THE MEASUREMENT OF SELECTION ON CORRELATED CHARACTERS

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Natural selection acts on phenotypes, regardless of their genetic basis, and produces immediate phenotypic effects within a generation that can be measured without recourse to principles of heredity or evolution. In contrast, evolutionary response to selection, the genetic change that occurs from one generation to the next, does depend on genetic variation. Animal and plant breeders routinely distinguish phenotypic selection from evolutionary response to selection (Mayo, 1980; Falconer, 1981). Upon making this critical distinction, emphasized by Haldane (1954), precise methods can be formulated for the measurement of phenotypic natural selection.

Correlations between characters seriously complicate the measurement of phenotypic selection, because selection on a particular trait produces not only a direct effect on the distribution of that trait in a population, but also produces indirect effects on the distribution of correlated characters. The problem of character correlations has been largely ignored in current methods for measuring natural selection on quantitative traits. Selection has usually been treated as if it acted only on single characters (e.g., Haldane, 1954; Van Valen, 1965a; O'Donald, 1968, 1970; reviewed by Johnson, 1976 Ch. 7). This is obviously a tremendous oversimplification, since natural selection acts on many characters simultaneously and phenotypic correlations between traits are ubiquitous. In an important but neglected paper, Pearson (1903) showed that multivariate statistics could be used to disentangle the direct and indirect effects of selection to determine which traits in a correlated ensemble are the focus of direct selection. Here we extend and generalize Pearson's major results.

The purpose of this paper is to derive measures of directional and stabilizing (or disruptive) selection on each of a set of phenotypically correlated characters. The analysis is retrospective, based on observed changes in the multivariate distribution of characters within a generation, not on the evolutionary response to selection. Nevertheless, the measures we propose have a close connection with equations for evolutionary change. Many other commonly used measures of the intensity of selection (such as selective mortality, change in mean fitness, variance in fitness, or estimates of particular forms of fitness functions) have little predictive value in relation to evolutionary change in quantitative traits. To demonstrate the utility of our approach, we analyze selection on four morphological characters in a population of pentatomid bugs during a brief period of high mortality. We also summarize a multivariate selection analysis on nine morphological characters of house sparrows caught in a severe winter storm, using the classic data of Bumpus (1899).

Direct observations and measurements of natural selection serve to clarify one of the major factors of evolution. Critiques of the "adaptationist program" (Lewontin, 1978; Gould and Lewontin, 1979) stress that adaptation and selection are often invoked without strong supporting evidence. We suggest quantitative measurements of selection as the best alternative to the fabrication of adaptive scenarios. Our optimism that measurement can replace rhetorical claims for adaptation and selection is founded in the growing success of field workers in their efforts to measure major components of fitness in natural populations (e.g., Thornhill, 1976; Howard, 1979; Downhower and Brown, 1980; Boag and Grant, 1981; Clutton-Brock et

al., 1982). The essential fact is that selection and adaptation *can* be measured.

Empirical Background

Before considering the theory, it will be useful to briefly review the kinds of data that can be analyzed with our methods. The basic data consist of a set of phenotypic measurements on individuals in a population before and after an episode of selection. In *longitudinal* studies individuals are observed (usually through a span of time) to score some component(s) of fitness, as well as a set of phenotypic characters, for each individual. *Cross-sectional* studies are performed on a population at a single point in time by comparing the phenotype distribution of cohorts of different age, to infer viability selection without actually measuring any aspect of fitness. Three features of the data are crucial to the interpretation of the results: which components of fitness are considered; whether the study is longitudinal or cross-sectional; and whether there is ontogenetic change in the characters.

Many workers have succeeded in measuring components of fitness in natural populations. Although the measurement of total lifetime fitness is a worthy goal, and one that can be achieved with some organisms such as annual plants, accurate estimates of major components of fitness also give valuable insights. The present methods for measuring selection can be applied to components of fitness as well as total lifetime fitness. Charlesworth (1980) and Lande (1982) treat the problem of measuring total fitness in populations with overlapping generations.

Longitudinal data have many advantages over cross-sectional data. Typically, cross-sectional studies are carried out by comparing the phenotype distributions of young and old individuals in a single population and assuming these to represent, respectively, samples before and after an interval of viability selection; any statistically significant change in the phenotype distribution is attributed to selection. The assumptions of cross-sectional studies are valid only if during the interval between the production of the young and old cohorts (1) there was no genetic evolution of the characters in the population, (2) the environment did not change in any way which would affect individual development of the characters, (3) differential immigration or emigration by different phenotypes did not occur, and (4) there was no ontogenetic change in the characters in the stages of the life cycle under study. Thus, cross-sectional studies are commonly applied to characters that do not change with age, such as meristic characters (Inger, 1942, 1943; Hecht, 1952; Hagen and Gilbertson, 1973; Fox, 1975; Beatson, 1976) and those with determinate growth (Kurtén, 1958; Van Valen, 1963, 1965b; Mason, 1964; Van Valen and Weiss, 1966). Organisms with accretionary growth can be used in cross-sectional studies to measure selection on characters of early ontogenetic stages (Weldon, 1901; di Cesnola, 1906; Sambol and Finks, 1977). Traits that change continuously during ontogeny can be analyzed with longitudinal data by using growth curve parameters of individuals as characters, instead of the original measurements (Cock, 1966; Kidwell et al., 1979; Atchley and Rutledge, 1981).

Directional Selection

Theoretical Results.—The directional aspect of selection is defined by its effect on the mean values of phenotypic characters in a population within a generation. In this section it is demonstrated that the forces of directional selection are best described by a vector of partial regression coefficients of individual relative fitness on the characters. This is a multivariate generalization of the results of Robertson (1966) and Price (1970, 1972), who showed that directional selection on a single trait can be expressed in terms of a covariance or regression of relative fitness on the character.

The change in the mean value of a phenotypic character produced by selection within a generation is known as the observed *directional selection differential* (Lush, 1945; Falconer, 1981). For a set of

characters, z_1, z_2, . . . , z_n, arranged in a column vector, z, the directional selection differential is

$$s = \bar{z}^* - \bar{z} \qquad (1)$$

in which $\bar{z}^*$ denotes the vector of mean values of the characters after selection. Let the phenotype distribution in the population before selection be $p(z)$. The absolute fitness of an individual, W, can be represented by the expected fitness for its phenotype, $W(z)$, plus an individual deviation which among individuals with phenotype z has a mean of zero (so that in the population as a whole $W - W(z)$ is uncorrelated with any phenotypic measure). The mean absolute fitness in the population is

$$\bar{W} = \int W(z)p(z)\mathrm{d}z \qquad (2a)$$

where the integration extends over all phenotypes in the population. Relative fitnesses are defined with respect to the mean fitness in the population, $w = W/\bar{W}$ so that the expected relative fitness of individuals with phenotype z is

$$w(z) = W(z)/\bar{W} \qquad (2b)$$

and $\bar{w} = 1$. After selection the phenotype distribution is $w(z)p(z)$ with mean value

$$\bar{z}^* = \int zw(z)p(z)\mathrm{d}z. \qquad (3)$$

$\bar{z}^*$ is the average of the product of individual relative fitness with the vector of characters. Because the mean relative fitness is unity, the observed directional selection differential can be expressed from (1) and (3) as the covariance of individual relative fitness with the vector of characters,

$$s = \mathrm{Cov}[w, z]. \qquad (4)$$

Now consider the influence of selection on the genetic evolution of the mean phenotype in a population. In the absence of genotype-environment interaction and correlation, individual phenotypes before selection can be decomposed into additive genetic effects (or breeding values), x, plus independent environmental effects, e, which include nonadditive genetic effects due to dominance and epistasis,

$$z = x + e \qquad (5a)$$

with $\bar{e} = 0$ (Kempthorne, 1969; Falconer, 1981). Denoting the variance-covariance matrices of the breeding values and the environmental (plus nonadditive genetic) parts respectively as G and E, the phenotypic variance-covariance matrix is $P = G + E$, which is taken to be nonsingular, $|P| \neq 0$. The regression of breeding values on phenotypes is assumed to be linear and homoscedastic,

$$x - \bar{x} = GP^{-1}(z - \bar{z}) + \varepsilon \qquad (5b)$$

where ε is an independent residual term with zero mean. Linearity and homoscedasticity of both regressions (5a) and (5b) imply that the phenotypes and breeding values (as well as environmental effects) jointly have a multivariate normal distribution (Kendall and Stuart, 1973 Ch. 28).

An important result due to Pearson (1903) is that phenotypic selection does not change the coefficients in the regression (5b). The change in the mean breeding value produced by phenotypic selection within a generation is therefore

$$\bar{x}^* - \bar{x} = GP^{-1}(\bar{z}^* - \bar{z}). \qquad (6a)$$

If there is no change in the mean environmental effect between generations, and no change in the mean breeding value caused by recombination or mutation, then the mean breeding value of selected parents is equivalent to the mean phenotype of their offspring, and the change in the mean phenotype across one generation produced by selection is, using (1),

$$\Delta\bar{z} = GP^{-1}s \qquad (6b)$$

(Lande, 1979). Thus, with the assumption that the characters have a multivariate normal distribution, the vector $P^{-1}s$ contains all of the information concerning the forces of directional selection on the phenotypes. For quantitative (polygenic) characters, the assumption of normality is often satisfied, at least approximately, on an appropriate scale of measurement, most often logarithmic (Wright, 1968 Ch. 10; Falconer, 1981 Ch. 17).

In view of (4), the vector $\beta = P^{-1}s$ is a set of partial regression coefficients of rel-

ative fitness on the characters (Kendall and Stuart, 1973 eq. 27.42). Under quite general conditions, the method of least squares indicates that the element β_i gives the slope of the straight line that best describes the dependence of relative fitness on character z_i, after removing the residual effects of other characters on fitness (Kendall and Stuart, 1973 Ch. 27.15). There is no need to assume that the actual regressions of fitness on the characters are linear, or that the characters have a multivariate normal distribution. For this reason, the partial regression coefficients β provide a general solution to the problem of measuring the forces of directional selection acting directly on the characters.

We can now partition the observed selection differential into the parts alluded to by Pearson. Writing $s = P\beta$, the observed selection differential on the ith character contains a term due to direct selection on that character plus a set of terms due to indirect selection on all characters that are phenotypically correlated with the ith character,

$$s_i = \sum_{j=1}^{n} P_{ij}\beta_j \qquad (6c)$$
$$= P_{i1}\beta_1 + \ldots + P_{ii}\beta_i \ldots + P_{in}\beta_n$$

where P_{ii} is the phenotypic variance of the ith character and P_{ij} is the phenotypic covariance between the ith and jth characters. The term $P_{ii}\beta_i$ represents the *direct effect* of selection in changing the mean of the ith character. The remaining terms represent the *indirect effects* of selection on all other characters in changing the mean value of the ith trait.

There is an interesting interpretation of the partial regression coefficients when the phenotypic traits follow a multivariate normal distribution, although the actual regression of fitness on the characters may be nonlinear. The vector of partial regression coefficients, $\beta = P^{-1}s$, is then equivalent to the average gradient of the relative fitness surface, weighted by the phenotype distribution. To establish this, let

$$p(z) = \sqrt{(2\pi)^{-n} |P|^{-1}} e^{-\frac{1}{2}(z - \bar{z})^{T}P^{-1}(z - \bar{z})}$$
$$(7)$$

where the superscript T signifies matrix transposition, and define the gradient operator

$$\partial/\partial z \equiv (\partial/\partial z_1, \ldots, \partial/\partial z_n)^{T}. \qquad (8)$$

Using integration by parts shows that if $w(z)$ is differentiable then its average gradient, weighted by $p(z)$, is

$$\int p(z)\frac{\partial w(z)}{\partial z}\,dz = p(z)w(z)\Big|_{-\infty}^{+\infty}$$
$$- \int w(z)\frac{\partial p(z)}{\partial z}\,dz.$$

Assuming $w(z)$ is bounded, the first term on the right side vanishes, and using (1), (3) and (7), the second term is

$$\int w(z)P^{-1}(z - \bar{z})p(z)dz =$$
$$P^{-1}(\bar{z}^* - \bar{z}) = P^{-1}s. \qquad (9)$$

Thus the forces of directional selection on the characters are given by the average gradient of the surface of individual relative fitness, weighted by the phenotype distribution. We therefore refer to the vector of partial regression coefficients of individual relative fitness on the characters as the *directional selection gradient*. In the section on stabilizing selection we show how the surface of individual fitness can be approximated by estimating its average gradient and average curvature in the neighborhood of the multivariate mean phenotype.

Components of Fitness.—Selection on major components of fitness, such as lifespan, fecundity, mating success, and parental effort, can be measured by coefficients in the regression of total fitness on its components. Selection on morphological, behavioral or physiological traits can be analyzed with respect to components of fitness as well as total fitness. Major components of fitness are expected to contribute positively to total fitness, and hence to be always under directional selection to increase, given that all other components of fitness are held constant. In a regression of total fitness on its major components, the finding of negative directional selec-

tion (or stabilizing selection) on a major fitness component indicates that this component is negatively correlated with another component of fitness which is missing from the analysis.

Missing Characters.—The analysis of directional selection on a set of correlated characters within a generation will be complete only if the characters under observation are phenotypically uncorrelated with any other characters that are undergoing appreciable directional selection. An objection can always be raised that some important trait(s) has been omitted from the analysis. This hypothesis can be tested by including the new character(s) in another study. If this is not feasible, then it must be admitted that the characters under observation may be responding in part to phenotypically correlated characters that have not been measured. This criticism is not necessarily fatal to the investigation, since a partial resolution of the influence of phenotypic correlations between characters is better than none at all. It is crucial to realize that an observed directional selection gradient on a given trait can *not* be ascribed to indirect selection on a correlated trait that *has* been included in the analysis.

Highly Correlated Characters.—If a group of characters are highly correlated phenotypically, or if a large number of traits are measured, the phenotypic variance-covariance matrix may be singular, with a determinant that vanishes, $|\mathbf{P}| = 0$, or nearly so. Then P cannot be inverted and the directional selection gradient cannot be calculated. In such cases a reduction of dimensionality should be accomplished by some method, such as by summing or averaging highly correlated characters, or by eliminating all but one trait in each highly correlated set, or by retaining only the first few principal components of phenotypic variation as characters. All of these techniques can produce a phenotypic matrix, P, that is nonsingular. Principal components have the advantage that they are uncorrelated. Consequently there can be no indirect effects of selection from one principal component

to the next and they can be analyzed separately or in any combination.

Selection on a Combination or Index of Traits.—In some situations it may be desirable to construct an index, or linear combination of characters, such that selection acting directly on that index alone would produce an observed directional selection differential. In other words, one might wish to know what combination of characters was in effect the focus of past selection. The appropriate linear combination is obtained by weighting each trait by the direct force of selection on it,

$$I = \beta^{\mathrm{T}}\mathbf{z} = \mathbf{s}^{\mathrm{T}}\mathbf{P}^{-1}\mathbf{z} =$$
$$\beta_1 z_1 + \ldots + \beta_n z_n. \tag{10}$$

When selection acts directly on the index I alone, the observed directional selection differential on the vector of characters z is proportional to its phenotypic covariance with I. Hence selection acting only on the index would produce an observed directional selection differential proportional to that on the original characters, since $\mathrm{Cov}[\mathbf{z}, I] = \mathrm{Cov}[\mathbf{z}, \mathbf{z}^{\mathrm{T}}]\mathbf{P}^{-1}\mathbf{s} = \mathbf{s}$. This index has been employed by animal breeders as a retrospective measure of directional selection observed within a generation, and a similar index has been used to describe observed evolutionary changes between generations (Dickerson et al., 1954, 1974; Harvey and Bearden, 1962; Marcus, 1964, 1969; Magee, 1965; Yamada, 1977; Lande, 1979).

Stabilizing and Disruptive Selection

Historical Background.—Stimulated by Galton's classic work on Natural Inheritance (1889), Pearson (1896, 1903, 1911) investigated fundamental problems in the theory of selection and evolution of correlated characters (cf. Pearson, 1920). In these papers, and others by Yule (1897, 1907), the methods of partial regression and correlation were greatly advanced (Seal, 1967). Pearson failed to achieve a clear understanding of heredity and evolution because he never accepted a Mendelian basis for the inheritance of quantitative variability, which was later confirmed by the experiments of Johann-

sen, Nilsson-Ehle, East, Hayes and Castle, and theoretical analyses by Yule, Weinberg, Fisher and Wright (reviewed by Wright, 1968 Ch. 15; Provine, 1971). Nevertheless, Pearson derived powerful methods for analyzing the immediate impact of phenotypic selection within a generation. He was especially concerned to distinguish between directly selected characters and non-selected or indirectly selected traits which change only due to their correlations with directly selected characters.

Assuming a multivariate normal phenotype distribution for the characters in a population before selection, Pearson (1903) proved that if a trait has been modified only by indirect selection, then its partial regression coefficients on any set of other traits, provided this includes all the directly selected characters, remain unchanged by selection. In contrast, selection within a generation produces changes in the means, variances and covariances of characters that are not themselves directly selected, if they are correlated with the selected character(s). For example, consider an arbitrary form of selection on a single character, z_1, which changes the phenotypic variance from P_{11} before selection to P^*_{11} after selection, and let the proportional decrease in the variance be denoted by $\kappa = 1 - P^*_{11}/P_{11}$. Then after selection the variance of a second character, z_2, not under direct selection but having a correlation ρ_{12} with the first character, is

$$P^*_{22} = P_{22}(1 - \kappa\rho^2_{12}). \qquad (11)$$

This demonstrates that selection which decreases the variance of the first character, $\kappa > 0$, also decreases the variance of the second character, whether the correlation between them is positive or negative. The covariance of the characters after selection on the first trait is $P^*_{12} = P_{12}(1 - \kappa)$. Equation (11), first derived by Pearson (1903), suggests that for a set of correlated characters under multivariate stabilizing selection, observed changes in the variance of a single character may overestimate the intensity of stabilizing selection acting directly on that trait, be-

cause of the indirect effects of stabilizing selection acting through correlated traits. This is shown more explicitly below.

Theoretical Results.—Combined with the modern view of polygenic inheritance of quantitative variation, Pearson's methods can be applied to the problem of predicting how phenotypic selection changes additive genetic variances and covariances within a generation. The formulation of this genetic change should suggest measures of stabilizing (or disruptive) selection. Consider an arbitrary form of selection acting on a multivariate normal phenotype distribution. Following Pearson (1903) and Lande (1980), equation (5b) can be used to derive the change in the variance-covariance matrix of breeding values within a generation (before mutation, segregation and recombination), as

$$\mathbf{G}^* - \mathbf{G} = \mathbf{G}\mathbf{P}^{-1}(\mathbf{P}^* - \mathbf{P})\mathbf{P}^{-1}\mathbf{G}. \quad (12)$$

Analogy with (6a) indicates that the phenotypic part of the expression on the right, $\mathbf{P}^{-1}(\mathbf{P}^* - \mathbf{P})\mathbf{P}^{-1}$, is a matrix measuring the forces of selection acting directly on the variances and covariances of the characters.

It is informative to express the observed change in the phenotypic variance-covariance matrix produced by selection within a generation in the form of a covariance of fitness with a function of the characters,

$$\mathbf{P}^* - \mathbf{P} = \int (z - \bar{z}^*)(z - \bar{z}^*)^T w(z) p(z) dz$$
$$- \int (z - \bar{z})(z - \bar{z})^T p(z) dz.$$

Substituting $\bar{z}^* = s + \bar{z}$ in the first integral, and using (4), yields

$$\mathbf{P}^* - \mathbf{P} = Cov[w, (z - \bar{z})$$
$$(z - \bar{z})^T] - ss^T \quad (13a)$$

which is valid for any distribution of characters under an arbitrary form of selection. The last term, $-ss^T$, gives the change in $\mathbf{P}$ that would be produced by a linear fitness function with the observed directional selection differential s. The covariance of relative fitness with a matrix of quadratic deviations of the characters from their mean values can therefore be taken as an observed *stabilizing selection differential,* C, which is independent of the influence of directional selection,

$$C \equiv \mathrm{Cov}[w, (z - \bar{z})(z - \bar{z})^{\mathrm{T}}]$$
$$= P^* - P + ss^{\mathrm{T}}. \qquad (13b)$$

In conjunction with (12) this implies that, for characters with a multivariate normal distribution before selection, the matrix

$$\gamma \equiv P^{-1}(P^* - P + ss^{\mathrm{T}})P^{-1}$$
$$= P^{-1}CP^{-1} \qquad (14a)$$

is the *stabilizing selection gradient* which measures the forces of stabilizing (or disruptive) selection acting directly on the characters, independent of the forces of directional selection, and accounting for the phenotypic correlations between characters. The diagonal elements measure the strength of stabilizing (or disruptive) selection directly on the variance of each character, and the off-diagonal elements measure the strength of selection directly on the covariances (i.e., the intensity of selection to positively or negatively correlate pairs of characters), after allowing for the changes produced by directional selection.

Formula (14a) can also be interpreted in terms of the shape of the relative fitness surface acting on the characters. Defining the curvature operator as the matrix of second partial derivatives

$$\partial^2/\partial z^2 \equiv \begin{pmatrix} \partial^2/\partial z_1^2 & \ldots & \partial^2/\partial z_1 \partial z_n \\ \cdot & & \cdot \\ \cdot & & \cdot \\ \cdot & & \cdot \\ \partial^2/\partial z_n \partial z_1 & \ldots & \partial^2/\partial z_n^2 \end{pmatrix}$$

and using integration by parts, it can be shown from (7) that if $w(z)$ is twice differentiable, then its average curvature is

$$\int p(z) \frac{\partial^2 w(z)}{\partial z^2} \, dz = \int w(z) \frac{\partial^2 p(z)}{\partial z^2} \, dz$$
$$= \int w(z) P^{-1}(z - \bar{z})(z - \bar{z})^{\mathrm{T}} P^{-1} p(z) \, dz$$
$$- P^{-1}.$$

Writing $P^{-1} = P^{-1}PP^{-1}$ and employing (13b) yields

$$\int p(z) \frac{\partial^2 w(z)}{\partial z^2} \, dz = P^{-1}CP^{-1} = \gamma. \qquad (14b)$$

Thus the stabilizing selection gradient is equivalent to the average curvature of the relative fitness surface, weighted by the multivariate normal distribution of characters.

The intensity of stabilizing or disruptive selection has often been measured using the observed effect of selection on the variance of single characters. To show how the observed changes in the phenotypic variances and covariances depend on the shape of the fitness surface acting on a multivariate normal character distribution, formula (11) can be generalized by rearranging (14a) as

$$P^* - P = P\gamma P - ss^{\mathrm{T}} \qquad (15a)$$

or in terms of the ijth element

$$P^*_{ij} - P_{ij} = \sum_{k=1}^{n} \sum_{l=1}^{n} P_{ik}\gamma_{kl}P_{lj} - s_i s_j. \quad (15b)$$

In the case where selection acts independently to stabilize the mean of each character toward an intermediate optimum, γ is a diagonal matrix with $\gamma_{jj} < 0$, and the observed change in the variance of the ith character is

$$P^*_{ii} - P_{ii} = \sum_{j=1}^{n} \gamma_{jj}P^2_{ij} - s^2_i. \qquad (15c)$$

This supports the notion that under multivariate stabilizing selection the intensity of stabilizing selection acting directly on a single character will be overestimated from observed changes in its variance, for two reasons: (i) indirect effects of stabilizing selection on every trait correlated with z_i decrease P_{ii}, regardless of the signs of the correlations, and (ii) an observed directional selection differential on z_i caused by a directional selection gradient on z_i or any correlated character also decreases P_{ii}. Thus a multivariate analysis of selection is necessary to accurately estimate the intensity of stabilizing selection acting directly on single traits, as measured by the shape of the fitness surface affecting them.

The Selective Surface Approximated by Quadratic Regression

Background.—The concept of a fitness function, a surface of selective value, or

an "adaptive landscape" played a central role in the evolutionary theories of Wright (1931, 1932, 1935), Fisher (1930, 1958 Ch. 2), Dobzhansky (1937, 1951) and Simpson (1944, 1953). As early as 1903 Pearson described selection in terms of a multidimensional surface, the height of which was individual fitness as a function of metrical characters represented by the other dimensions. (In Wright's adaptive landscape the height is the mean fitness in the population as a function of gene frequencies along the other axes.) If the characters in a population follow a multivariate normal distribution both *before and after* an episode of selection within a generation, then the individual fitness surface must have a generalized Gaussian form. Pearson (1903) showed that the parameters of such a selective surface can be estimated from the observed changes in the means, variances and covariances of the characters produced by selection. An equivalent approach was applied by Karn and Penrose (1951) to describe the dependence of early survival in human neonates on birth weight and gestation time. Manly (1976, 1977) analyzed mortality selection using a multivariate fitness function with a double exponential form.

In the preceding sections we generalized Pearson's result to an arbitrary form of selection acting on a distribution of characters that is multivariate normal *before* selection. It was shown that the directional and stabilizing selection gradients are equivalent respectively to the average slope and curvature of the surface of relative individual fitness. In this section we demonstrate that for any form of selection, the coefficients in the best quadratic approximation to the selective surface measure the forces of directional and stabilizing selection on the characters, if these have a multivariate normal distribution before selection. The regression method can also be extended to the general case in which no assumption is made about the form of selection or the distribution of characters. Even in the general case, measures of selection can be obtained by linear and qua-

dratic approximations to the surface of individual relative fitness.

Theoretical Results.—To simplify subsequent notation, suppose that all characters are measured as deviations from their means before selection, so that $\bar{z} = 0$. At first it is assumed that the characters have a multivariate normal distribution in the population before selection (but not necessarily after selection), and any form of fitness function is allowed. Consider the quadratic regression of relative fitness on the characters, listing each quadratic term once,

$$w - 1 = \sum_{j=1}^{n} \beta_j z_j + \sum_{k=1}^{n} \sum_{l=k}^{n} (1 - \tfrac{1}{2}\delta_{kl})\gamma_{kl}$$
$$\cdot [z_k z_l - P_{kl}] + \varepsilon \qquad (16)$$

where $\delta_{kl} = 1$ if $l = k$ and zero otherwise. The method of least squares can be employed to minimize the mean squared error with respect to changes in the linear and quadratic coefficients, β_j and γ_{kl},

$$Q = \int \varepsilon^2 p(z) dz.$$

For the multivariate normal distribution all third moments vanish, hence the linear and quadratic terms are uncorrelated and $\partial Q/\partial \beta_i = 0$ implies

$$\text{Cov}[w, z_i] - \sum_{j=1}^{n} P_{ij}\beta_j = 0,$$

or in matrix form

$$\beta = P^{-1}\text{Cov}[w, z] \qquad (17)$$

which is equivalent·to the directional selection gradient $P^{-1}s$. The fourth moments of the multivariate normal distribution can be expressed in terms of the second moments (Kendall and Stuart, 1976 eq. 41.97),

$$\int z_i z_j z_k z_l p(z) dz = P_{ij}P_{kl} + P_{ik}P_{jl} + P_{il}P_{jk}$$

so that $\partial Q/\partial \gamma_{ij} = 0$ implies

$$\text{Cov}[w, z_i z_j] - \sum_{k=1}^{n} \sum_{l=1}^{n} P_{ik}P_{jl}\gamma_{kl} = 0,$$

or in matrix form,

$$\gamma = P^{-1}\text{Cov}[w, zz^T]P^{-1} \qquad (18)$$

which is equivalent to the stabilizing se-

lection gradient (14) with $\bar{z} = 0$. The second derivatives of Q with respect to β_i and γ_{ij} are constants and demonstrate that the solutions (17) and (18) specify a unique minimum error variance.

The coefficients of the linear and quadratic terms in the regression (16) therefore measure the forces of directional and stabilizing selection acting directly on the characters, if these have a multivariate normal distribution before selection. The utility of least-squares regression is that it can be readily generalized to provide estimates of intensities of directional and stabilizing selection on correlated characters regardless of their distribution before selection.

When no assumption is made about the distribution of the characters, or the form of the fitness function, a problem exists with the use of the regression (16) alone. If the character distribution before selection displays multivariate skewness (nonzero third moments), the linear and quadratic terms are correlated and estimates of β depend on whether or not the quadratic terms are included in the regression. Stability of estimates of β can be achieved through a system of quadratic polynomials that are uncorrelated with the linear terms (see Appendix).

In practice, the simplest method of computing the measures of selection, and the quadratic approximation to the fitness surface acting on the characters, is by employing automated programs for multiple regression, which are available at most computation centers. Linear multiple regression can be used first to estimate the forces of directional selection, β, and their standard errors. Then a quadratic multiple regression (16) or (A1), can be used to estimate the forces of stabilizing selection, γ, with their standard errors. The regression (16) provides the best quadratic approximation to the selective surface (although valid estimates of β can be obtained only from a purely linear regression, or by using the orthogonal regression (A1)).

Calculation of the stabilizing selection gradient, γ, may require a rather large data set. Multiple regression can not be performed on a given sample of data unless the number of individuals in the sample, N, exceeds the number of coefficients to be estimated: n (the number of characters) for directional selection, plus $n(n + 1)/2$ for stabilizing (or disruptive) selection. If there are too few individuals in the sample, the number of coefficients to be estimated can be reduced, either by neglecting stabilizing selection, or by reducing the number of characters (e.g., by performing the selection analysis on the first few principal components of variation, instead of on the original characters). Especially when many characters are involved, limited sample size will usually make it impractical to estimate coefficients of more than second degree in the regression of relative fitness on the characters.

Cross-sectional Analysis.—Regression techniques for estimating selection coefficients are not applicable to cross-sectional data, because there are no measurements of individual fitnesses. All inferences about selection must then be drawn from a comparison of the phenotype distributions in cohorts of different age sampled from a single population at a point in time. If the basic assumptions of cross-sectional analysis (discussed above) are satisfied, the directional selection gradient which produced an observed change in the mean phenotypes between a young cohort and an old cohort can be estimated from formula (6) with $\bar{z}^*$ and $\bar{z}$ being the mean phenotype vectors in the old and young cohorts respectively, and P being the phenotypic variance-covariance matrix of the young cohort. The stabilizing selection gradient can be estimated from the observed change in the phenotypic variance-covariance matrix between cohorts, adjusted for the effect of directional selection, as in formula (14a) with P* being the phenotypic variance-covariance matrix of the old cohort.

The derivation of expressions (6) and (14), and their application in cross-sectional analysis, requires multivariate normality of the character distribution in the

young cohort (before selection). For this reason, and because of the additional assumptions required, cross-sectional analysis of selection is less general and powerful than longitudinal analysis by regression techniques.

Preliminaries for Data Analysis

Transformation of Characters.—For the analysis of cross-sectional data, the most important assumption is that the distribution of characters in the young cohort (before selection) is multivariate normal. There are many types of departure from normality, but these can often be corrected with simple transformations discussed by Wright (1968 Chs. 10, 11). Normality of the separate univariate distributions for each character is a necessary, but not sufficient, condition for multivariate normality.

Major components of fitness, as measured in longitudinal studies, will hardly ever be normally distributed. However, the estimation of selection coefficients from longitudinal data does not depend on any distributional assumptions concerning fitness. No attempt should be made to transform fitness to a more normal distribution, since such transformation will lead to invalid estimates of the forces of selection. Absolute fitnesses need only be transformed to relative fitnesses by dividing each absolute measure by the mean absolute fitness, because selection differentials and gradients are relationships between relative fitness and the characters.

In practice there will almost always be some departure from multivariate normality in the distribution of characters, and it is important to realize which results and interpretations are affected. We emphasize that in longitudinal studies employing the regression methods outlined above, departure from multivariate normality of the character distribution will *not* affect the estimates of selection differentials and gradients, or their standard errors. In contrast, tests of significance for selection differentials and gradients generally assume a normal distribution of *errors from the regression* of relative fitness on the char-acters (Kendall and Stuart, 1973 Ch. 19.10).

Standardized Selection Coefficients.— The observed selection differential on a particular character is often expressed in terms of phenotypic standard deviations, $s'_i = s_i/\sigma_i$ (Falconer, 1981). Coefficients in the regression of fitness on the characters can also be standardized by adopting units of standard deviations for every character, except fitness. The standardized measures of the intensities of directional and stabilizing selection, $\beta'_i = \beta_i\sigma_i$ and $\gamma'_{ij} = \gamma_{ij}\sigma_i\sigma_j$ respectively, are the coefficients in the linear and quadratic regressions of relative fitness on the standardized characters, $z'_i = z_i/\sigma_i$.

Selection in an Hemipteran

On the morning of April 19, 1981 adult pentatomid bugs (*Euschistus variolarius* PB) were found along the shoreline of Lake Michigan in Porter Co., Indiana. The bugs, along with several species of carabid and chrysomelid beetles, were common in the zone of waft debris, about 1 to 3 m from the water's edge. The first 94 bugs encountered in this zone were collected and of these only 39 were alive. The 55 dead bugs were in excellent condition and had apparently died recently. We suppose that the bugs were knocked down into the lake during a storm as they attempted to migrate north over Lake Michigan and were then washed ashore. There was a light rain during the morning when the collection was made, and live bugs were inactive and apparently incapable of taking flight. These circumstances suggest that we obtained an unbiased sample of bugs washed ashore during the storm.

The bugs were sorted into live and dead groups and preserved in 70% ethanol within two hours after collection. Subsequently, four linear measurements were made on each individual (head width, width of thorax [pronotum], length of scutellum, and length of forewing), using a dissecting microscope at 6-fold magnification with an ocular micrometer. All measurements were transformed to natural logarithms.

A multivariate analysis of variance gave no indication of sexual dimorphism in the mean phenotype (Wilks' lambda = .98; $F(4,85) = .51$, $P > 0.7$). Consequently, male and female samples were pooled for subsequent analysis. Basic statistics for the sample are shown in Table 1. The coefficients of variation of the characters range from about 3% to 6%, which is fairly typical for linear measurements.

Directional selection differentials were calculated as the covariances between relative fitness and each character; these represent the changes in character means produced by direct and indirect selection. The directional selection gradient was estimated from the partial regression coefficients of relative fitness on the characters (Table 2). The stabilizing selection gradient was estimated from a multiple regression of relative fitness on the four characters and the ten product variables (head × head, head × thorax, . . . , scutellum × wing, wing × wing). None of the quadratic coefficients were statistically significant, possibly due to the small sample size, hence the analysis of stabilizing selection is not reported here.

Interpretation of Results.—The pentatomid data provide some striking contrasts between selection differentials and gradients (Table 2). For example, there was no significant directional selection differential on the thorax, indicating that no appreciable change in mean thorax width resulted from selection. Nevertheless, in the selection gradient the coefficient for thorax is highly significant. Thus there was substantial selection directly on the thorax, but this was masked in the selection differential by indirect selection through some correlated character(s). Apparently, direct selection to decrease wing length (which is positively correlated with thorax width) produced negative indirect selection on the thorax, counteracting the direct effect of selection to increase thorax width (eq. 6b).

Selection on the scutellum is another example of the distinction between the selection differential and the selection gradient. Despite a significant decrease in

TABLE 1. *Statistics of the hemipteran population before selection, with all characters transformed to natural logarithms.*

Character	Sample size,[†] N	Mean, $\bar{z}$	Standard deviation, σ
Head	94	.880	.034
Thorax	93	2.038	.049
Scutellum	94	1.526	.057
Wing	91	2.337	.043
Correlations[‡]			

Character	Head	Thorax	Scutellum	Wing
Head	1	.72	.50	.60
Thorax		1	.59	.71
Scutellum			1	.62
Wing				1

[†] Thorax and wing dimensions could not be measured on all individuals due to damage
[‡] All correlations are significant at the .001 level

mean scutellum length, there was no significant directional selection on this character. The observed selection differential for the scutellum is therefore attributable to the indirect effects of selection acting on correlated characters. Because the two traits undergoing substantial directional selection (thorax and wing) are about equally variable and have nearly the same correlation with the scutellum, it appears that the somewhat stronger selection to decrease wing length (compared with that to increase thorax width) produced the overriding indirect effect on the scutellum. These examples clearly illustrate how the observed selection differential can give a misleading picture of the selective forces acting directly on the characters.

The magnitudes of the standardized selection coefficients reveal rather strong directional selection on two of the characters. On average in the population, an increase in thorax length alone by one standard deviation would have increased relative fitness by about 58%, while an increase in wing length alone by one standard deviation would have decreased relative fitness by about 74%. The proportion of variance in relative fitness explained by the multiple regression is highly significant ($R^2 = .23$).

Two interpretations can be made of the

TABLE 2. *Directional selection differential* (s) *and gradient* ($\beta \pm$ *standard error) for the hemipteran population. Standardized selection coefficients* (s' *and* β') *are also given in units of phenotypic standard deviations.*

Character	s†	s'	$\beta \pm$ SE	$\beta' \pm$ SE
Head	−.004	−.11	−.7 ± 4.9	−.03 ± .17
Thorax	−.003	−.06	11.6** ± 3.9	.58** ± .19
Scutellum	−.016*	−.28*	−2.8 ± 2.7	−.17 ± .15
Wing	−.019**	−.43**	−16.6** ± 4.0	−.74** ± .18
	$\sigma_w^2 = 1.43$		$R^2 = .23**$	

* Significant at the 05 level ** Significant at the 01 level
† Significance levels are for Spearman rank correlations of relative fitness with the characters

differing signs on the coefficients for the wing and thorax in the directional selection gradient. First, selection can be viewed as acting separately on the characters, one force favoring large thorax and another force favoring small wings. A second interpretation is that directional selection acted on a character combination or index, rather than separately on wing and thorax. The results are consistent with selection on the index 11.6 thorax−16.6 wing (eq. 10). Since the characters are measured on logarithmic scales this is nearly equivalent to saying that selection favored bugs with proportionally small wings in relation to thorax length. In turbulence and/or precipitation such bugs may have been better fliers and spent less time in the lake water during the storm. This hypothesis could be tested with aerodynamic studies.

Selection in the House Sparrow

On the morning of February 1, 1898 after a severe winter ice storm, immobilized house sparrows (*Passer domesticus*) were common on the ground in Providence, Rhode Island. Bumpus (1899) obtained a sample of 136 of these sparrows and upon bringing them into his laboratory, about half of the birds revived. Bumpus weighed all the birds and then prepared them as specimens, keeping track of the survivors and nonsurvivors. He made eight linear measurements on each specimen (total length, wing extended, skull width, and lengths of beak plus head, humerus, femur, tibiotarsus, and keel of sternum), and published the raw data in his original report.

We transformed all the linear measurements to natural logarithms. Body weight was also transformed to natural logarithms, after taking the cube root in order to make its dimensionality the same as that of the other characters (Lande, 1977). Bumpus classified males into juvenile and adult subsamples, based on plumage appearance. Multivariate Analysis of Variance showed no significant age effects on the mean vectors of the metrical traits (Wilks' lambda = .92; $F(9,77) = .74$, $P > .7$) and accordingly the juvenile and adult males were pooled for subsequent analysis. The lack of age effects probably reflects a cessation of skeletal growth soon after fledging, as has been documented for song sparrows by Smith and Zach (1979). MANOVA did reveal significant sexual dimorphism (Wilks' lambda = .52; $F(9,126) = 12.86$, $P < .0001$), and univariate analysis of variance showed significant differences between the sexes in total length, weight, wing extended, humerus, and sternum. Hence males and females were analyzed separately. The variability of the characters is consistent with the typically small coefficients of variation of linear measures in birds, between about 2% and 5%. Significant positive correlations occur for all pairs of characters, ranging from .26 to .88 in males, and from .46 to .83 in females.

Directional selection differentials and gradients were estimated for each sex. The only significant coefficients in the directional selection gradients were for weight in both sexes (male $\beta' = -.27 \pm .09$, female $\beta' = -.52 \pm .25$) and for total length in males ($\beta' = -.52 \pm .10$). The stan-

dardized selection coefficients reveal apparently strong directional selection on these traits. The proportion of total variance in relative fitness explained by the multiple regression was highly significant for males ($R^2 = .46$), while that for females was not significant ($R^2 = .20$).

The samples are not large enough to analyze stabilizing selection on all nine characters. The full quadratic regression would contain nine coefficients of directional selection and 45 coefficients of stabilizing selection. With only 49 females and 87 males there were not enough degrees of freedom to estimate all of the selection coefficients in females, or to do so precisely in males. Substantial positive correlations between all characters suggested that a reduction of dimensionality could be carried out by using the first few principal components of variation in each sex, while still retaining most of the total variation in the characters. Ordinary principal components (eigenvectors) were computed from the phenotypic variance-covariance matrices. In both cases more than 70% of the total character variance was accounted for by the first two principal components. We therefore restricted the analysis of stabilizing selection to the first two principal components of variation in each sex. All characters contributed positively to the first principal component in both sexes, which can be viewed as an index of general size. The second principal component of variation had a large positive contribution from the sternum and lesser negative contributions from humerus, femur and tibiotarsus lengths in both sexes, and can be viewed as an index of sternum size in relation to limb dimensions.

Directional and stabilizing selection gradients on the first two principal components were estimated using the method of quadratic regression described above (and in the Appendix). There was (barely) significant stabilizing selection on the first principal component of females only. The standardized selection coefficient ($\gamma'_{11} = -.45 \pm .22$) indicates that on average in the female population a random change in the first principal component alone by (plus or minus) one standard deviation would

have decreased relative fitness by about 45%.

Interpretation of Results.—The sample of sparrows obtained by Bumpus has definite limitations that should be kept in mind in interpreting our selection analysis. Because Bumpus collected birds that were immobilized by a storm, some individuals may have survived without falling to the ground and these would necessarily be missing from the sample. Thus the selection measured is conditional on the event of immobilization and may not represent the selection experienced by the entire population. In addition, the selection observed only pertains to mortality on a single night of unusually severe weather. This brief episode of selection may not reflect the forces acting throughout the year. (Similar qualifications apply to the above interpretation of selection on pentatomid bugs.)

The winter storm apparently favored small birds. This pattern of winter selection seems difficult to explain on functional grounds, since it is opposite to that which would be predicted from Bergman's rule (larger geographic races in colder climates). Johnston et al. (1972) have suggested that sparrows surviving the storm may have lost weight by metabolizing longer than those which perished, but this would not account for the highly significant decrease in male body length.

The analysis of selection on the first two principal components failed to reveal significant directional selection on either sex. Although significant directional selection was detected for some of the original characters, combination with other apparently unselected characters rendered the directional selection gradient on the first principal component nonsignificant. There was, however, strong but barely significant stabilizing selection on the first principal component of females.

DISCUSSION

We have shown that selection coefficients which appear in dynamical equations for the evolution of correlated characters can be estimated from purely phenotypic data. These same coefficients

describe a surface of phenotypic selective value acting on a population. Multiple regression of individual relative fitness on the characters can be used to estimate the forces of directional selection, given by the steepest uphill slope (or gradient) in the best linear approximation to the selective surface; the forces of stabilizing or disruptive selection are given by the curvature of the best quadratic approximation to the selective surface. Even if the quadratic approximation to the selective surface has a maximum, so that an optimal phenotype exists, the population mean may differ substantially from the optimum, indicating maladaptation of the mean phenotype. Disruptive selection on one or more characters suggests that the population is in a valley or saddle between two or more adaptive peaks. Some important questions which can be approached with the techniques we have described include the following: Do selective surfaces commonly have multiple peaks? How frequent is maladaptation of the mean phenotype in a population? What is the magnitude of geographical and temporal variation in selective surfaces? Studies designed to answer such questions should be done on a number of animal and plant populations. Only then will we have adequate information on the intensity and pattern of phenotypic natural selection.

The examples we have analyzed leave much to be desired. They have, nevertheless, illustrated the application of partial regression analysis in the measurement of directional and stabilizing selection on correlated characters. The analysis of directional selection on pentatomid bugs showed that the observed change in the mean phenotype within a generation may be a very poor indicator of the actual forces of selection estimated by the selection gradient; indirect selection through correlated characters can cause the mean value of a trait to change against the force of selection on it. The analysis of Bumpus' data on sparrows demonstrated one technique for the reduction of dimensionality that may often be necessary when estimating forces of stabilizing selection on multiple

characters. Our analysis differed from most previous treatments of the Bumpus data which employed univariate selection theory and mainly compared surviving and dead samples, rather than those before and after selection (Bumpus, 1899; Harris, 1911; Calhoun, 1947; Grant, 1972; Johnston et al., 1972; O'Donald, 1973; for an exception see Manly, 1976). Grant (1972) commented that the sparrow characters were strongly correlated so that a univariate selection theory is inadequate to identify which characters were the actual target of selection.

In both the pentatomid and sparrow populations we detected apparently intense directional selection during brief periods of high mortality (see also Van Valen, 1963; Hagen and Gilbertson, 1973; Boag and Grant, 1981). Because the persistence of a population requires that the total selective mortality not exceed the reproductive rate, these results suggest that in some populations most of the directional selection within a generation may be concentrated in a few relatively short periods of high mortality.

Attempts have frequently been made to measure the intensity of stabilizing selection by its effect on the variance of single traits. We have demonstrated, however, that purely directional selection (defined by a linear fitness surface) decreases character variance (eq. 13a), and have therefore proposed to measure stabilizing selection in terms of the curvature of the best quadratic approximation to the selective surface. Furthermore, stabilizing selection on any character indirectly decreases the variance of correlated characters, whether the correlations are positive or negative (eqs. 11, 15c). For these two reasons, most previous studies (reviewed by Johnson, 1976 Ch. 7) have probably seriously overestimated the strength of stabilizing selection acting directly on single characters. This may explain why the only significant stabilizing selection we detected in the Bumpus data was on the first principal component of variation in females, although these data have been considered a classic example of stabilizing selection.

Summary

Multivariate statistical methods are derived for measuring selection solely from observed changes in the distribution of phenotypic characters in a population within a generation. Selective effects are readily detectable in characters that do not change with age, such as meristic traits or adult characters in species with determinate growth. Ontogenetic characters, including allometric growth rates, can be analyzed in longitudinal studies where individuals are followed through time.

Following an approach pioneered by Pearson (1903), this analysis helps to reveal the target(s) of selection, and to quantify its intensity, without identifying the selective agent(s). By accounting for indirect selection through correlated characters, separate forces of directional and stabilizing (or disruptive) selection acting directly on each character can be measured. These directional and stabilizing selection coefficients are respectively the parameters that describe the best linear and quadratic approximations to the selective surface of individual fitness as a function of the phenotypic characters.

The theory is illustrated by estimating selective forces on morphological characters influencing survival in pentatomid bugs and in house sparrows during severe weather conditions.

Acknowledgments

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APPENDIX

Writing the orthogonal quadratic regression of relative fitness on the characters, setting $\bar{z} = 0$, and listing each quadratic term once,

$$w - 1 = \sum_{j=1}^{n} \beta_j z_j + \sum_{k=1}^{n} \sum_{l=k}^{n} (1 - \tfrac{1}{2}\delta_{kl})\gamma_{kl}\xi_{kl} + \varepsilon \tag{A1}$$

the quadratic polynomials are the usual quadratic deviations in (16) with an additional linear factor that corrects for skewness of the character distribution,

$$\xi_{kl} = z_k z_l - P_{kl} - \tau^T_{kl} P^{-1} z. \tag{A2}$$

$\tau^T_{kl} = (\tau_{1kl}, \ldots, \tau_{nkl})$ is a vector of all third moments of the distribution involving characters z_k and z_l,

$$\tau_{jkl} = \int z_j z_k z_l p(z)dz. \tag{A3}$$

Each of the polynomials ξ_{kl} is evidently uncorrelated with all of the z_j since

$$\text{Cov}[z, \xi_{kl}] = \tau_{kl} - \text{Cov}[z, z^T]P^{-1}\tau_{kl} = 0.$$

The coefficients in the orthogonal regression (A1) are found by minimizing the mean squared error, $Q,$ as before. $\partial Q/\partial \beta_j = 0$ implies (17), which is what would be obtained from an ordinary linear regression (omitting the quadratic terms or polynomials in (16) or (A1)). For the coefficients of the quadratic polynomials, $\partial Q/\partial \gamma_{ij} = 0$ implies the same equations (involving fourth moments of the character distribution) that would be obtained from (16) without any distributional assumptions. The orthogonal regression (A1) is also useful for calculating separate proportions of variance in relative fitness due to directional and stabilizing selection, expressed as the squared multiple correlation coefficients, R^2, of relative fitness with the linear terms and the quadratic polynomials.