The Measurement of Selection on Size and Growth

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1 Introduction

A good deal of interest in natural selection is focused on the size of individuals or individual parts. For example, the significance of size-selective predation has long been a dominant theme in research on zooplankton ecology (Brooks and Dodson 1965; Kerfoot 1980; Lynch 1980). Much of the theory on the evolution of complex life histories is focused on the interaction of size-specific growth and mortality rates (Wilbur 1980; Werner and Gilliam 1984; Werner 1986 and this Vol.). Size-dependent competition and reproductive performance are central issues in plant population biology (Harper 1977; Dirzo and Sarukhán 1984; see also Ebenman this Vol.). In order to couch studies of these phenomena in an evolutionary framework, techniques are required for analyzing the intensity of natural selection on components of size and growth. A methodology for the measurement of selection on age-invariant characters (e.g., size at age x) has been outlined in Lande and Arnold (1983) and Mitchell-Olds and Shaw (1987), but selection on ontogenetic patterns raises some practical difficulties that were not addressed in those papers.

A conceptual difficulty arises in the analysis of selection on size. Because the size at any age is a sum of growth increments during previous age intervals, the question can arise as to whether selection is operating on size per se or on growth rate. From the standpoint of evolutionary interpretation, this is not a trivial circularity, since different agents of selection may operate on size and growth rate. For example, given a population of available prey, a predator will often select prey items solely on the basis of current size regardless of their previous rates of growth. On the other hand, individuals of identical size but different growth rates may vary in their vulnerability to predation if variation in growth rate is a consequence of selection for habitats that vary in resource level as well as in predation risk. Since selection may often act simultaneously on size and growth rate, a method is needed for measuring the direct forces of selection on both types of characters.

As an example of an evolutionary phenomenon whose analysis requires a quantification of the forces of selection operating on size and growth rate, consider compensatory growth in which individuals tend to converge on the same mature size despite differences in size at birth and early growth rate (Monteiro and

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Falconer 1966; Atchley 1984; Riska et al. 1984). Such a growth pattern requires that weight gains during some successive growth intervals exhibit negative phenotypic correlations (Lynch this Vol.). Perhaps the simplest hypothesis that can account for the evolution of compensatory growth is strong stabilizing selection on size at sexual maturity with weaker selection on size at earlier ages. Alternatively, correlational selection may favor a negative tradeoff between growth in adjacent age intervals with little selection operating directly on size. Multivariate selection gradients, a subject of this chapter, provide the relevant parameter estimates for testing these and other hypotheses.

Growth components are fundamentally different from sets of morphological traits that are expressed simultaneously. An individual reveals each growth component only during a single interval of time and only if it lives through that interval. Thus, mortality during the period of study will result in individuals with incomplete data. The data set becomes progressively smaller for traits expressed later in life. This raises a technical problem. To properly correct for the effects of correlation among traits when measuring selection, we need to know the phenotypic covariance matrix for the traits before selection (Pearson 1903; Lande and Arnold 1983). However, we can only estimate a complete matrix for the subset of individuals that survived until the last measurement. If selection has operated on growth rate, size, or any other correlated trait, the latter matrix will be a biased estimate of the former.

In the following sections, we show how estimates of the phenotypic covariance matrices that prevailed before selection can be obtained. This is accomplished in a stepwise fashion by applying information on the strength and direction of selection for individual growth intervals. The age-specific parameter estimates can then be used to estimate the total forces of directional, stabilizing, and correlational selection operating on size and growth characters. Some simple algebraic relationships between selection on size and growth will be pointed out, and path analysis will be shown to provide a means of partitioning the variance of fitness into components attributable to variation in age-specific size and/or growth rate.

2 Conditional Selection Differentials and Gradients

As in Lynch (this Vol.), we express the size of an individual at time t, z_t, as the sum of an initial size at birth and a series of growth increments between various measurements,

$$z_t = z_0 + (z_1 - z_0) + (z_2 - z_1) + \ldots + (z_t - z_{t-1}) = z_0 + \sum_{i=1}^{t} \Delta z_i \ , \qquad (1)$$

where z_0 is the size at the first census. We start with a cohort of same-aged individuals. At each of a series of censuses, we record whether each individual is alive or dead and measure the live ones. Figure 1 provides an example of the type of growth data that may arise from such a longitudinal study on a hypothetical cohort of 15 individuals. Size is measured on all survivors at three points (i = 0, 1, 2) in time. A fourth census is necessary to evaluate the survival of individuals

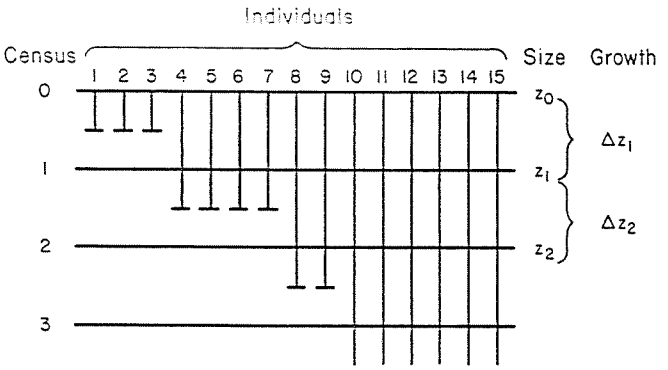

Fig. 1. A schematic for a longitudinal analysis of size and growth data on 15 hypothetical individuals. *Cross-hatches* denote times of death. Measurements are made at censuses 0, 1, and 2, allowing the computation of three size and two growth measures. Measurements are not necessarily taken at census 3, but this census is required to evaluate survivorship of the individuals that were alive at census 2. A later census could be taken to evaluate total lifetime fitness of individuals that survived to census 3

expressing all five size and growth characters, and a later survey may be taken to evaluate reproductive performance. Since three individuals died prior to the second census, size at birth is the only character available for the initial cohort of 15 individuals. The reduced cohort of 12 individuals alive at census 1 can be characterized by z_0, z_1, and Δz_1. The remaining 8 individuals at census 2 (6 of which have nonzero fitness) are fully characterized for traits z_0, z_1, z_2, Δz_1, and Δz_2. The individuals alive at the i^{th} census are assigned a conditional relative fitness measure w(i) of 0 or 1/p(i), where p(i) is the fraction of the cohort that survives to i+1, depending on whether they died or survived in the interval (i, i+1).

For each of the three censuses, a conditional phenotypic covariance matrix **P**(i) can be constructed for the subset of individuals alive at that census. The diagonal elements of this matrix are variances, while the off-diagonal elements are covariances between characters. Due to the expression of new characters at each census, the dimensionality of this matrix will increase with census number. For example, **P**(0) consists of a single element, the variance of z_0 for all of the members of the initial cohort. **P**(1) contains additional variances and covariances. Since these are computed from the subset of individuals that survived to census 1, the variance of z_0 in **P**(1) is likely to differ from that in **P**(0) as well as that in **P**(2) and later matrices.

In reality, the complete set of size and growth characters cannot be analyzed simultaneously. Because the growth increments are computed from sequential sizes, inclusion of all of the available size and growth characters in **P**(i) would cause this matrix to be singular. This is a problem since the analysis of multivariate selection requires that the conditional covariance matrices be invertible. The choice of which characters to include will depend somewhat on the objectives of the analysis, but the elimination of the singularity problem requires that none of the characters employed in the analysis be linear functions of any of the other characters included. This means that with n censuses, no more than n size and/or growth characters can be employed in an analysis. For example, if size were

measured on two occasions, a selection analysis could be performed on z_0 and z_1 or on z_0 and Δz_1 or on z_1 and Δz_1, but not on z_0, z_1, and Δz_1 since $\Delta z_1 = z_1 - z_0$. When measurements are taken on three occasions, the maximum number of characters that can be analyzed at any one time is three, but there are seven combinations of characters that can be analyzed: (z_0, z_1, z_2), $(z_0, z_1, \Delta z_2)$, $(z_0, z_2, \Delta z_1)$, $(z_0, z_2, \Delta z_2)$, $(z_0, \Delta z_1, \Delta z_2)$, $(z_1, \Delta z_1, \Delta z_2)$, and $(z_2, \Delta z_1, \Delta z_2)$.

For each census, it is also possible to calculate a conditional directional selection differential **S**(i). This differential is conditional in the sense that it is based only on those individuals alive at census i. Each element of the vector **S**(i) represents a different character and is the difference in mean phenotype (at time i) between individuals that survived to census i+1 and those that were present at census i. For example, the conditional directional selection differential for birth weight at census 1, is the difference in birth weight of individuals alive at census 2 and those alive at census 1. As in the case of **P**(i), the dimensionality of **S**(i) will usually increase with census number, as one has the opportunity to include additional characters.

The conditional directional selection gradient for each interval of time is the vector $\beta(i) = \mathbf{P}^{-1}(i) \cdot \mathbf{S}(i)$. Since the elements of **S**(i) are equivalent to the covariance of relative fitness and phenotypic value (Robertson 1966), this formula is equivalent to the standard least-squares solution to a multiple regression, in this case of w(i) on the phenotypic traits measured at census i. Each element of $\beta(i)$ is a partial regression coefficient, providing a measure of the slope of the regression of relative fitness on the respective character when all other characters are held constant. Provided that the conditional phenotype distribution is multivariate normal at census i, the elements of $\beta(i)$ can be interpreted as the average gradient of the relative fitness surface weighted by the phenotype distribution (Lande and Arnold 1983). The preservation of multivariate normality throughout the period of study requires that the initial phenotype distribution be multivariate normal and that all subsequent selection functions be Gaussian in form, a rather unlikely situation. It should be noted, however, that the actual analysis of data is not contingent upon multivariate normality.

By computing all of the elements of $\beta(i)$ at each census, we allow for the possibility that age-specific size and growth traits, although expressed only once, may influence fitness at all future ages. This will be important if unobserved characters that are acted upon by natural selection are correlated with earlier size and or growth rate. It is conceivable that the conditional selection gradients computed for the same character at different censuses may vary substantially in magnitude and/or direction.

A conditional stabilizing selection differential **C**(i) can also be calculated for each census. This is a square matrix, each element being the covariance of relative fitness and the cross-product of two traits measured as deviations from the mean phenotype at census i. For example, the diagonal element involving size at birth for individuals alive at census 1 is $\mathrm{Cov}[w(1),[z_0 - \bar{z}_0(1)]^2]$, where $\bar{z}_0(1)$ is the mean size at birth for the subset of individuals alive at census 1. For the population in Fig. 1, 12 individuals would be involved in this computation, four (individuals 4–7) with w(1) = 0 and eight (individuals 8–15) with w(1) = 1/(8/12) = 1.5. For the same census, the off-diagonal element involving size at birth and growth dur-

ing the first increment is $\mathrm{Cov}[w(1), \{[z_0 - \bar{z}_0(1)][\Delta z_1 - \overline{\Delta z_1}(1)]\}]$. Each element of $\mathbf{C}(i)$ is an estimate of the change in the variance (diagonal element) or covariance (off-diagonal element) of characters resulting from selection. Using $\mathbf{C}(i)$ we can now compute the conditional stabilizing selection gradient, $\gamma(i) = \mathbf{P}^{-1}(i)\mathbf{C}(i) \times \mathbf{P}^{-1}(i)$ [cf. Lande and Arnold 1983, Eq. (14a)].

The elements of $\gamma(i)$ describe the average curvature of the conditional fitness surface weighted by the phenotype distribution. Positive and negative diagonal elements in $\gamma(i)$ indicate disruptive and stabilizing selection on the respective characters, whereas the signs of the off-diagonal elements indicate whether pairs of characters are being selected to become positively or negatively correlated. A detailed discussion of the relationship between these coefficients and the topography of the fitness surface is provided in Phillips and Arnold (in prep.).

3 Reconstruction of the Phenotypic Covariance Matrix

While the conditional selection gradients introduced in the previous section describe specific episodes of selection operating on a cohort, it will usually be of interest to quantify the total forces of selection over the entire period of study. This requires an estimate of the phenotypic covariance matrix for all of the characters prior to selection. Only at the final census do we have an estimate of the complete covariance matrix, and this will be a biased estimate of the matrix that existed before selection. Nevertheless, in conjunction with the conditional selection gradients, the final phenotypic covariance matrix can be used to derive an estimate of the initial matrix.

Let us now represent the full covariance matrix for individuals alive at census i as $\mathbf{P}_i$, with $\mathbf{P}_n = \mathbf{P}(n)$. (From here on, conditional matrices will be denoted with parentheses while complete matrices will be subscripted.) Each of these matrices has dimensionality $(n+1)\times(n+1)$. However, for the ith matrix, only $(i+1)\times(i+1)$ of the elements are known; these are the elements that were included in $\mathbf{P}(i)$. At each census, the complete directional selection gradient, β_i, is simply the vector $\beta(i)$ with zeroes added to yield the desired dimensionality of $(i+1)\times 1$. Such treatment entails the assumption that selection does not operate on growth or size characters prior to their expression. By similar reasoning, the complete stabilizing selection gradient at census i, $\mathbf{C}_i$, is simply $\mathbf{C}(i)$ with zeroes filled in for the missing elements.

Estimates of the missing elements of $\mathbf{P}(i)$ are obtained by noting that the within-generation dynamics of the elements of the phenotypic covariance matrix are defined completely by the directional and stabilizing selection gradients [Lande and Arnold 1983, Eq. (13)],

$$\mathbf{P}_i = \mathbf{P}_{i-1} + \mathbf{P}_{i-1}\gamma_{i-1}\mathbf{P}_{i-1} - \mathbf{P}_{i-1}\beta_{i-1}[\mathbf{P}_{i-1}\beta_{i-1}]^T , \tag{2}$$

where T denotes transpose. Since $\mathbf{P}_i$ is a symmetrical matrix, Eq. (2) amounts to a set of $(n+1)(n+2)/2$ equations with the unknowns being the missing elements of $\mathbf{P}_{i-1}$. Starting with $i = n$, the first step is to solve for the $n+1$ missing elements of $\mathbf{P}_{n-1}$; these are the elements that occupy the last row (and column) of $\mathbf{P}_{n-1}$. The elements of $\mathbf{P}_n$ that are also observed directly in $\mathbf{P}_{n-1}$ are defined

solely in terms of the latter and are of no use in this solution. Thus, filling out the missing elements of $\mathbf{P}_{n-1}$ involves the solution of $n+1$ equations in $n+1$ unknowns.

If it is necessary to back-track a further step to $\mathbf{P}_{n-2}$, then the newly completed matrix $\mathbf{P}_{n-1}$ is substituted for $\mathbf{P}_i$ in Eq. (2), and the entire procedure is repeated with $\mathbf{P}_{n-2}$, β_{n-2}, and γ_{n-2} on the right. This analysis would involve the solution of $2n+1$ equations in $2n+1$ unknowns (the last two rows (and columns) of $\mathbf{P}_{n-2}$). By this means, information on the conditional selection gradients allows a progressive extrapolation of $\mathbf{P}_n$ back to $\mathbf{P}_0$. At each (xth) step in the process there are $\sum_{i=1}^{x} (n+2-i)$ equations to solve in the same number of unknowns. This procedure involves no assumptions regarding the form of the phenotype distribution or of the selection function.

4 Total Selection on Growth and Size Caused by Selective Mortality

Having reconstructed the phenotypic covariance matrix throughout the period of study, the stage-specific conditional selection gradients can be assembled into composite measures describing the total forces of selection operating on the cohort. It was necessary at the outset to break the analysis down into intervals of selection to account for the fact that even those individuals that die before expressing a character are relevant to the evolution of that character if it is correlated with size and growth components that have been expressed and selected upon. The total changes in the means and variances of size and growth attributes caused by selection can be partitioned into components describing the effects of direct selection on the characters and those resulting indirectly from selection on phenotypically correlated characters. Letting $l(i)$ be the proportion of the initial cohort that survives to the i^{th} census, the total directional selection differential for the j^{th} character is, using Eq. (6c) from Lande and Arnold (1983),

$$S_j = \sum_{i=0}^{n-1} l(i)\left[\beta_j(i)\,\sigma_{jj}(i) + \sum_{\substack{k=1 \\ k\neq j}}^{n+1} \beta_k(i)\,\sigma_{jk}(i)\right] , \tag{3}$$

where $\beta_j(i)$ is the conditional directional selection gradient on the j^{th} trait over the period $(i, i+1)$ and $\sigma_{jk}(i)$ is the jk^{th} element of $\mathbf{P}_i$. The first set of terms on the right is the sum of direct effects of selection acting on trait j over the various census periods, while the second set of terms is the sum of indirect effects of selection acting on correlated traits. Letting $\mathbf{S}$ be the vector of the estimates of S_j, the total directional selection gradient caused by mortality is $\beta = \mathbf{P}_0^{-1}\mathbf{S}$.

Similarly, the total correlational selection differential for the j^{th} and k^{th} characters is, using equation 14a from Lande and Arnold (1983),

$$C_{jk} = \sum_{i=0}^{n-1} l(i)\left[\sum_{k=1}^{n+1}\sum_{l=1}^{n+1}\sum_{m=1}^{n+1} \sigma_{jk}(i)\,\gamma_{kl}(i)\,\sigma_{jm}(i)\right] , \tag{4}$$

where $\gamma_{kl}(i)$ is the conditional stabilizing selection gradient for the k^{th} trait $(k = l)$ or the conditional correlational selection gradient for traits k and l $(k \neq l)$.

One of the terms in this expression represents the change in covariance of traits j and k due to selection acting directly on the trait product $[z_j - \bar{z}_j(i)][z_k - \bar{z}_k(i)]$, while the remaining sum of terms represents indirect effects on the covariance of traits j and k due to stabilizing and correlational selection on correlated traits. When j = k, C_{jk} is the stabilizing selection differential for the j^{th} trait. Letting **C** be the matrix of estimates of C_{jk}, the total stabilizing selection gradient due to mortality selection is $\gamma = \mathbf{P}_0^{-1}\mathbf{C}\mathbf{P}_0^{-1}$, with stabilizing selection gradients on the main diagonal and correlational selection gradients elsewhere.

5 Selection on Size Versus Growth Rate

The problem of whether natural selection operates on size per se and/or growth rate is a fundamental issue that has attracted little attention from field biologists. In the previous sections, we have developed a general method that can be applied to the entire lifespan of a cohort. We now point out a useful simplification for evaluating the selective pressures operating on average size and growth rate within any interval.

Suppose that a cohort of individuals is measured on two occasions (censuses 0 and 1) and a third survey is taken to identify the survivors among those individuals that lived to census 1. There are two ways to parameterize the data. The procedures outlined in the preceding sections can be applied directly to the size characters z_0 and z_1 to obtain estimates of the elements of the directional selection gradient, β_0 and β_1, as well as of the elements of the stabilizing selection gradient, γ_{00}, γ_{01}, and γ_{11}. Alternatively, the data can be transformed to yield $z_s = (z_0 + z_1)/2$ as a measure of size and $z_g = z_1 - z_0$ as a measure of growth rate. These transformed variables can be used to obtain the selection coefficients β_s, β_g, γ_{ss}, γ_{sg}, and γ_{gg}, where the subscripts s and g denote size and growth rate respectively.

Recalling that the selection gradients are equivalent to the partial regression coefficients of relative fitness (w) on phenotype (Lande and Arnold 1983), we have the alternative expressions

$$E(w) = \alpha + \beta_0 z_0 + \beta_1 z_1 + \tfrac{1}{2}\gamma_{00} z_0^2 + \tfrac{1}{2}\gamma_{11} z_1^2 + \gamma_{01} z_0 z_1 \ , \tag{5a}$$

$$E(w) = \alpha + \beta_s z_s + \beta_g z_g + \tfrac{1}{2}\gamma_{ss} z_s^2 + \tfrac{1}{2}\gamma_{gg} z_g^2 + \gamma_{sg} z_s z_g \ , \tag{5b}$$

where E denotes expectation. The intercept α is obtained by substituting 1 for E(w) and the means for the other parameters, e.g., $\bar{z}_0$ for z_0, and $\overline{z_0 z_1}$ for $z_0 z_1$. These formulae yield the relationships

$$\begin{aligned}
\beta_s &= \beta_0 + \beta_1 \ , \\
\beta_g &= \tfrac{1}{2}(\beta_1 - \beta_0) \ , \\
\gamma_{ss} &= \tfrac{1}{2}\gamma_{00} + \gamma_{01} + \tfrac{1}{2}\gamma_{11} \ , \\
\gamma_{sg} &= \tfrac{1}{2}(\gamma_{11} - \gamma_{00}) \ , \\
\gamma_{gg} &= \tfrac{1}{2}\gamma_{00} - \gamma_{01} + \tfrac{1}{2}\gamma_{11} \ .
\end{aligned}$$

Thus, the force of directional selection on average size is simply the sum of the forces of directional selection acting on size at the two ages. The force of direc-

tional selection on growth rate is one half the difference between the force of directional selection at the second and first ages. Positive selection for growth rate is equivalent to greater directional selection for size at the second age. In other words, there is no directional selection on the rate of growth when the directional selection gradients for size at the two ages are equal. Similar logic can be used to explain the existence of stabilizing, disruptive, or correlational selection on mean size and growth rate.

By use of Eq. (5a) [or equivalently (5b)], the selection gradients can be used to portray a fitness surface that describes the relationship between relative fitness, size, and growth rate. Starting with a bivariate surface in z_0 and z_1, the axes for mean size and growth rate are obtained by a 45° rotation of the original axes (Fig. 2). The topographical features of the fitness surface can be described by a series of contours connecting character combinations with equal fitness (Fig. 3).

We first consider some simple situations in which there is no stabilizing, disruptive, or correlational selection ($\gamma_{00} = \gamma_{01} = \gamma_{11} = 0$). Under these circumstances the selection surface is a plane whose orientation depends on the magnitudes of β_0 and β_1 (or equivalently β_s and β_g). Figure 3a shows selection for increased size at age 0 but no selection on size at age 1. When viewed on the z_s, z_g coordinate system, it is seen that such a fitness surface corresponds to selection for an increase in average size but a decrease in the growth rate in the interval (0, 1). Figure 3b illustrates the fitness surface when there is selection for increased size at the second age but no selection on size at the first age. This corresponds to selection for increased average size and higher growth rate. In Fig. 3c,

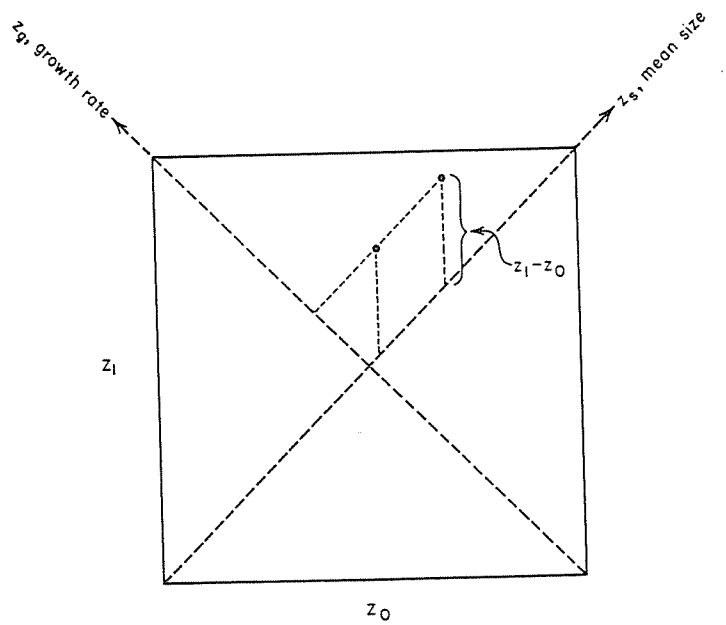

Fig. 2. Alternative coordinate systems for age-specific sizes (*solid lines*) and mean size and growth rate (*dashed lines*) The two points refer to individuals with different age-specific sizes (z_0, z_1) but the same growth rate ($z_1 - z_0$)

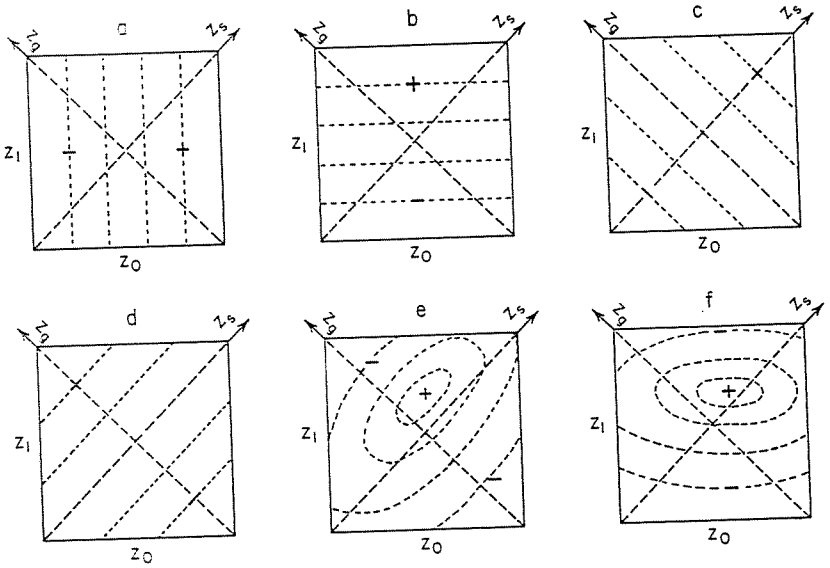

Fig. 3a–f. Selection surfaces (*dotted lines*) on the age-specific size (*solid lines*) and mean size-growth rate (*dashed lines*) coordinate systems. The gradient of fitness is uphill from contours marked with − to those marked with +. **a** $\beta_0 > 0$, $\beta_1 = 0$. **b** $\beta_0 = 0$, $\beta_1 > 0$. **c** $\beta_0 = \beta_1 > 0$. **d** $\beta_0 = -\beta_1 < 0$. **e** Selection towards intermediate optimum sizes at both ages; the axes of the selection surface are aligned with the axes of the mean size-growth rate coordinate system. **f** Selection towards intermediate optimum sizes at both ages; the axes of the selection surface are aligned with the axes of the age-specific size coordinate system

selection favors increased size at both ages. However, because selection for size is equally strong at both ages, there is no selection on the rate of growth. Figure 3d illustrates the opposite case, in which selection favoring increased size at age 1 is balanced by an equal intensity of selection for decreased size at age 0. This is equivalent to selection for high growth rate with no selection on mean size.

When the stabilizing and/or correlational selection gradients are nonzero, the fitness surface will contain a peak, a basin, a saddle, or a ridge (Phillips and Arnold in prep.). We will only consider two simple situations in which there is selection for an intermediate optimum size at both ages. In the first case (Fig. 3e), there is no correlational selection for growth and size ($\gamma_{sg} = 0$), but there is stronger stabilizing selection on growth rate than on mean size ($\gamma_{gg} < \gamma_{ss} < 0$). This disparity in the strengths of stabilizing selection operating on z_s and z_g translates into positive correlational selection between the sizes at both ages. In the second case (Fig. 3f), there is no correlational selection between size at the two ages, but stabilizing selection on size at the second age is stronger than that at the first age. This is equivalent to negative correlational selection between average size and growth rate. In other words, selection promotes a negative correlation between average size and growth rate.

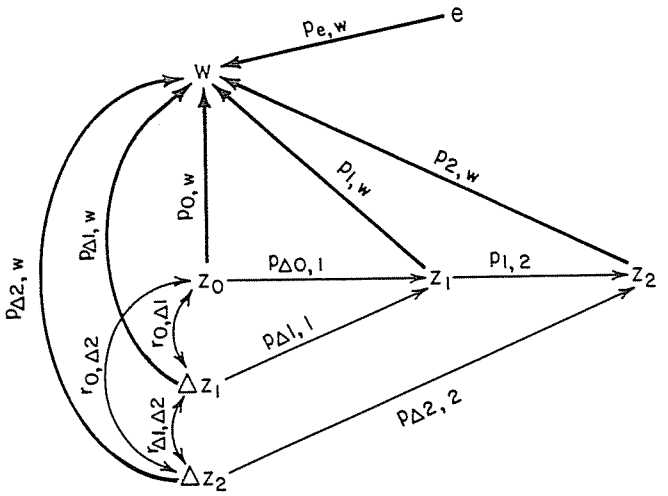

Fig. 4. A path diagram showing the effects of directional selection on relative fitness, w. The figure shows only the size, z_i, and growth variables, Δz_i, that could be computed by taking measurements at three ages (including at birth), as in Fig. 1. Correlations between growth variables are indicated with *narrow, double-headed arrows.* The path from e represents residual (unexplained) effects on fitness. Definitions of the remaining path coefficients are given in the text

6 Path Analysis of the Variance in Fitness Attributable to Size and Growth

The techniques outlined above are readily merged with the path analytical techniques described in Lynch (this Vol.) to evaluate the fractions of the variance in fitness that are associated with direct selection on size and growth components and those that are associated with correlations between characters. For clarity, just the directional effects of selection are summarized in Fig. 4. The squared path coefficients on the arrows leading from the size and growth characters to relative fitness (w) define the fraction of the variance in fitness caused by the direct effects of selection on the character. For the jth character, the path coefficient to w is simply the total directional selection gradient on the character multiplied by the ratio of phenotypic standard deviations of the character (obtained from $\mathbf{P}_0$) and fitness. For example, $p_{0w} = \beta_{z_0}[\sigma_0^2(z_0)/\sigma_0^2(w)]^{1/2}$ where $\sigma_0^2(z_0)$ is the estimated variance of size at birth among the initial members of the cohort and $\sigma_0^2(w)$ is the variance of relative fitness. The fraction of the variance in fitness not explained by the model is $p_{e,w}^2$.

The portion of the path diagram denoted by narrow lines defines the correlational structure of the growth and size attributes. The quantities on the double-headed arrows are ordinary phenotypic correlations obtained from the elements of $\mathbf{P}_0$. The path coefficients are simply the ratios of the standard deviations of the variables at the blunt and pointed tips of the arrows. The contribution of any indirect path to the variance in fitness is twice the product of the coefficients along the path. For example, the proportion of variance in fitness attributable to joint selection on size at birth (z_0) and growth in the first interval (Δz_1) is $2p_{0,w}r_{0,\Delta 1}p_{\Delta 1,w}$. The fractional contribution attributable to joint selection on

Δz_1 and z_2 is obtained by tracing down two paths: $2p_{\Delta 1,w}p_{1,2}p_{2,w}(p_{\Delta 1,1} + r_{0,\Delta 1}p_{\Delta 0,1})$.

The complete path diagram is given in Fig. 4 only for heuristic purposes. As noted above, a complete selection analysis of all of the size and growth components is not possible, so all of the paths cannot be computed. However, analyses involving different combinations of characters can be evaluated for their relative abilities to explain the variance in fitness by comparing the squared multiple regression coefficients, which in the context of Fig. 4 are equivalent to $1-p^2_{e,w}$. If, as in the previous section, the study involves only estimates of mean size and growth during one interval, a complete analysis is possible. The path diagram contains only two variables, z_s and z_g, connected by a correlation.

7 Discussion

The primary motivation of this paper has been to develop an approach for estimating selection on characters that undergo developmental change and/or are missing from selected members of the population. Although we have focused on size and growth, our technique for the reconstruction of the phenotypic covariance matrix provides a general solution to the problem of missing data and can be applied to any phenotypic traits that change with age. For example, if the dimensions of different body parts are measured at each age, selection on shape and shape change can be analyzed. Maturational changes in behavior such as feeding rate, movement pattern, or territorial defense can also be analyzed with the present approach. With plants, the technique can be used to study the form of selection operating on the mean time of flowering versus the duration of flowering.

Thus far our discussion has been limited to viability selection. In certain circumstances, the technique can be extended to the analysis of fecundity selection. For example, in semelparous organisms such as annual plants, in which a single reproductive bout follows viability selection, the phenotypic covariance matrix for individuals attaining sexual maturity can be estimated directly. Using that matrix, the conditional selection gradients corresponding to fecundity selection could be estimated as described by Lande and Arnold (1983).

We also emphasize that our focus has been on the estimation of parameters. Of equal importance is the need for testing for the significance of sample statistics. Substantial sampling problems may arise with the present approach as a consequence of estimating one statistic from many others. For example, the estimation of $\mathbf{P}_0$ will inevitably compound sampling errors, since $\mathbf{P}_0$ is computed from estimates of variances and covariances at several censuses. This problem may be minimized by having relatively few censuses (ages) and large samples at each census, but it should not be taken lightly. A resampling procedure (Efron 1982; Mitchell-Olds and Shaw 1987) may aid in evaluating the confidence that can be placed in the final estimates of β and γ.

There are other methods for dealing with incomplete data sets when the missing data are a consequence of selection (Curnow 1961; Thompson 1973; Rubin 1976; Little and Rubin 1987). As maximum likelihood procedures, these methods

have some restrictive assumptions, such as multivariate normality, which may not adequately describe the growth process. Our procedure is more general in the sense that it makes no assumption regarding the phenotype distribution. However, if the normality assumption is justifiable, the maximum likelihood approach should yield a more reliable estimate of $\mathbf{P}_0$ than our technique, since the former utilizes all of the data simultaneously.

High correlations between traits can sometimes frustrate the estimation of selection gradients by causing the phenotypic covariance matrix to be singular. For example, size at one census and growth during the next time interval may be highly correlated if growth is a linear function size. In such circumstances, it may not be possible to measure simultaneously selection on age-specific size and growth rate in adjacent intervals. This problem can usually be solved by deleting some highly correlated traits from the analysis (Lande and Arnold 1983; Mitchell-Olds and Shaw 1987).

In closing, we emphasize the obvious. The present results are directly applicable to laboratory or field populations in which individuals can be unambiguously classified as alive or dead at each census. This is not a problem for most plants, but in many natural animal populations, live individuals may elude the census-taker. If the phenotypes of dispersing and/or missing individuals are not random with respect to the population prior to selection, selection theory should not be applied.

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