficiently large we would not be able to distinguish between these very different types of selection even if we could show that $\gamma_{11}, \gamma_{22} < 0$, and $\gamma_{12} > 0$.

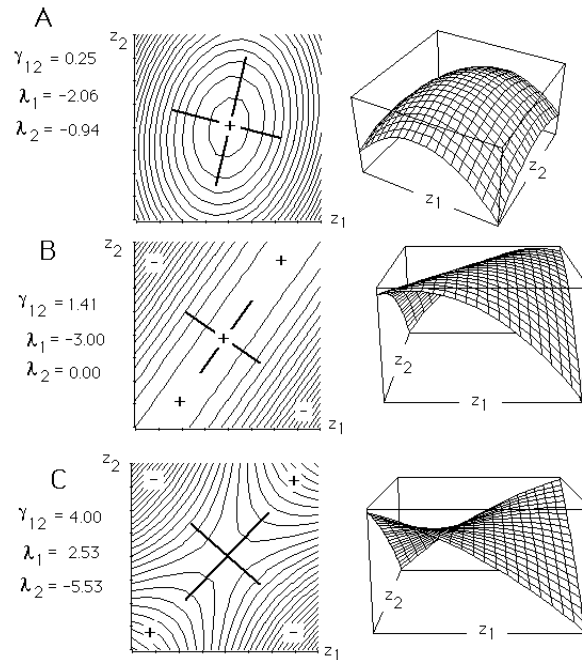


Figure 20.3. Three quadratic fitness surfaces, all of which have $\gamma_{11} = -2$ and $\gamma_{22} = -1$ and $\mathbf{b} = \mathbf{0}$. On the left are curves of equal fitness values, with peaks being represented by a +, and valleys by a -. Axes of symmetry of the surface (the canonical or principal axes of γ) are denoted by the thick lines. These axes correspond to the eigenvectors of γ . On the right are three dimensional plots of individual fitness as a function of the phenotypic values of the characters z_1 and z_2 . **Top:** $\gamma_{12} = 0.25$. This corresponds to stabilizing selection on both characters, with fitness falling off more rapidly (as indicated by the shorter distance between contour lines) along the z_1 axis than along the z_2 axis. **Middle:** $\gamma_{12} = \sqrt{2} \simeq 1.41$, in which case γ is singular. The resulting fitness surface shows a ridge in one direction with strong stabilizing selection in the other. **Bottom:** When $\gamma_{12} = 4$, the fitness surface now shows a saddle point, with stabilizing selection along one of the canonical axes of the fitness surface and disruptive selection along the other.

Thus, even for two characters, visualizing the individual fitness surface is not trivial and can easily be downright misleading. The problem is that the cross-product terms (γ_{ij} for $i \neq j$) make the quadratic form difficult to interpret geometrically. Removing these terms by a change of variables so that the axes of new variables coincide with the axes of symmetry of the quadratic form (its canonical axes) greatly facilitates visualization of the fitness surface. Motivated by this, Phillips and Arnold (1989) suggest using two slightly different versions of the

canonical transformation of γ to clarify the geometric structure of the best fitting quadratic fitness surface. From Equation 31.19 and 31.23, if we consider the matrix \mathbf{U} whose columns are the eigenvalues of γ , the transformation $\mathbf{y} = \mathbf{U}^T \mathbf{z}$ (hence $\mathbf{z} = \mathbf{U} \mathbf{y}$ since $\mathbf{U}^{-1} = \mathbf{U}^T$ as \mathbf{U} is orthonormal) removes all cross-product terms in the quadratic form,

$$\begin{aligned} w(\mathbf{z}) &= a + \mathbf{b}^T \mathbf{U} \mathbf{y} + \frac{1}{2} (\mathbf{U} \mathbf{y})^T \gamma (\mathbf{U} \mathbf{y}) \\ &= a + \mathbf{b}^T \mathbf{U} \mathbf{y} + \frac{1}{2} \mathbf{y}^T (\mathbf{U}^T \gamma \mathbf{U}) \mathbf{y} \\ &= a + \mathbf{b}^T \mathbf{U} \mathbf{y} + \frac{1}{2} \mathbf{y}^T \mathbf{A} \mathbf{y} \\ &= a + \sum_{i=1}^n \theta_i y_i + \frac{1}{2} \sum_{i=1}^n \lambda_i y_i^2 \end{aligned} \tag{20.20}$$

where $\theta_i = \mathbf{b}^T \mathbf{e}_i$, $y_i = \mathbf{e}_i^T \mathbf{z}$, with λ_i and \mathbf{e}_i the eigenvalues and associated unit eigenvectors of γ . Alternatively, if a stationary point \mathbf{z}_0 exists (e.g., γ is nonsingular), the change of variables $\mathbf{y} = \mathbf{U}^T (\mathbf{z} - \mathbf{z}_0)$ further removes all linear terms (Box and Draper 1987), so that

$$w(\mathbf{z}) = w_o + \frac{1}{2} \mathbf{y}^T \mathbf{A} \mathbf{y} = w_o + \frac{1}{2} \sum_{i=1}^n \lambda_i y_i^2 \tag{20.21}$$

where $y_i = \mathbf{e}_i^T (\mathbf{z} - \mathbf{z}_0)$ and w_o is given by Equation 20.19b. Equation 20.20 is called the **A canonical form** and Equation 20.21 the **B canonical form** (Box and Draper 1987). Both forms represent a rotation of the original axis to the new set of axes (the canonical axes of γ) that align them with axes of symmetry of the quadratic surface. The B canonical form further shifts the origin to the stationary point \mathbf{z}_o . Since the contribution to individual fitness from $\mathbf{b}^T \mathbf{z}$ is a hyperplane, its effect is to tilt the fitness surface. The B canonical form “levels” this tilting, allowing us to focus entirely on the curvature (quadratic) aspects of the fitness surface.

The orientation of the quadratic surface is determined by the eigenvectors of γ while the eigenvalues of γ determine the nature and amount of curvature of the surface along each canonical axis. Along the axis defined by y_i , the individual fitness function has positive curvature (is concave) if $\lambda_i > 0$, has negative curvature (is convex) if $\lambda_i < 0$, or has no curvature (is a plane) if $\lambda_i = 0$. The amount of curvature is indicated by the magnitude of λ_i , the larger $|\lambda_i|$ the more extreme the curvature.

An alternative way to think about this canonical transformation is that the original vector \mathbf{z} of n characters is transformed into a vector \mathbf{y} of n independent selection indices (Simms 1990). Directional selection on the index y_i is measured by θ_i , while quadratic selection is measured by λ_i .

Returning to Figure 20.3, we see that the axes of symmetry of the quadratic surface are the canonical axes of γ . For $\gamma_{12} = 0.25$, $\lambda_1 = -2.06$ and $\lambda_2 = -0.94$

so that the fitness surface is convex along each canonical axis, with more extreme curvature along the y_1 axis. When $\gamma = \sqrt{2}$, one eigenvalue is zero while the other is -3 , so that the surface shows no curvature along one axis (it is a plane), but is strongly convex along the other. Finally, when $\gamma_{12} = 4$, the two eigenvalues differ in sign, being -5.53 and 2.53 . This generates a saddle point with the surface being concave along one axis and convex along with other, with the convex curvature being more extreme.

If $\lambda_i = 0$, the fitness surface along y_i has no curvature, so that the fitness surface is a ridge along this axis. If $\theta_i = \mathbf{b}^T \mathbf{e}_i > 0$ this is a rising ridge (fitness increases as y_i increases), it is a falling ridge (fitness decrease as y_i increase) if $\theta_i < 0$, and is flat if $\theta_i = 0$. Returning to Figure 20.3B, the effect of \mathbf{b} is to tilt the fitness surface. Denoting values on the axis running along the ridge by y_1 , if $\theta_1 > 0$ the ridge rises so that fitness increases as y_1 increases. Even if γ is not singular, it may be nearly so, with some of the eigenvalues being very close to zero. In this case, the fitness surface shows little curvature along the axes given by the eigenvectors associated with these near-zero eigenvalues. From Equation 31.20, the fitness change along a particular axis (here given by \mathbf{e}_i) is $\theta_i y_i + (\lambda_i/2) y_i^2$. If $|\theta_i| \gg |\lambda_i|$, the curvature of the fitness surface along this axis is dominated by the effects of linear (as opposed to quadratic) selection. Phillips and Arnold (1989) present a nice discussion of several other issues relating to the visualization of multivariate fitness surfaces, while Box and Draper (1987) review the statistical foundations of this approach.

Unmeasured Characters and Other Biological Caveats

Even if we are willing to assume that the best-fitting quadratic regression is a reasonable approximation of the individual fitness surface, there are still a number of important biological caveats to keep in mind (Chapter 30). For example, the fitness surface can change in both time and space, often over short spatial/temporal scales (e.g., Kalisz 1986, Stewart and Schoen 1987, Scheiner 1989, Jordan 1991), so that one estimate of the fitness surface may be quite different from another estimation at a different time and/or location (Figure 20.4). Hence, considerable care must be used before pooling data from different times and/or sites to improve the precision of estimates. When the data are such that selection gradients can be estimated separately for different times or areas, space/time by gradient interactions can be tested for in a straightforward fashion (e.g., Mitchell-Olds and Bergelson 1990b).

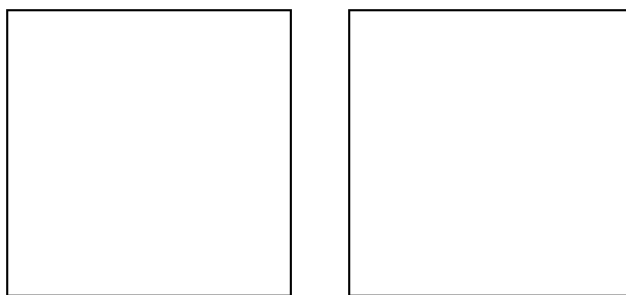


Figure 20.4. The selection surface can change over time. These two surfaces are the best-fitting quadratic surface for relative fitness as a function of stem diameter and internode length for a population of the annual plant *Diodia teres* at Surf City, North Carolina. **Left.** Estimate for June 1985 data. **Right.** Estimate for July 1985 data. From Jordon (1991).

Population structure can also influence fitness surface estimation in other ways. If the population being examined has overlapping generations, fitness data must be adjusted to reflect this (e.g., Stratton 1992). Likewise, if members in the population differ in their amount of inbreeding, measured characters and fitness may show a spurious correlation if both are affected by inbreeding depression (Willis 1993).

Perhaps the most severe caveat for the regression approach of estimating $w(z)$ is unmeasured characters — estimates of the amount of direct selection acting on a character are biased if that character is phenotypically correlated to unmeasured characters also under selection (Lande and Arnold 1983, Mitchell-Olds and Shaw 1987). Adding one or more of these unmeasured characters to the regression can change initial estimates of β and γ . Conversely, selection acting on unmeasured characters that are phenotypically *uncorrelated* with those being measured has no effect on estimates of β and γ .

The Bias due to Environmental Correlations Between Fitness and Characters

A problem related to that of unmeasured characters is that environmental correlations between characters and fitness can bias estimates of how phenotypes influence fitness (Rausher 1992). Suppose plant size and total seed set in an annual plant are both influenced by the soil concentration of nitrogen, so that plants in nitrogen-rich soil have both large size and large seed set, while plants in nitrogen-poor soil have small size and small seed set. Thus, even though we may observe a positive correlation between plant size and seed set, size per se may have no effect on seed set.

To express this effect formally, decompose the phenotype of the i th character as $z_i = g_i + E_i$, where g represents the genetic contribution and E the environ-

mental contribution (assume no genotype \times environment interaction and that g and E are independent). Decomposing the covariance between phenotypic value and fitness gives

$$s_i = \sigma(w, z_i) = \sigma(w, g_i + E_i) = \sigma(w, g_i) + \sigma(w, E_i)$$

The first term is the covariance between genotypic value and fitness, while the second (which concerns us here) is the covariance between fitness and the environmental deviation of z_i . Provided that E_i does not influence fitness other than through its effect on phenotype ($E_i \rightarrow z_i \rightarrow w$), the environmental covariance does not bias our view of the phenotype-fitness association. However, if E_i also has an effect on fitness **independent** of its effect on the phenotype (e.g., $E_i \rightarrow w$ without passing through z_i), this augments the covariance over that from the phenotypic effects on fitness alone. Following Rausher (1992), we use the method of path analysis (Appendix 2) to examine the amount of bias created by such environmental correlations. Figure 20.5 shows a simplified version for two characters.

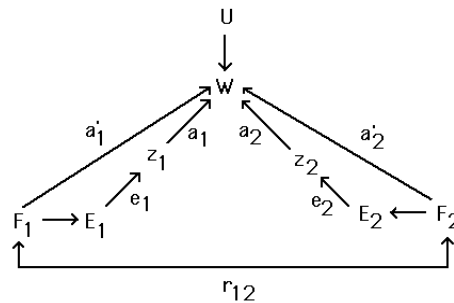


Figure 20.5. A path analysis model incorporating character-fitness correlations due to shared environmental effects. Here relative fitness w is determined by the phenotypic value of two characters (z_1 and z_2) and by three environmental values F_1 , F_2 , and U . See text for further details. After Rausher (1992).

Without loss of generality, assume that E_i is completely determined by the environmental factor F_i . We wish to decompose the correlation between E_i ($= F_i$) and w into a component due to the direct association between phenotype and fitness and a component due to association between environmental value and fitness *independent* of the phenotypic value. For two characters, the path diagram in Figure 20.5 shows four paths creating correlations between w and E_1 . The paths $F_1 \rightarrow E_1 \rightarrow z_1 \rightarrow w$ and $F_1 \leftrightarrow F_2 \rightarrow E_2 \rightarrow z_2 \rightarrow w$ represent the contribution of the environmental effects through their effect on phenotypes. The first path represents the phenotypic contribution through z_1 (with path coefficient product of $e_1 \cdot a_1$), the second the contribution from z_2 due to the correlation between

environmental effects of z_1 and z_2 (path product = $r_{12} \cdot e_2 \cdot a_2$). The effects of the environment on fitness independent of phenotypic value are given by the two remaining paths, $F_1 \rightarrow w$ and $F_1 \leftrightarrow F_2 \rightarrow w$ (with products a'_1 and $r_{12} \cdot a'_2$, respectively). Summing all four paths gives the correlation between fitness and the environmental deviation of character i as

$$\rho(w, E_i) = (e_1 \cdot a_i + r_{12} \cdot e_2 \cdot a_2) + (a'_1 + r_{i1} \cdot a'_2)$$

This correlation can be expressed in terms of a covariance, with $\sigma(w, E_i) = \sigma(w) \cdot \sigma(E_i) \cdot \rho(w, E_i)$. More generally, consider n characters where r_{ij} is the correlation between E_i and E_j , e_i the path coefficient for the effect of the environmental deviation on phenotype ($E_i \rightarrow z_i$), a_i the path coefficient for the effect of phenotype on fitness ($z_i \rightarrow w$), and a'_i the path coefficient for the effect of E_i on fitness, independent of phenotypic value ($E_i \rightarrow w$). In this case

$$\sigma(w, E_i) = \sigma(w) \cdot \sigma(E_i) \cdot \left(\left[e_i a_i + \sum_{j \neq i} r_{ij} e_j a_j \right] + \left[a'_i + \sum_{j \neq i} r_{ij} a'_j \right] \right) \quad (20.22)$$

The contribution from the association of phenotypic value and fitness are given by the first set of terms (those involving a_i), while the second set (those involving a'_i) represents the contribution from associations of environmental values and fitness that are independent of phenotypic value. This set of terms alters the phenotype-fitness covariance over that created by the phenotypic influence on fitness alone. Subtracting off this additional covariance term, viz.,

$$s_i - \sigma(w) \cdot \sigma_E(z_i) \cdot \left(a'_i + \sum_{j \neq i} r_{ij} a'_j \right) \quad (20.23)$$

removes this bias. Since we almost never have knowledge of the a'_i , the utility of Equation 20.23 is in exploring just how important these effects might be, given various assumptions. As we discuss in the next Chapter, Rausher suggests an alternative method, based on regressing relative fitness on breeding values (rather than phenotypic value) to remove some of these sources of bias.

PATH ANALYSIS AND FITNESS ESTIMATION

As we discussed in LW Appendix 2, path analysis and multivariate regressions are very closely connected, with path coefficients simply being standardized regression coefficients for the linear model suggested by the path diagram. Nevertheless, regression methods and path analysis offer complementary methods to examine associations between phenotypes and fitness. The purpose of a regression analysis is to predict fitness given character value, while path analysis provides

a description of the nature of character covariances and how they interact with fitness.

Example 4. Mitchell-Olds and Bergelson (1990b) measured fitness (adult size) in the annual plant *Impatiens capensis* as a function of five characters – seed weight, germination date, June size, early growth rate, and late growth rate. Figure 20.6 displays the significant paths between these variables and fitness. Note that the path diagram provides a description of the actual nature of the correlations, in particular, the causal connections assumed between variables.

From this path diagram, we can examine the contribution to relative fitness from the direct effect of a character and from its indirect effects through its effect on other characters. For example, the direct effect of early growth is 0.37 (the path $EG \rightarrow w$). Thus the correlation coefficient between the direct effect of EG and fitness is 0.37, so that this path accounts for 13 percent of the variation in fitness (as $0.37^2 \sim 0.13$). Early growth also influences fitness through an indirect path in that it influences late growth rate which in turns has a direct effect on fitness ($EG \rightarrow LG \rightarrow w$), which has product $0.8 \cdot 0.48 = 0.38$. Thus the total effect of early growth on fitness is the sum of the direct and indirect effects, or 0.76. Considering the other characters,

Character	Direct Effect	Indirect Effect
Seed weight	0.04	0.10
Germinate date	-0.08	-0.32
June Size	-0.02	0.52
Early growth rate	0.37	0.38
Late growth rate	0.48	0.00

Showing that indirect effects are more important than direct effects for most characters.

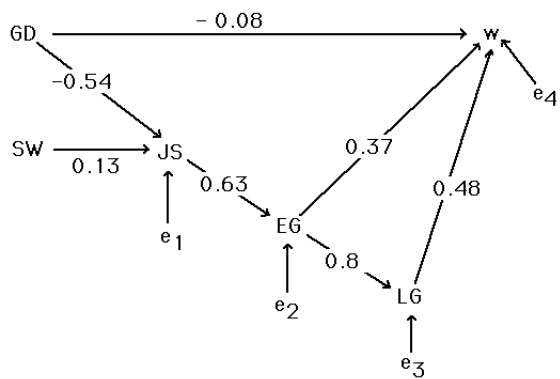


Figure 20.6. An example of the use of path analysis in describing multivariate selection is Mitchell-Olds and Bergelson (1990b), who examined fitness (measured by adult size) for the annual plant *Impatiens capensis*. Germination date (GD), seed weight (SW), June size (JS), early growth rate (EG), and late growth rate (LG) were the measured characters. Only significant paths are shown, with the standardized partial regression coefficient (or path coefficient) given above each path. After Mitchell-Olds and Bergelson (1990b).