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The aim of this paper is to illustrate an approach to the empirical measurement of selection that is directly related to formal evolutionary theory. Recent field studies have demonstrated that it is feasible to measure fitness in natural populations. The most successful studies have yielded accurate tallies of survivorship, mating success and fertility (e.g., Tinkle, 1965; Howard, 1979; Downhower and Brown, 1980; Lennington, 1980; Kluge, 1981; Clutton-Brock et al., 1982). Despite this success, no concensus has been reached on how to analyze the data and relate them to evolutionary theory. We present here a mode of data analysis that describes selection in useful, theoretical terms, so that field or experimental results will have a tangible relationship to equations for evolutionary change.

Multivariate, polygenic theory (Lande, 1979, 1980, 1981; Bulmer, 1980) is particularly useful as a conceptual framework because it is concerned with the evolution of continuously distributed traits such as those commonly studied in laboratory and field situations. Multivariate equations have been used for many years by plant and animal breeders in order to impose selection and predict its impact (Smith, 1936; Hazel, 1943; Dickerson et al., 1954, 1974; Yamada, 1977), but this quantitative genetic theory has only recently been applied to evolutionary problems.

Definitions and Aims. — It is critical to distinguish between *selection* and *evolutionary response to selection* (Fisher, 1930; Haldane, 1954). Selection causes observable changes within a generation in the means, variances and covariances of phenotypic distributions. Thus selection can be described in purely phenotypic terms without recourse to the inheritance of characters. In contrast, evolutionary response to selection, for example, the change in phenotypic mean from one generation to the next, certainly does depend on inheritance. In the following sections we show how knowledge of inheritance can be combined with purely phenotypic measures of selection to predict evolutionary response to selection. By distinguishing between selection and response to selection we can measure selection on characters whose mode of inheritance may be unknown and make prediction of evolutionary response a separate issue. Thus knowledge of inheritance is essential for complete

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evolutionary analysis but is not required for the measurement of selection on phenotypic characters.

The statistical relationship between fitness and phenotypic characters can be deduced from the changes that occur within a generation in the means, variances and covariances of phenotypic traits. The covariance between relative fitness and a quantitative character is mathematically equivalent to the shift in mean induced within a generation by directional selection (Robertson, 1966; Price, 1970; Bulmer, 1980). This covariance, or change in mean before and after selection, is called the *selection differential* (Lush, 1945; Falconer, 1981). However, the mean may shift within a generation for two reasons: (1) because selection has acted directly on the character, or (2) because selection has acted on a correlated character (Pearson, 1903). The direct and indirect effects of selection can be partitioned with multivariate statistics if the correlated characters that are actually under selection are included in the data. The partial regression of relative fitness on a character measures the direct force of selection on that character and is known as the *selection gradient* (Lande, 1979; Lande and Arnold, 1983).

One of the primary aims of this paper is to show how selection, measured by selection differentials or gradients, can be separated into parts corresponding to segments of the life cycle. We refer to these life cycle segments as *episodes of selection*. The recognition of separate episodes of selection is useful because the direction or magnitude of selection on particular characters may change from one life cycle segment to the next. We present a formal solution that permits partitioning of selection differentials and gradients into parts corresponding to an arbitrary number of selection episodes. We treat the general case in which selection acts simultaneously on a whole suite of characters, but we deal here only with directional selection. The measurement of stabilizing and disruptive selection is discussed in Lande and Arnold (1983).

The *opportunity for selection* can be conveniently measured as the variance in relative fitness (Crow, 1958). Variance in fitness constrains the evolution of fitness itself and the intensity of selection that can act on any character. When there is no variance in fitness, there can be no selection: when there is a large variance in fitness, there is a great opportunity for selection. The fact that the opportunity for selection can be expressed as a variance is important because we can treat many apparently unsolved problems in the analysis of selection as well-studied problems in the analysis of variance. One such problem is a primary topic of this paper: How can we measure the selection opportunities corresponding to separate stages in the life cycle? We use a multiple-level analysis of fitness variance to solve this problem. The mode of analysis is illustrated in a companion paper (Arnold and Wade, 1984) with fitness data from frog, lizard and insect populations.

Measures of Selection in Relation to Evolutionary Theory

In order to place our results in a conceptual framework, it will be useful to review briefly some recent developments in multivariate selection theory. In nature, selection will usually act simultaneously on a whole set of phenotypic characters. Furthermore, the characters may be phenotypically and genetically correlated. *Genetic correlation* means that the characters are genetically coupled due to pleiotropy and/or linkage disequilibrium (Falconer, 1981). Under these common circumstances, one cannot predict the evolution of a single character by merely knowing its heritability and the strength of selection. Thus the usual equation for response to selection (response to selection equals the product of heritability and selection differential) cannot be used to model multivariate evolution in nature (Falconer, 1981).

Evolution in nature can be modeled using Lande's (1979, 1982) equation for response to multivariate selection. In Lande's generalization of the standard

univariate equation, $\Delta \bar{z}$ is a column vector representing the change in the mean of each phenotypic character from one generation to the next, G is the additive genetic variance-covariance matrix for the characters, P is the phenotypic variance-covariance matrix assessed before selection with the matrix inverse P^{-1}, S is a column vector of selection differentials and $\beta = P^{-1}S$ is a column vector of selection gradients. The selection differential measures both direct and indirect effects of selection, whereas the selection gradient measures only direct effects. Assuming that selection acts directly on phenotypic values, Lande (1979) shows that the deterministic evolution of phenotypic means can be modeled by the equation

$$\Delta \bar{z} = GP^{-1}S = G\beta. \qquad (1)$$

Focusing on the first character in the set, z_1, the change in mean across one generation is

$$\Delta \bar{z}_1 = G_{11}\beta_1 + G_{12}\beta_2 + G_{13}\beta_3 \\ + \ldots + G_{1n}\beta_n, \qquad (1b)$$

where G_{11} is the additive genetic variance for the first character, G_{1j} is the additive genetic covariance between the first and the jth character and β_j is the selection gradient for the jth character. The selection gradient represents the direct force of selection on a character, accounting for phenotypic correlations with the other characters (Lande, 1979) and is formally equivalent to the partial regression of relative lifetime fitness on the character holding all other characters constant (Lande, 1982; Lande and Arnold, 1983). In the above equation, the first term represents the direct response to selection on the character, $G_{11}\beta_1$, while the other terms represent the correlated responses to selection.

We will now show that the selection gradient can be partitioned into additive parts corresponding to episodes of selection. We begin by deriving a partitioning of the selection differential.

RESULTS

Partitioning the Selection Differential

A partitioning of the selection differential into additive parts corresponding to an arbitrary number of selection episodes follows directly from Lande's (1980) discussion of selection differentials when sexual selection follows natural selection (an example of the two episode case). Successive episodes of selection might shift the mean in different directions, but the total shift in mean after all episodes must be equal to the sum of the shifts imposed by each episode. Thus, the total shift in mean, or the selection differential, after m episodes of selection is

$$\begin{aligned} S &= \bar{z}_m - \bar{z} \\ &= (\bar{z}_m - \bar{z}_{m-1}) + (\bar{z}_{m-1} - \bar{z}_{m-2}) \\ &\quad + \ldots + (\bar{z}_1 - \bar{z}) \\ &= \sum_{k=1}^{m} (\bar{z}_k - \bar{z}_{k-1}), \qquad (2) \end{aligned}$$

where $\bar{z}$ is the character mean before selection, $\bar{z}_m$ is the mean after m episodes of selection, $\bar{z}_k$ is the mean after k intermediate episodes of selection and $(\bar{z}_k - \bar{z}_{k-1})$ is the shift induced by the kth episode of selection.

In order to calculate the mean of the character after some arbitrary number of episodes, we will need to know how fitness and the character frequency distribution change with each selection episode.

Let W_k be the *absolute* fitness of an individual at episode k of selection. Let p be the frequency of individuals with phenotype z before selection and let p_k be the frequency of these same individuals after the kth episode of selection. Let the components of fitness be multiplicative, such that the total absolute fitness of an individual is

$$W = \prod_{k=1}^{m} W_k. \qquad (3a)$$

Let the *relative* fitness of an individual at episode k of selection be

$$w_k = W_k/\bar{W}_k, \qquad (3b)$$

where $\bar{W}_k$ is the average absolute fitness at the kth episode.

The initial frequency distribution of the phenotypes, p, changes as a result of each episode of selection: from p to $p_1 = pw_1$ after the first episode, to $p_2 = p_1 w_2$ after the second episode and so forth. In general, after k episodes of selection, the frequency of individuals of phenotype z will be

$$p_k = p_{k-1} w_k. \qquad (4)$$

Thus the average absolute fitness at the kth selection episode is

$$\bar{W}_k = \sum p_{k-1} W_k. \qquad (5)$$

The mean phenotype before the onset of selection is, by definition,

$$\bar{z} = \sum pz \qquad (6a)$$

and the mean of the phenotypic character after k episodes of selection will be

$$\bar{z}_k = \sum p_k z$$
$$= \sum p_{k-1} w_k z. \qquad (6b)$$

We can now show that each component of the partitioned selection differential is itself a covariance of character value and relative fitness. Since the shift in mean due to the kth episode of selection is

$$\bar{z}_k - \bar{z}_{k-1} = \left(\sum p_k z \right) - \bar{z}_{k-1}$$
$$= \left(\sum p_{k-1} w_k z \right)$$
$$- \bar{z}_{k-1}, \qquad (7a)$$

and since $\bar{z}_{k-1}$ is the character mean at the onset of the kth selection episode and $\bar{w}_k = 1$, expression (7a) is a standard expression for a covariance. Thus the selection differential corresponding to the kth episode of selection is

$$\bar{z}_k - \bar{z}_{k-1} = \text{Cov}(z, w_k), \qquad (7b)$$

which is the covariance between phe-

notypic value and the kth component of relative fitness, S_k. Consequently, using (2) and (7b),

$$S = \sum_{k=1}^{m} \text{Cov}(z, w_k)$$
$$= \sum_{k=1}^{m} S_k. \qquad (8)$$

This accomplishes an additive partitioning of the selection differential for an arbitrary number of selection episodes. The extension to the partitioning of the multivariate selection gradient, S, is straightforward, since expression (8) can be applied individually to each element in the column vector.

Partitioning the Selection Gradient

The partitioning of the selection gradient, β, follows simply from the above results. Substituting the column vector version of (8) into the expression $\boldsymbol{\beta} = \boldsymbol{P}^{-1}\boldsymbol{S}$ yields the m-episode partitioning of the selection gradient. Thus the total selection gradient for a particular character,

$$\beta = \sum_{k=1}^{m} \beta_k.$$

This derivation also reveals that the components of the partitioned selection gradient, namely $\boldsymbol{\beta}_k$, are themselves partial regressions of relative fitness at the kth episode on phenotypic value holding all other phenotypic characters constant.

In the preceding derivation the selection gradient corresponding to a particular selection episode was calculated using the phenotypic variances and covariances before selection, $\boldsymbol{P}$. These phenotypic variances and covariances may be changed by selection. Consequently in order to describe the partial regression of relative fitness on character at a particular selection episode, k, one might use the phenotypic variance-covariance matrix corresponding to the onset of that episode, $\boldsymbol{P}_k$, so that

$$\boldsymbol{\beta^*}_k = \boldsymbol{P}_k^{-1} \boldsymbol{S}_k.$$

This selection gradient might give a more accurate picture of selection at that episode than $\beta_k = P^{-1}S_k$, but it has the disadvantage that individual selection gradients might not sum to the total selection gradient β.

The Opportunity for Selection and its Partitioning

Variance in Fitness as the Opportunity for Selection.—There are three reasons for viewing variance in fitness as the opportunity for selection. First, as Crow (1958) pointed out, the change in mean fitness within a generation due to selection is equivalent to the variance in relative fitness. Consequently, if fitness were completely heritable, the change in fitness from one generation to the next would be equivalent to the variance in relative fitness. Second, if selection is not frequency-dependent, the change in fitness across generations will equal the additive genetic variance in fitness (Fisher, 1930, 1958). Since this genetic variance cannot exceed the phenotypic variance in fitness, fitness variance can be viewed as a constraint on fitness evolution. Finally, as we show in a later section, fitness variance places an upper bound on the force of selection that can act on any phenotypic character.

The opportunity for selection, I, has also been called the "index of total selection" and the "intensity of selection" (Crow, 1958, 1962; Wade, 1979; Wade and Arnold, 1980). Many of our colleagues prefer "opportunity for selection" because it gives a more accurate impression of the meaning of I. "Opportunity for selection" is also preferable because it avoids confusion with the standardized selection differential, i, which has also been called the "intensity of selection" (Hartl, 1980; Falconer, 1981).

The Relationship Between the Opportunity for Selection, the Selection Differential and the Selection Gradient.—These three measures of selection are related by the standard statistical relationship between variance, covariance and regres-
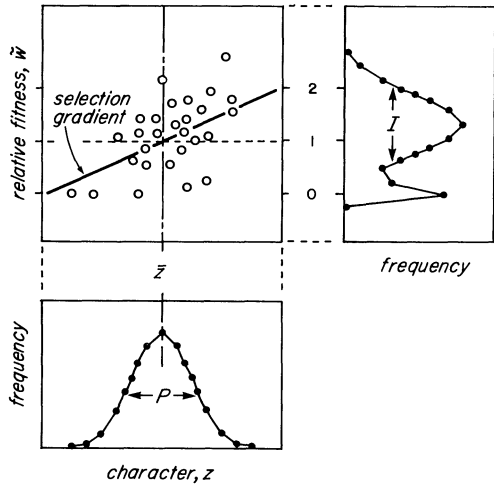

FIG. 1. A plot of hypothetical data showing the relationship between the univariate selection gradient and the opportunity for selection, I. In the center of the figure relative fitness, w, is shown as a function of phenotypic character value, z. The univariate selection gradient is the slope of the regression of relative fitness on character, z. The covariance of w and z is the selection differential. The marginal distribution of relative fitness is shown on the right hand side. The variance in relative fitness is I, the opportunity for selection.

sion. The opportunity for selection is the variance in relative fitness, the selection differential is the covariance between relative fitness and character, and the selection gradient is the partial regression of relative fitness on character, holding all other characters constant. The relationships are easiest to visualize in the univariate case in which selection acts directly on a single phenotypic character (Fig. 1). In this case the selection gradient is the ordinary regression of relative fitness on character (covariance of relative fitness and character divided by the character's phenotypic variance before selection, P). The opportunity for selection, I, is the variance of the marginal distribution of relative fitness.

Since the squared correlation coefficient must be equal to or less than unity, the squared selection differential must be equal or less than the product of phenotypic variance in a character before selection and the total opportunity for se-

lection, $S^2 \leq PI$. Since $S/P^{1/2}$ is the intensity of directional selection on the character, i, the absolute value of this intensity must be equal to or less than the square root of the total selection opportunity or the standard deviation in relative fitness,

$$|i| \leq I^{1/2}.$$

In other words, the number of phenotypic standard deviations that a character can be shifted by directional selection will always be equal to or less than the standard deviation in relative fitness.

Partitioning the Total Opportunity for Selection. — The total opportunity for selection, I, is defined as the variance in total relative fitness (Crow, 1958, 1962). This is equivalent to the variance in absolute total fitness divided by the square of mean total fitness. Crow also showed that the total opportunity of selection is equal to the change in relative total fitness caused by selection,

$$
\begin{align}
I &= V_w \tag{9a}\\
&= V_W / \bar{W}^2 \tag{9b}\\
&= (\bar{W}_T - \bar{W})/\bar{W} \tag{9c}\\
&= \Delta\bar{w}, \tag{9d}
\end{align}
$$

where V_w and V_W are, respectively, the variances in relative and absolute total fitness, $\bar{W}$ is the mean absolute fitness before selection and $\bar{W}_T$ is the mean absolute fitness after selection (Crow, 1958; O'Donald, 1970).

If the total force of selection can be subdivided into separate, more or less discrete, episodes of selection acting at different points in the life cycle of an organism, then I can similarly be partitioned into components. Crow (1958) derived such a partitioning for two independent episodes of selection.

The advantage of our partitioning is that we do not assume independent episodes of selection. In contrast Crow (1958, 1962) assumed that there was no correlation between fitness at different episodes (see also Doyle and Myers, 1982). We also permit an arbitrary number of selection episodes. A further critical feature of our approach is that we

evaluate the means, variances and covariances of fitness components using the phenotypic distribution that is present at the start of each episode. Thus while our formulation gives the same total opportunity for selection, I, as Crow's approach, it gives a different partitioning.

These differences between the two partitionings are particularly important in the measurement of selection in natural populations. With our partitioning lack of knowledge regarding a previous episode of selection does not influence the measured opportunity for selection for subsequent episodes; with Crow's partitioning, however, the measurement is necessarily affected.

Suppose there are a total of m episodes of selection. The mean absolute fitness before selection will be

$$\bar{W} = \sum pW, \tag{10}$$

where p is the frequency of individuals with fitness W. After m episodes of selection the mean total absolute fitness will be

$$\bar{W}_T = \sum p_m W. \tag{11}$$

Because our equations (10) and (11) define $\bar{W}$ and $\bar{W}_T$ in the same manner as Crow (1958), the total opportunity for selection, I, is the same. Substituting (3a) into (10), using (4) and (5), we find that

$$\bar{W} = \prod_{k=1}^{m} \bar{W}_k,$$

and so, substituting (10) and (11) into (9c)

$$
\begin{align}
I &= \bar{W}^{-1}\left[\sum p_m W - \sum pW\right]\\
&= \sum p_m w - \sum pw\\
&= \sum p_m w - 1\\
&= n^{-1}\sum w^2 - 1, \tag{12}
\end{align}
$$

in which n is the number of individuals in the population.

We can now derive a partitioning of this total opportunity for selection. We

desire a partitioning that includes variances in relative fitness at the separate episodes, I_k. Consider the case in which total selection is composed of three selection episodes. The total variance in relative fitness is, from exp. (12),

$$I = \sum p(w - 1)^2$$
$$= n^{-1} \sum w^2 - 1. \qquad (13)$$

The opportunity for selection at the first episode is

$$I_1 = \sum p(w_1 - 1)^2$$
$$= n^{-1} \sum w_1^2 - 1. \qquad (14)$$

Similarly, I_2 and I_3 are given by

$$I_2 = \sum p_1(w_2 - 1)^2$$
$$= n^{-1} \sum w_1 w_2^2 - 1, \qquad (15)$$

$$I_3 = \sum p_2 (w_3 - 1)^2$$
$$= n^{-1} \sum w_1 w_2 w_3^2 - 1. \qquad (16)$$

In general, the opportunity for selection at the kth episode is

$$I_k = p_{k-1}(w_k - 1)^2$$
$$= n^{-1} \sum \prod_{r=1}^{k-1} w_r w_k^2 - 1. \qquad (17)$$

In general, the episode opportunities will not sum to the total opportunity, even when selection acts independently at each episode. The discrepancy between the sum of the episode opportunities and the total is due to covariance between selection episodes. For example, when there are three selection episodes,

$$I = I_1 + I_2 + I_3 + C, \qquad (18)$$

where C is a residual term representing a sum of covariances between fitness components. These covariances have two sources: non-independence of selection and induction by zero fitnesses at some early episode. We have not been able to separate these two kinds of contributions but we give a decomposition of the residual term into constituent covariances in the APPENDIX.

If fitness components are multiplicative, one can obtain a simpler decomposition of fitness variance by taking the logarithms of fitness components and using the standard equation for the variance of a sum. A major disadvantage of this approach arises if fitness components take zero values, for in such cases logarithms are undefined. One could bypass this difficulty by adding a constant to all fitnesses before taking logarithms but the resulting fitness variances bear no simple relationship to dynamic equations for evolutionary change.

Selection Gradients for Fitness Components

In order to model the evolution of fitness components we need to know their selection gradients. If fitness components are defined so that their product is total lifetime fitness, then their selection gradients take a remarkably simple form.

Lande (1979) shows that the selection gradient for phenotypic character z is equivalent to the partial derivative of mean total fitness with respect to the character mean,

$$\beta = \frac{\partial \bar{W}}{\bar{W} \partial \bar{z}}.$$

If we define multiplicative fitness components such that $\bar{W} = \prod_{r=1}^{m} \bar{W}_r$, then taking the partial derivative of $\bar{W}$ with respect to $\bar{W}_k$, using the chain rule, we find that

$$\frac{\partial \bar{W}}{\partial \bar{W}_k} = \prod_{\substack{r=1 \\ r \neq k}}^{m} \bar{W}_r$$
$$= \bar{W} / \bar{W}_k.$$

Dividing this expression by mean total fitness, we find that the selection gradient on the kth component of fitness is

$$\beta_{w_k} = \frac{\partial \bar{W}}{\bar{W} \partial \bar{W}_k} \qquad (19a)$$

$$= \frac{1}{\bar{W}_k}. \qquad (19b)$$

So we have the simple result that the selection gradient on a multiplicative component of fitness is equal to the reciprocal of that component's mean value. For example, if fecundity is the kth fitness component, then the expected change in total fitness resulting from a unit change in fecundity, holding all other fitness components constant, is equal to the reciprocal of average fecundity. In other words, the episode of selection in which selection is the strongest (smallest $\bar{W}_k$), will have the largest selection gradient.

We can model the evolution of a fitness component, of a life history trait, using exp. (19) and exp. (1). Application of the latter equation assumes a multinormal distribution of fitness components. For example, the change in the mean of the first fitness component, across generations, is

$$\Delta \bar{W}_1 = G_{11}/\bar{W}_1 + G_{12}/\bar{W}_2 + G_{13}/\bar{W}_3 \\ + \ldots + G_{1m}/\bar{W}_m \quad (20)$$

and similarly for any other fitness component in the multiplicative series. Expression (20) shows that the evolution of a fitness component directly depends only on its additive genetic variance and mean phenotypic value and on its additive genetic covariances with other fitness components and the mean values of those other fitness components. Neither the phenotypic variances of fitness components nor phenotypic correlations between fitness components have direct effects on the evolution of fitness components. The crucial role of additive genetic covariances in life history evolution is further discussed by Lande (1982).

DISCUSSION

We have shown how selection can be measured in statistical terms that have a direct relationship to equations for evolutionary change. Selection can be measured in phenotypic terms without knowledge of character inheritance. Furthermore, the measures we discuss make no assumptions about the form of selection. For example, one need not assume that truncation or purely directional selection acts on the characters.

Using extensions of the methods we outline, one can measure forces of stabilizing and disruptive selection and reconstruct the selection surface that acts on phenotypic characters (Lande and Arnold, 1983). Arnold (1983) discusses the relationship to measures of performance used in physiological ecology and functional morphology.

Selection Opportunities, Differentials, Intensities and Gradients. — These four measures of selection have different uses. The opportunity of selection measures the overall constraint on the evolution of fitness and phenotypic characters that is imposed by variance in fitness. The selection differential measures both the direct force of selection on a character and indirect forces due to selection on related characters. The selection intensity (standardized selection differential) is useful for population comparisons because it measures the force of selection in units of phenotypic standard deviation. All of these measures of selection are unaffected by the particular choice of phenotypic characters. The selection gradient is affected by the characters that are included in a multivariate study, because it is a partial regression. The virtues of the selection gradient are that it measures only the direct forces of selection on a character and it has the most direct relationship to equations for evolutionary change.

One of our primary results is a technique for partitioning directional selection into parts corresponding to segments of the life cycle. This result has many empirical and conceptual applications. In a companion paper we review some of these applications (Arnold and Wade, 1984). An important aspect of our approach is that it can be applied to phenotypic characters. Prout (1965) and Christiansen and Frydenberg (1973) discuss analogous partitionings of selection on gene frequencies but there is no simple way to apply their solutions to polygenic phenotypic characters.

SUMMARY

The primary contributions of this paper are, first, an elucidation of the relationship between various measures of selection and their relationships to predictive equations for evolutionary change. We show that the opportunity for selection (variance in relative fitness) places an upper bound on the amount that the mean of any character can be shifted by directional selection. Second, we offer several solutions to the problem of analyzing multiple selection episodes (e.g., sexual versus natural selection). We show how the total effect of directional selection can be partitioned into parts corresponding to particular selection episodes or fitness components. The opportunity for selection cannot be so readily partitioned because of covariances between fitness components. We present a rather complex partitioning which may nevertheless be useful in particular applications.

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APPENDIX. Covariances among selection episodes when fitness components are multiplicative.

In order to account for the general case of non-independent selection we must consider covariances between fitness at successive episodes. We will refer to these covariances between relative fitnesses as *cointensities* and denote them *COI*.

The covariance between relative fitness components corresponding to the first two episodes, weighting individuals equally, is

$$COI(1, 2) = \sum p(w_1 - 1)(w_2 - 1)$$
$$= 1 - n^{-1} \sum w_2. \qquad (A1)$$

This covariance is changed by selection, so that after the first episode the covariance between the first two fitness components is

$$COI(1, 2 \mid 1) = \sum p_1(w_1 - 1)(w_2 - 1)$$
$$= n^{-1} \sum w_1^2 w_2 - n^{-1} \sum w_1^2. \qquad (A2)$$

The initial covariance between relative fitness after the first two episodes, $w_1 w_2$, and the second fitness component, w_2, is

$$COI(12, 2) = \sum p(w_1 w_2 - 1)(w_2 - 1)$$
$$= n^{-1} \sum w_1 w_2^2 - n^{-1} \sum w_2, \qquad (A3)$$

in which each individual is weighted equally. After the first selection episode, the covariance between $w_1 w_2$ and w_2 will be

$$COI(12, 2 \mid 1) = \sum p_1(w_1 w_2 - 1)$$
$$\cdot (w_2 - 1)$$
$$= n^{-1} \sum w_1^2 w_2^2$$
$$- n^{-1} \sum w_1^2 w_2, \qquad (A4)$$

in which each individual is weighted by its fitness at the first episode or w_1.

We can now show that the total variance in relative fitness after the first two episodes, I_{12}, is the sum of a series of variances and covariances. The opportunity for selection after the first two episodes is

$$I_{12} = \sum p(w_1 w_2 - 1)^2$$
$$= n^{-1} \sum w_1^2 w_2^2 - 1$$
$$= I_1 + I_2$$
$$+ COI(1, 2) + COI(1, 2 \mid 1)$$
$$+ [COI(12, 2 \mid 1) - COI(12, 2)]. \qquad (A5)$$

The final term in expression (A5) is the change in covariance between fitness after the first two episodes and the second fitness component caused by selection during the first episode.

In order to account for the selection opportunity that occurs after the first two episodes, we need to consider some additional covariance terms. The initial covariance between fitness after the first two episodes, $w_1 w_2$, and the third fitness component, w_3, is

$$COI(12, 3) = \sum p(w_1 w_2 - 1)(w_3 - 1)$$
$$= 1 - n^{-1} \sum w_3, \qquad (A6)$$

in which each individual is weighted equally. It is interesting to note that this covariance is the sum of the covariance between the first and third fitness components, $COI(1, 3)$, and the covariance between the second and third fitness components, $COI(2, 3)$:

$$COI(1, 3) = \sum p(w_1 - 1)(w_3 - 1)$$
$$= n^{-1} \sum w_1 w_3 - n^{-1} \sum w_3,$$
$$COI(2, 3) = \sum p_1(w_2 - 1)(w_3 - 1)$$
$$= 1 - n^{-1} \sum w_1 w_3, \qquad (A7)$$

so that

$$COI(12, 3) = COI(1, 3) + COI(2, 3). \qquad (A8)$$

$COI(12, 3)$ is changed by selection, so that after the second episode, the covariance between $w_1 w_2$ and w_3 is

$$COI(12, 3 \mid 2) = \sum p_2(w_1 w_2 - 1)(w_3 - 1)$$
$$= n^{-1} \sum w_1^2 w_2^2 w_3$$
$$- n^{-1} \sum w_1^2 w_2^2. \qquad (A9)$$

We need two additional covariance terms. The

initial covariance between total relative fitness, $w_1w_2w_3 = w$, and the third fitness component is

$$COI(123, 3) = \sum p(w_1w_2w_3 - 1)$$
$$\cdot (w_3 - 1)$$
$$= n^{-1} \sum w_1w_2w_3^2$$
$$- n^{-1} \sum w_3, \qquad (A10)$$

in which each individual is weighted equally. This covariance is changed by selection, so that after the first two episodes of selection the covariance between $w_1w_2w_3$ and w_3 is

$$COI(123, 3|2) = \sum p_2(w_1w_2w_3 - 1)$$
$$\cdot (w_3 - 1)$$
$$= n^{-1} \sum w_1^2w_2^2w_3^2$$
$$- n^{-1} \sum w_1^2w_2^2w_3$$
$$= n^{-1} \sum w^2$$
$$- n^{-1} \sum w_1^2w_2^2w_3. \quad (A11)$$

We derive the partitioning for the total opportunity of selection using the above expressions:

$$I = I_1 + I_2 + I_3$$
$$+ COI(1, 2) + COI(1, 2|1)$$
$$+ COI(12, 3) + COI(12, 3|2)$$
$$+ [COI(12, 2|1) - COI(12, 2)]$$
$$+ [COI(123, 3|2) - COI(123, 3)] \quad (A12)$$

In general, after m episodes of selection, the total opportunity for selection can be partitioned into the following terms

$$I = \sum_{k=1}^{m} I_k$$
$$+ \sum_{k=1}^{m-1} COI\left(\prod_{r=1}^{m-1} r, k + 1\right)$$
$$+ \sum_{k=1}^{m-1} COI\left(\prod_{r=1}^{m-1} r, k + 1|k\right)$$
$$+ \sum_{k=1}^{m-1} \left[COI\left(1 \prod_{r=2}^{k+1} r, k + 1|k\right) \right.$$
$$\left. - COI\left(1 \prod_{r=2}^{k+1} r, k + 1\right) \right] \quad (A13)$$

in which, when for example $m = 4$, the symbol $\prod_{r=1}^{m-1} r$ denotes 123, and when $k = 2$, the symbol $1 \prod_{r=2}^{k+1}$ denotes 123. This result accomplishes the desired, additive partitioning of the total opportunity for selection into parts corresponding to the separate episodes of selection. The large number of covariance terms is unfortunate, but these will often be biologically interesting. An example of interpretable cointensities in a three episode analysis of selection is provided in the companion paper (Arnold and Wade, 1984). The additive nature of the partitioning is preserved even when successive episodes are collapsed or not formally recognized.

Collapsing Episodes of Selection.—The partitioning of the total selection opportunity has the property that, if two successive episodes cannot be distinguished and are considered as one, say episodes 1 and 2 are collapsed to represent 1*, then I becomes

$$I = I_{1*} + I_3$$
$$+ COI(1*, 3)$$
$$+ COI(1*, 3|1*)$$
$$+ [COI(1*3, 3|1*)$$
$$- COI(1*3, 3)], \quad (A14)$$

where

$$I_{1*} = I_1 + I_2$$
$$+ COI(1, 2)$$
$$+ COI(1, 2|1)$$
$$+ [COI(12, 2|1)$$
$$- COI(12, 2)],$$
$$COI(1*, 3) = COI(12, 3),$$
$$COI(1*, 3|1*) = COI(12, 3|2)$$
$$[COI(1*3, 3|1*) - COI(1*3, 3] = [COI(123, 3|2)$$
$$- COI(123, 3)].$$

$$(A15)$$