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THE ADDITIVE PARTITIONING OF SELECTION GRADIENTS

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The action of environmental forces on continuously distributed phenotypic traits changes the mean, variance, and other moments of the phenotypic distribution. Changes in the phenotypic distribution that occur within a generation can be attributed to the effects of development and natural selection, and those that occur across generations, from parents to offspring, are attributed to transmission. In this paper, we will ignore the effects of development and assume that within-generation change is caused by selection (Fisher, 1930; Lande and Arnold, 1983; Arnold and Wade, 1984a, 1984b). Our purpose is to reexamine recent methods for measuring selection (Lande and Arnold, 1983; Arnold and Wade, 1984a, 1984b), particularly in those instances where selection can be separated into episodes or components corresponding to different portions of the life cycle. We will restrict our attention to within-generation changes in the mean and variance of the phenotypic distribution. Change in the mean has been called *directional selection* (Lande and Arnold, 1983; Arnold and Wade, 1984a, 1984b) and is mathematically equivalent to the *selection differential* or covariance between relative fitness and character value (Robertson, 1966). The *selection gradient*, the vector of (partial) regression coefficients of relative fitness on character value, has been recommended as a better descriptor of the force of directional selection on a particular trait for reasons discussed in Lande and Arnold (1983 p. 1220).

Change in the variance of the phenotypic distribution can be interpreted as disruptive or stabilizing selection, depending upon whether the phenotypic variance is enhanced or diminished (Lande and Arnold, 1983). There are alternative definitions of stabilizing selection as selection favoring individuals with intermediate values and disruptive selection as that favoring individuals with extreme values (Mitchell-Olds and Shaw, 1987). Because directional selection itself changes the phenotypic variance, Lande and Arnold (1983 p. 1215) limited the definition of stabilizing selection to that portion of the change in the phenotypic variance attributable to the covariance between relative fitness and the squared deviation of the character value from its mean (quadratic selection).

Any change in the phenotypic variance, whether owing to directional or quadratic selection, prohibits an additive partitioning of the selection gradient in the manner suggested by Arnold and Wade (1984a p. 712). If the phenotypic variance changes at one episode of selection, say i , then the components of the total selection gradient given by Arnold and Wade (1984a p. 712) are not the gradients that one would observe by measuring the population at episodes $i + k$ of selection where $k > 1$. This happens because the Arnold and Wade (1984a) partitioning is correct only if the phenotypic variance is constant over the entire period. To illustrate this, consider the total selection gradient on a single character, $\beta_T = S_T/P_0$, where S_T is the covariance between character value and fitness and P_0 is the phenotypic variance before selection. Let $\beta_i = S_i/P_{i-1}$ be the selection gradient at the i th episode of selection, where S_i and P_i are the respective covariances and variances. Lastly, let $S_T = \sum S_i$. The Arnold and Wade partitioning states that $\beta_T = \sum \beta_i$, which can be true only if $P_i = P_0$ for all i . Although the total selection differential can be partitioned, the gradients, as ratios of selection differentials to variances, cannot. For this reason, Arnold and Wade partitioned only the numerator of β_T and stated that "individual selection gradients might not sum to the total selection gradient" (Arnold and Wade, 1984a p. 713). They cannot sum to the total whenever selection at an early episode affects the phenotypic variances or covariances among traits (Kalisz, 1986). Thus, the utility of that partitioning is open to question, because its components do not have the properties of true selection gradients (Kalisz, 1986). In illustrating their partitioning, Arnold and Wade (1984b) chose a data set from Howard (1979) in which the phenotypic variance was not observed to change significantly at any of the episodes of selection, and this problem was not an issue. However, selection in natural populations will not always have this property. In this note, we illustrate how an additive partitioning of the total selection gradient into components that are themselves weighted selection gradients can be accomplished. Because the partitioning is additive, it is useful for comparative purposes, and the weight-

ings have a natural interpretation. In our analysis, we assume that each individual in the population manifests each character from birth. For a treatment of selection on traits manifested only at certain ages, see Lynch and Arnold (1988).

Lande (1979) illustrated how genetic correlations among characters can limit the response to selection; the change across generations in the mean value of a trait depends upon the effects of selection on all genetically correlated traits. Our partitioning shows how phenotypic correlations can limit the action of selection within a generation. We show how changes in phenotypic correlations among characters at one episode of selection can enhance or diminish the operation of selection in later episodes within the same generation. The effect of natural selection on the mean value of a trait in later episodes of selection is constrained by the phenotypic variance and covariance with other characters at earlier episodes of selection.

Derivation of the Additive Partitioning

Let there be m episodes of selection and let the fitness of an individual with character vector \mathbf{z} be $W_k(\mathbf{z})$ at the k th episode of selection. The total fitness, $W(\mathbf{z})$, of an individual with character vector \mathbf{z} , is thus equal to the product

$$W(\mathbf{z}) = \prod W_k(\mathbf{z}). \tag{1}$$

We let $p_k(\mathbf{z})$ be the distribution of phenotypic values in the population after the k th episode of selection; $p_0(\mathbf{z})$ is the initial distribution of phenotypes before any selection. The relationship between $p_k(\mathbf{z})$ and $p_{k-1}(\mathbf{z})$ is thus

$$p_k(\mathbf{z}) = p_{k-1}(\mathbf{z})\tilde{W}_{k-1}(\mathbf{z}) \tag{2}$$

where

$$\tilde{W}_k(\mathbf{z}) = W_k(\mathbf{z}) \left\{ \int p_{k-1}(\mathbf{z})W_k(\mathbf{z}) d\mathbf{z} \right\}^{-1}. \tag{3}$$

The total change in the phenotypic distribution is

$$\Delta\tilde{\mathbf{z}}_{\text{total}} = \mathbf{S} = \text{Cov}[\mathbf{z}, \tilde{W}(\mathbf{z})] \tag{4}$$

where

$$\tilde{W}(\mathbf{z}) = W(\mathbf{z}) \left\{ \int p_0(\mathbf{z})W(\mathbf{z}) d\mathbf{z} \right\}^{-1} \tag{5}$$

and

$$\text{Cov}[\mathbf{z}, \tilde{W}(\mathbf{z})] = \int zp_0(\mathbf{z})\tilde{W}(\mathbf{z}) d\mathbf{z} - \int zp_0(\mathbf{z}) d\mathbf{z}. \tag{6}$$

β_{total} , the selection gradient on \mathbf{z} , is the vector of standardized selection differentials given by multiplying Equation (6) by the inverse of the phenotypic variance-covariance matrix of \mathbf{z} , \mathbf{P}_0^{-1}

$$\beta_{\text{total}} = \mathbf{P}_0^{-1}\mathbf{S}. \tag{7}$$

In order to partition the vector into additive components we rewrite Equation (7) as

$$\beta_{\text{total}} = \mathbf{P}_0^{-1} \left\{ \sum \mathbf{P}_{k-1}\mathbf{P}_{k-1}^{-1}\mathbf{S}_k \right\} \tag{8}$$

where \mathbf{P}_k is the phenotypic variance-covariance matrix at the end of the k th episode of selection and \mathbf{S}_k is the selection differential at that episode. We note that

$$\beta_k = \mathbf{P}_{k-1}^{-1}\mathbf{S}_k \tag{9}$$

is the vector that would be observed at the k th episode of selection. We can rewrite Equation (8) as

$$\beta_{\text{total}} = \sum \mathbf{a}_{k-1}\beta_k \tag{10}$$

where $\mathbf{a}_{k-1} = \mathbf{P}_0^{-1}\mathbf{P}_k$.

We have now written a decomposition of the vector of total selection gradients into a weighted sum of the vectors of selection gradients observed at each component episode. Each weighting, \mathbf{a}_k , in Equation (10) is the product of the phenotypic variance-covariance matrix at the beginning of an episode of selection (\mathbf{P}_{k-1}) and the inverse of the original phenotypic variance-covariance matrix (\mathbf{P}_0^{-1}). Whenever selection affects the phenotypic variance-covariance matrix, this ratio will be different from \mathbf{I} , the identity matrix. Lande and Arnold (1983 p. 1215) emphasize that even directional selection will alter the elements in the phenotypic variance-covariance matrix.

These weighting elements, \mathbf{a}_k , have a natural interpretation: they represent the cumulative change by selection in the phenotypic variance-covariance matrix up to this point in the life cycle. Clearly, to perform the partial regression of fitness on one trait in the vector of phenotypes at a given episode of selection, we require the variance of that trait at the start of that episode as well as the covariances of that trait with other components of the vector of phenotypes. The contribution of this episode to the total change by selection in the mean value of the trait must then itself be weighted by the relative amount of phenotypic variance available for selection at the start of that episode. The original phenotypic variance-covariance matrix, \mathbf{P}_0 , is the natural scale or standard of comparison.

Summary

Any change in the phenotypic variance at one episode of selection, whether owing to directional or quadratic selection on a measured or unmeasured character, prohibits an additive partitioning of the directional selection gradient in the manner suggested by Arnold and Wade (1984a p. 712). If the phenotypic variance of a trait, z , is changed by one episode of selection, the components of the directional selection gradient given by Arnold and Wade (1984a) are not the gradients that one would measure at subsequent episodes of selection. Thus, these components do not have the properties of true selection gradients. In this note, we derived a true additive partitioning of the total selection gradient into components. The components of this partitioning consist of selection gradients corresponding to each episode of selection and multiplicative weighting factors that represent the relative change in the phenotypic variance-covariance matrix. Because the partitioning is additive, it is useful for comparative purposes, such as determining whether or not selection on body size at one stage in the life history is more intense than at some other stage (see Kalisz [1986] for an application of our method). The weightings have a natural interpretation that conforms to common evolutionary expectation: selection at one episode in the life history can limit (or enhance) the phenotypic variation available for selection at a later stage in the life history.

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COMMENT ON A RATE TEST

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Turelli et al. (1988) proposed a "rate test" regarding whether the speed of evolution is too fast or too slow to be explained by drift under certain assumptions. Their test involves the count *t* of generations of a lineage, the absolute change *z* in the mean of a phenotypic trait over that span of generations, and the new genetic variance σ_m^2 introduced by mutation per zygote per generation. Evolution has been too fast to be explained by drift if

$$\sigma_m^2 < \frac{z^2}{2t(2.2414)^2}$$

and has been too slow to be explained by drift if

$$\sigma_m^2 > \frac{z^2}{2t(0.03134)^2}$$

(Turelli et al., 1988 eqs. 9 and 10). I have cancelled a factor σ^2 from both sides and substituted more accurate normal tails for the values 2.24 and 0.03 used by Turelli et al. Together the formulas delimit one possible 95% confidence interval around the null hypothesis of drift. This particular interval covers a range of *z*'s in the ratio of 2.2414 : 0.03134, which is 71.5 to 1.

When phenotypic means are available at an adequate number of intermediate times, a far more powerful statistical test for the "slow" side of this same distinc-

tion is available from the theory of random walk. Instead of the measure *z* of absolute change from end to end of the series, one should use the maximum excursion *z**, the largest (absolute) deviation from the starting sample mean *anywhere* in the series of *t* generational means. Then, under the assumptions of the "mutation-drift-equilibrium" model, as summarized in Turelli et al. (1988 eq. 6), evolution is too fast to be explained by drift if

$$\sigma_m^2 < \frac{(z^*)^2}{2t(2.4977)^2}$$

and is too slow to be explained by drift if

$$\sigma_m^2 > \frac{(z^*)^2}{2t(0.56014)^2}$$

The range of the implied 95% confidence interval for drift, again on the multiplicative scale, is 2.4977: 0.56014, which is 4.46 to 1, a 16-fold improvement over the bound supplied by Turelli et al.

These bounds on the ratio z^*/σ_m are a consequence of a fundamental theorem about Brownian motion proved by Erdős and Kac in 1946 but suspected by the economist Bachelier around the turn of the century (see Spitzer, 1964). The theorem is stated and one proof