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Short-term Changes in the Mean: The Breeders' Equation

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Our examination of selection of quantitative characters, and its consequences, comprises the remainder of this book. We start by discussing the simplest models — changes in the mean of a single character following a single generation of selection. As the reader will see over the next several chapters, even these simple models are not without complications. Over subsequent chapters we build on these models, making them more complex and biologically realistic.

Selection changes the distribution of both phenotypic and genotypic values from one generation to the next. While it is convenient to assume that only the means of these distributions change, this is generally not the case. Rigorous prediction of the expected change in the mean over several generations requires predictions of how higher moments (such as the variance and skew) of the genotypic distribution change as well (Chapters 9, 10). Unfortunately, this requires considerable knowledge about the underlying distributions of allelic effects and frequencies, both of which are almost always unknown. Despite this gloomy initial assessment, the change in mean over a few generations of selection can often be accurately projected using estimates of genetic variances from an unselected base population. This chapter considers the basis for much of this success: models that assume a linear parent-offspring regression and short-term stability of the genetic variance (i.e., over short time scales, selection-induced changes in variance are assumed to be negligible).

We will have much to say about selection-induced changes in the genetic variances and covariances in subsequent chapters (Chapters XX -XX). For now, the assumption of the infinitesimal model (a very large number of underlying loci, each with very small effect) ensures that negligible change in allele frequencies will occur over only a few generations of selection. However (Chapter 6), even under the infinitesimal model, *genotypic* frequencies can change, due to selection generating gametic-phase disequilibrium, even while allele frequencies remain essentially unchanged. Over longer time scales, changes in variances can be sub-

stantial and are extremely difficult to predict. Thus, while the results presented here hold for a single generation, they are expected to become increasingly less accurate as the number of generations of selection increases.

Besides the constancy of variances and linearity of parent-offspring regression, the third major assumption required here is that there is no selection acting on characters correlated to our character of interest. Breeders have the luxury of artificial selection and hence fairly precise control over the nature of selection, while evolutionary biologists face the additional problem of estimating the form of selection acting on the character(s) under consideration. However, even in the most controlled breeding designs, natural selection can also be acting on the character of interest (either directly, or through correlations with other characters under selection). Accounting for selection on multiple characters is discussed in Chapters 17-20.

There is a huge literature on different selection schemes that exploit special features of specific organisms (such as artificial insemination in large farm animals or complex crosses of selfed plants). Our focus in this chapter is **individual** (or **mass**) **selection**, wherein individuals are chosen solely on the basis of their phenotypic value (i.e., information from relatives, other characters, etc. is ignored). **Family selection**, where individuals are chosen based on either their family mean or their relative ranking within a family is discussed in Chapter 6. Using such information from relatives can improve our ability to accurately predict breeding values and hence increase response relative to individual selection. The general theory for selection using information from relatives relies on index selection and BLUP (LW Chapter 26), both of which are discussed in Chapter 20. Additional complications (such as threshold traits, overlapping generations, inbreeding, and group selection) are examined in Chapters XX, XX, XX. Finally, the reader is also referred to Turner and Young (1969), Pirchner (1983), Ollivier (1988), Weller (1994), Cameron (1997), and Simm (1998) for specialized applications in animal breeding and to Namkoong (1979), Hallauer and Miranda (1981), Wricke and Weber (1986), Mayo (1987), Stoskopf et al. (1993), Bernardo (2002), and Gallais (2003) for specialized applications in plant breeding.

SINGLE-GENERATION RESPONSE: THE BREEDERS' EQUATION

The simplest selection model is the classic **breeders' equation**

$$R = h^2 S \quad (4.1)$$

which relates response to heritability times the selection differential. This is perhaps the most well known expression in quantitative genetics. The actual origin of the breeders' equation is somewhat unclear, but it was clearly suggested (in multivariate form) in the early writings of Pearson and popularized by Lush (1937). The simplicity of this equation is compelling, relating the change in mean *across*

a generation (the response R) to the product of the *within*-generation change in the mean (the **directional selection differential** S) with a measure of how character value is passed across generations (the slope h^2 of the midparent-offspring regression). The breeders' equation immediately follows by assuming the parent-offspring regression is linear. In particular, the expected phenotypic value z_o of an offspring given the mean phenotypic value of its parents z_{mp} is given by the midparent-offspring regression,

$$z_o = \mu + h^2(z_{mp} - \mu)$$

Taking the average over all the selected parents, $E_s[z_{mp} - \mu] = S$, and likewise the difference between the expected value of the offspring from such parents and the overall mean is the response R , giving

$$E_s[z_o - \mu] = R = h^2 E_s[z_{mp} - \mu] = h^2 S$$

Even when the parent-offspring regression is not assumed to be linear, the breeders' equation still approximately holds (Equations XX9.31b and XX9.35b).

Response is the Change in Mean Breeding Value

A key concept is that response (being the change in offspring mean) equals the mean breeding value of the selected parents. Recall that (non-inbred, sexually reproducing) parents pass along only a fraction of their total genotypic value, namely their breeding value A , to their offspring. The expected offspring value is then just the average breeding values of its parents (LW Chapter 4). In an unselected base population with a nonzero σ_A^2 , potential parents show a range of breeding values distributed about an expected breeding value of zero. Selection response occurs by choosing parents with breeding values favorable to character improvement, and the expected change in offspring mean from this set of parents is simply the average breeding value of the selected parents.

Hence, one goal of selection is to choose those parents in a sample with the most favorable breeding values. The problem is that we cannot completely predict the breeding value of an individual from its phenotype alone (unless $h^2 = 1$). Hence, phenotype is an imperfect predictor of breeding value, and hence the offspring of phenotypically exceptional parents are generally not themselves as exceptional. To see the direct connection with the breeders' equation, recall that the predicted value \hat{A} of an individual's breeding value given their phenotypic value z is just

$$\hat{A} - \mu_A = \frac{\sigma(A, z)}{\sigma_z^2}(z - \mu_z), \quad \text{or} \quad \hat{A} = h^2(z - \mu_z)$$

This follows from standard regression theory as (i) the mean of the regression passes through the mean of A and z , which are 0 and μ_z (respectively), and (ii) the

slope of the regression for predicting A given z is just $\sigma(z, A)/\sigma_z^2 = \sigma_A^2/\sigma_z^2 = h^2$. Hence, the expected breeding value for a set of selected parents is just

$$E_s[h^2(z - \mu_z)] = h^2 E_s[z - \mu_z] = h^2 S$$

The change in the mean value of their offspring (relative to the base population) is just the mean parental breeding value. Thus response = $h^2 S$ and we recover the breeders' equation via another route.

Thinking of terms of breeding values will prove a most useful way of treating many features of selection. As we will see, a number of selection schemes (such as using information from relatives) have been proposed to improve response by improving our ability to estimate the breeding value of potential parents. Further, thinking about the breeding values of individuals will prove a helpful way of considering selection of multiple characters.

The Importance of Linearity

A variety of factors can result in a nonlinear parent-offspring regression (Chapter 10, LW Chapter 17). In such cases, the mean of the selected parents (and hence the selection differential S) is not sufficient to predict the offspring mean. As Figure 4.1 shows, two selected parental populations with the same mean, but different variances, can have different expected responses when the parent-offspring regression is nonlinear. Even if phenotypes are normally distributed and the character is completely determined by additive loci (no dominance or epistasis), if the underlying distribution of genotypic values shows skew, selection on the variance also results in a change in the mean (see Equation XX9.35b). A sufficient condition for linearity is that the joint distribution of breeding and phenotypic values is bivariate normal (Chapter 15, LW Chapter 8).

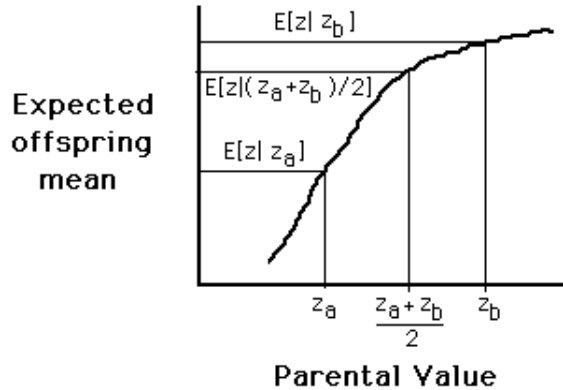


Figure 4.1. The importance of linearity in the parent-offspring regression. If

this regression is nonlinear, different subsets of the population with the same mean can have different offspring means. Suppose equal numbers of parents with values z_a and z_b are chosen. Denoting the expected value of offspring from parents with value z_x by $E[z | z_x]$, the offspring mean is given by $(E[z | z_a] + E[z | z_b]) / 2$. Conversely, choosing parents all with value $(z_a + z_b)/2$, gives the same parental mean and hence the same S , but the expected offspring mean is now $E[z | (z_a + z_b)/2]$, which, as shown, can deviate considerably from $(E[z | z_a] + E[z | z_b]) / 2$.

Selection generally causes the distribution of genotypic values to depart from normality, creating at least slight departures from linear parent-offspring regressions. Response under such non-normal distributions can be very complicated, depending on underlying genetic factors that do not easily translate into standard (and measurable) variance components (see Chapters 9 and 10).

Response Under More General Parent-Offspring Regressions

The regression coefficients for parent-offspring regressions can vary with the sex of both parents and offspring. In such cases, the breeders' equation can be extended by incorporating these sex-dependent regression coefficients. To see how this is done, denote the phenotypic values of the father and mother by z_{fa} and z_{mo} and an offspring by z_o (if its sex is unimportant) or by z_{so} and z_{da} for sons and daughters (respectively) when sex is important. Let $E(z_o | z_{fa}, z_{mo})$ be the expected phenotypic value of an offspring whose parents have phenotypic values z_{mo} and z_{fa} . The importance of this conditional expectation (the **biparental regression**) is that the expected character value in the next generation (assuming no fertility differences) is the average of $E_s(z_o | z_{fa}, z_{mo})$ over all selected parents. Taking expectations is particularly straightforward when the biparental regression is linear, i.e.,

$$E(z_o | z_{fa}, z_{mo}) = \mu_o + b_{o,fa}(z_{fa} - \mu_{fa}) + b_{o,mo}(z_{mo} - \mu_{mo}) \quad (4.2)$$

where μ_{fa} and μ_{mo} are the mean character values of males and females before selection and μ_o the mean for the offspring sex being considered. Denoting the expectation taken over all selected parents by E_s , the expected offspring mean after selection is

$$E_s[E(z_o | z_{fa}, z_{mo})] = \mu_o + b_{o,fa}S_{fa} + b_{o,mo}S_{mo} \quad (4.3)$$

where S_{fa} and S_{mo} are the directional selection differentials on fathers and mothers (respectively).

Equations 4.2 and 4.3 allow for the possibility of differences between sexes in regression coefficients, in which case separate equations for sons and daughters are required. For example, the expected change in the mean character value of

daughters, R_{da} , equals the expected mean of daughters of selected parents minus the mean of females before selection. Applying Equation 4.3,

$$E_s [E(z_{da} | z_{fa}, z_{mo})] = \mu_{mo} + b_{da,fa} S_{fa} + b_{da,mo} S_{mo}$$

implying

$$R_{da} = b_{da,fa} S_{fa} + b_{da,mo} S_{mo} \quad (4.4a)$$

where $b_{da,fa}$ is the regression coefficient of daughters on their fathers and $b_{da,mo}$ the mother-daughter regression coefficient. Likewise, for sons

$$R_{so} = b_{so,fa} S_{fa} + b_{so,mo} S_{mo} \quad (4.4b)$$

Example 1. Coyne and Beecham (1987) estimated the following parent-offspring regression coefficients for abdominal bristle number in laboratory populations of *Drosophila melanogaster*:

Mother-son	$b_{so,mo} = 0.39 \pm 0.08$
Mother-daughter	$b_{da,mo} = 0.32 \pm 0.08$
Father-son	$b_{so,fa} = 0.13 \pm 0.10$
Father-daughter	$b_{da,fa} = 0.40 \pm 0.08$

Note that the father-son regression has a significantly smaller slope than the three other parent-offspring sex combinations. Assume that these estimated values are indeed the true values and that different amounts of selection are applied to fathers and mothers. Suppose the mean increase in bristle number in selected fathers is 2, while selected mothers show a mean decrease of 1 bristle. What is the expected change in mean bristle number in the male and female offspring using these estimated regression coefficients, assuming all parent-offspring regressions are linear? Here $S_{mo} = -1$ and $S_{fa} = 2$, and from Equation 4.4a, the expected change in bristle number in females is

$$R_{da} = b_{da,mo} S_{mo} + b_{da,fa} S_{fa} = 0.32(-1) + 0.40(2) = 0.48$$

Likewise, from Equation 4.4b, the expected change in males is

$$R_{so} = b_{so,fa} S_{fa} + b_{so,mo} S_{mo} = 0.13(2) + 0.39(-1) = -0.13$$

Even though we selected for increased bristle number in males and decreased number in females, the expected response is the exact opposite: a decrease in males and an increase in females.

Equation 4.4 is very general, requiring only that the biparental regression is linear, in which case $b_{o,fa}$ and $b_{o,mo}$ are partial regression coefficients and can be obtained from covariances between relatives. Again, linearity is ensured if the joint distribution of both parents and their offspring is multivariate normal. If there is no correlation between the phenotypes of parents (which is guaranteed under random mating), the partial regression coefficients are standard univariate regression coefficients (LW Chapter 8), so that LW Equation 3.14b gives

$$b_{o,fa} = \frac{\sigma(z_o, z_{fa})}{\sigma^2(z_{fa})} \quad \text{and} \quad b_{o,mo} = \frac{\sigma(z_o, z_{mo})}{\sigma^2(z_{mo})}$$

If mating is random, and genotype \times environmental interactions, shared environmental effects, epistasis, and sex-specific effects can all be neglected, the regression slope (for each parent-offspring combination) is $b_{o,p} = h^2/2$ (LW Chapters 7, 17). Defining the total selection differential as the average of both parental values, $S = (S_{fa} + S_{mo})/2$, recovers the breeders' equation

$$R = \frac{h^2}{2} S_{fa} + \frac{h^2}{2} S_{mo} = h^2 S \quad (4.5)$$

Equation 4.5 shows how differential selection on parents is incorporated into the breeders' equation. For example, consider selection on dioecious plants. If plants to form the next generation are chosen *after* pollination, fathers (pollen donors) are chosen at random with respect to the character under selection and $S_{fa} = 0$, giving $R = (h^2/2)S_{mo}$. Conversely, if parents are selected before pollination with equal amounts of selection (S) on both sexes, $R = h^2S$.

The Selection Intensity, \bar{i}

While the selection differential S is a convenient and simple measure of the selection, it does not really tell us much about the *strength* of selection. Consider selection acting on the same character in two different populations. In one, the largest five percent of measured individuals are allowed to reproduce while in the second the largest 25 percent reproduce. Clearly selection is more intense in the first population. However, if the characters are normally distributed, Equation 4.22a (below) gives the selection differentials for these two populations as $S_1 = 2.06 \sigma_1$ and $S_2 = 1.27 \sigma_2$, where σ_k^2 is the character variance in population k . Provided the second population is sufficiently more variable than the first, it can have the larger selection differential even though it clearly experiences less intense selection.

A better measure is to use the **standardized directional selection differential** (or **selection intensity**)

$$\bar{i} = S/\sigma_z \quad (4.6)$$

The selection intensity accounts for differences in the phenotypic variances, much akin to the correlation being a better measure of the strength of association than is

the covariance (LW Chapter 3). Substituting $\bar{i}\sigma_z$ for S gives the selection intensity version of the breeders' equation,

$$R = h^2 \bar{i}\sigma_z = \bar{i} h \sigma_A \quad (4.7)$$

Equation 4.7 will prove to be a useful starting point for generalizations (developed below) of the Breeders' Equation to accommodate more general types of selection.

Correcting for Reproductive Differences: Effective Selection Differentials

In artificial selection experiments, S is usually estimated as the difference between the mean of the selected adults and the sample mean of the population before selection. Selection need not stop at this stage. For example, strong artificial selection to increase a character might be countered by natural selection due to a decrease in the fertility of individuals with extreme character values. Biases introduced by such differential fertility can be removed by randomly choosing the same number of offspring from each selected parent, ensuring equal fertility.

Alternatively, biases introduced by differential fertility can be accounted for by using **effective selection differentials**, S_e ,

$$S_e = \frac{1}{n_p} \sum_{i=1}^{n_p} \left(\frac{n_i}{\bar{n}} \right) (z_i - \mu_z) \quad (4.8)$$

where z_i and n_i are the phenotypic value and total number of offspring of the i th parent, n_p the number of parents selected to reproduce, \bar{n} the average number of offspring for selected parents, and μ_z is the mean before selection. If all selected parents have the same number of offspring ($n_i = \bar{n}$ for all i), then S_e reduces to S . However, if there is variation in n_i among selected parents, S_e can be considerably different from S . This corrected differential is also referred to as the **realized selection differential**.

Example 2. Consider a trait with a heritability of 0.3 and a (before selection) mean of 30. Suppose 5 parents are selected, with the following trait values and offspring number:

Parent	Phenotypic value	Number of offspring
1	45	1
2	40	2
3	35	3
4	33	5
5	32	5

The resulting (unweighted) mean is 37, giving $S = 7$ and an expected response of $R = 0.3 \cdot 7 = 2.1$.

However, computing the effective selective differential by weighting the selected parents proportional to the number of offspring they leave gives

i	z_i	n_i	n_i/\bar{n}
1	45	1	0.3125
2	40	2	0.6250
3	35	3	0.9375
4	33	5	1.563
5	32	5	1.563

$$\frac{1}{n_p} \sum_{i=1}^{n_p} \left(\frac{n_i}{\bar{n}} \right) z_i = 34.69$$

Hence, $S_e = 4.69$, for an expected response of $R = 0.3 \cdot 4.69 = 1.4$. In this case, not using the effective differential results in a very significant overestimation of the expected response.

The derivation of Equation 4.8 follows directly from applying the Robertson-Price identity (LW Equation 3.21), $S = \sigma(z, w)$, which expresses the selection differential as a covariance between trait value z and relative fitness w . (Relative fitness is simply fitness scaled to have a mean value of one, i.e., the relative fitness of individual i is its absolute fitness divided by the mean population fitness, $w_i = W_i/\bar{W}$.) If a total of n potential parents are examined, n_p of which are selected as parents, then

$$S = \sigma(z, w) = E[wz] - E[z]E[w] = \frac{1}{n} \sum_{i=1}^n \left(\frac{W_i}{\bar{W}} \right) z_i - \mu_z \cdot 1$$

where the fitness of individual i is $W_i = n_i$ (with $n_i = 0$ for individuals not chosen as parents). The mean fitness becomes

$$\bar{W} = \frac{1}{n} \sum_{i=1}^n n_i = \frac{\bar{n} n_p}{n}, \quad \text{where} \quad \bar{n} = \sum_{i=1}^n n_i/n_p$$

so that \bar{n} is the mean number of offspring left by adults selected to reproduce. Hence

$$\frac{W_i}{\bar{W}} = \frac{n_i n}{\bar{n} n_p}, \quad \text{giving} \quad \sigma(z, w) = \sum_{i=1}^n z_i \frac{n_i}{\bar{n} n_p} - \mu_z$$

Rearranging recovers Equation 4.8. Chapter 14 examines individual fitness and fitness calculations such as this in detail.

EXPANDING THE BASIC BREEDERS' EQUATION

Accuracy

Under appropriate linearity assumptions, the breeders' equation generalizes to much more general settings, predicting the mean of character y measured in one group when selection occurs on character x measured in another group. Assuming the regression of y on x is linear, standard regression theory (LW Equation 3.14) gives

$$E[y - \mu_y | x] = \frac{\sigma(x, y)}{\sigma_x^2} (x - \mu_x)$$

giving the expected change in y from selection on x as

$$R_y = \mu_y^* - \mu_y = \frac{\sigma(x, y)}{\sigma_x^2} (\mu_x^* - \mu_x) = \frac{\sigma(x, y)}{\sigma_x^2} S_x = \frac{\sigma(x, y)}{\sigma_x} \bar{t}_x \quad (4.9)$$

where μ^* denotes the mean following selection.

Example 3. As an example of applying Equation 4.9, consider selection on clones or other pure lines. With clones, parents pass on their entire genome to their offspring. The phenotypic value z of an offspring from a parent with genotypic value G can be written as $z = G + E$, so that parent-offspring covariance (in the absence of any genotype \times environment covariance and/or interactions) equals the total genetic variance σ_G^2 . The resulting parent-offspring regression has slope $b_{op} = \sigma_G^2 / \sigma_z^2 = H^2$, the **broad-sense heritability** (LW Chapter 19), giving

$$R = H^2 S$$

Since $H^2 \geq h^2$ (as $\sigma_G^2 \geq \sigma_A^2$), the single-generation response to selection is larger for clones than for a sexual population with the same variance components. When selection continues for several generations, using clones is expected to be less efficient than using a sexual population. Selection among clones very rapidly removes genetic variation from the population without any mechanism (other than mutation) to generate new variation. With selection among sexual individuals, recombination generates an almost endless supply of new variation if a large number of segregating loci underlie the trait. For this reason, selection schemes involving clones often randomly mate lines every few generations to allow for recombination, generating variation required for continued response.

The selection intensity version of Equation 4.9 is

$$R_y = \frac{\sigma_{x,y}}{\sigma_x} \bar{t}_x = \bar{t}_x \sigma_y \rho(x, y) \quad (4.10a)$$

where $\rho(x, y)$ is the correlation between x and y . This correlation is referred to as the **accuracy** in predicting the response in y from knowledge of x , and one immediately sees that by improving the accuracy of our selection scheme, we improve the response. Expressing Equation 4.10a in terms of the **relative response**, the change in y in phenotypic standard deviations of y , gives

$$\frac{R_y}{\sigma_y} = \bar{i}_x \rho(x, y) \quad (4.10b)$$

Equation 4.10b allows one to compare the relative efficiencies of different selection schemes. Fixing the selection intensity \bar{i} , the maximal expected response in y occurs when we select on the measure x that has the largest correlation with y . The relative response of two different schemes (x_1 versus x_2) is given by $\rho(x_1, y)/\rho(x_2, y)$.

Most commonly, y is the breeding value A of an individual so that R_y is the change in breeding value from selection on x , giving

$$R_A = \bar{i}_x \rho(x, A) \sigma_A \quad (4.11)$$

Hence, the breeders equation can be consider as the following product:

$$\text{Response} = (\text{Intensity}) * (\text{Accuracy in Predicting Breeding Value}) * (\sqrt{\text{Usable Variance}})$$

If x is the phenotypic value z of the character whose breeding value is of interest, the correlation between x and y here is the correlation between an individual's phenotype z and its breeding value A ,

$$\rho(z, A) = \sigma(z, A)/(\sigma_z \sigma_A) = \sigma_A/\sigma_z = h$$

recovering Equation 4.7.

In evaluating other breeding schemes h is replaced by the appropriate correlation between the breeding value and the measure x being selected on. For example, we could take x to be the family mean of the character for the individual being considered, in which case the correlation between an individual's breeding value and its family mean determines the response to selection under this scheme (Chapter XX6). Assuming \bar{i} and σ_A are constant, the largest response occurs by taking the measure x that gives the largest correlation with breeding value. This idea forms the foundation of index selection (Chapters XX19, XX20) wherein x is a linear combination of several characters $x = \sum a_i z_i$.

Example 4. Progeny testing, using the mean of a parent's offspring to predict the parent's breeding value, is an alternative predictor of an individual's breeding value. In this case, the correlation between the mean of n offspring and the breeding value of the parent is

$$\rho(x, A) = \sqrt{\frac{n}{n+a}}, \quad \text{where } a = \frac{4-h^2}{h^2}$$

From Equation 4.11, the response to selection under progeny testing is

$$R = i\sigma_A \sqrt{\frac{n}{n+a}} = i\sigma_A \sqrt{\frac{h^2 n}{4 + h^2(n-1)}}$$

Note that for very large n that the accuracy approaches one. Progeny testing gives a larger response than simple selection on the phenotypes of the parents (**mass selection**) when

$$\sqrt{\frac{n}{4 + h^2(n-1)}} > 1, \quad \text{or} \quad n > \frac{4 - h^2}{1 - h^2}$$

In particular, $n > 4, 5,$ and $7,$ for $h^2 = 0.1, 0.25,$ and $0.5.$ Also note that the ratio of response for progeny testing (R_{pt}) to mass selection (R_{ms}) is just

$$\frac{R_{pt}}{R_{ms}} = \frac{1}{h} \sqrt{\frac{h^2 n}{4 + h^2(n-1)}} = \sqrt{\frac{n}{4 + h^2(n-1)}}$$

which approaches $1/h$ for large $n.$

Stratified Mass Selection

An interesting modification of the breeders' equation is Gardner's (1961) scheme of **stratified mass selection.** Here the population is stratified into a number of blocks, potentially representing different microenvironments, and selection occurs within each block. The motivation for Gardner's method was to improve individual selection for yield in maize. At the time of Gardner's paper, selection based solely on individual phenotype for yield resulted in a very poor response, largely because environmental effects overwhelm genetic differences. Simply by selecting for plants within blocks of presumable similar environments, Gardner was able to use mass selection to obtain fairly significant gains (about 4% per year).

Stratified mass selection is performed as follows. Suppose n individuals are measured within each block, and selection occurs on the deviation from the block mean, e.g. on $z_{ij} - \bar{z}_i$ where z_{ij} is the j th individual from block i and \bar{z}_i is the block mean. An individual's phenotypic value can be expressed as its genotypic value G_{ij} plus an environmental value consisting of a block effect bl_j and the residual environmental value $e_{ij},$

$$z_{ij} = \mu + G_{ij} + bl_j + e_{ij} \tag{4.12a}$$

The total environmental variance equals the variance between blocks σ_{bl}^2 plus the within-block variance $\sigma_{Wbl}^2,$ giving the total variance as

$$\sigma_z^2 = \sigma_G^2 + \sigma_E^2 = \sigma_G^2 + \sigma_{bl}^2 + \sigma_{Wbl}^2 \tag{4.12b}$$

To predict the response to selection under stratified mass selection, we use Equation 4.9, where the selection criteria x here is $z_{ij} - \bar{z}_i$ and y is the breeding value A_{ij} of individual z_{ij} . The resulting covariance required for Equation 4.9 is

$$\begin{aligned}\sigma(x, y) &= \sigma(z_{ij} - \bar{z}_i, A_{ij}) = \sigma(z_{ij}, A_{ij}) - \frac{1}{n} \sum_{k=1}^n \sigma(z_{ik}, A_{ij}) \\ &= \sigma_A^2 \left(1 - \frac{1}{n}\right) \simeq \sigma_A^2\end{aligned}\quad (4.13)$$

as the assumption is that individuals within blocks are unrelated and that a large number of individuals are scored within each block. The phenotypic variance within the block is $\sigma_z^2 = \sigma_G^2 + \sigma_{Wbl}^2$, giving the response under stratified mass selection as

$$R = \frac{\sigma(x, y)}{\sigma_x} \bar{i} = \frac{\bar{i} \sigma_A^2 (1 - 1/n)}{\sqrt{\sigma_G^2 + \sigma_{Wbl}^2}} \simeq \frac{\bar{i} \sigma_A^2}{\sqrt{\sigma_G^2 + \sigma_{Wbl}^2}} \quad (4.14a)$$

In contrast, if the effects of blocks are ignored and individuals are simply selected from the entire population, the response becomes

$$R = \frac{\bar{i} \sigma_A^2}{\sqrt{\sigma_G^2 + \sigma_{bl}^2 + \sigma_{Wbl}^2}} \quad (4.14b)$$

where σ_{bl}^2 is the variance between blocks in environmental effects. The relative efficient of stratification (assuming the block size is modest to large so that $1 - 1/n \simeq 1$) is

$$\sqrt{\frac{\sigma_G^2 + \sigma_{bl}^2 + \sigma_{Wbl}^2}{\sigma_G^2 + \sigma_{Wbl}^2}} = 1 + \sqrt{\frac{\sigma_{bl}^2}{\sigma_G^2 + \sigma_{Wbl}^2}} \quad (4.15)$$

Thus if the between-block variance is considerable, the response can be significantly improved by taking blocks into consideration.

Adjustments for Non-overlapping Generations

So far, we have been assuming non-overlapping generations — all parents only reproduce in one generation interval. In most settings, domesticated animals live multiple years and can have progeny over different years. In such cases, the response should be expressed in terms of response per year. To express the breeders' equation in terms of *rate of response* (typically the response per year), we first need to compute the **generation intervals** L_x (the average age of parents when progeny are born) for both sexes.

Example 5. Compute L_s and L_d for the following age structure:

	Age of Birth at Progeny				
Sires Number	year 2 60	year 3 30	year 4 0	year 5 0	Total 90
Dams Number	year 2 400	year 3 600	year 4 100	year 5 40	Total 1140

The resulting sire generation interval is

$$L_s = \frac{2 \cdot 60 + 3 \cdot 30}{60 + 30} = 2.33,$$

while the dam generation interval is

$$L_d = \frac{2 \cdot 400 + 3 \cdot 600 + 4 \cdot 100 + 5 \cdot 40}{400 + 600 + 100 + 40} = 2.81$$

Incorporating the generation intervals, the yearly rate of response can be expressed as

$$R_y = \left(\frac{\bar{l}_s + \bar{l}_d}{L_s + L_d} \right) h^2 \sigma_p = \left(\frac{\bar{l}_s + \bar{l}_d}{L_s + L_d} \right) h \sigma_A \tag{4.16}$$

Thus, one way to increase response is to *reduce the generation intervals*, for example by using younger parents. The problem is that there is a tradeoff between generation interval and selection intensity. In species that are reproductively-limited (few offspring per dam), using younger dams means that a higher fraction of the dams must be chosen to replace the population (i.e., to keep the same number of animals in a herd). As a consequence, the selection intensity on these parents (which increases as fewer parents are chosen) is reduced. Chapter XX examines the effects of age structure on selection response in much greater detail.

Maximizing Response Under the Breeders' Equation

More generally, we can combine both selection accuracy and generation interval to give a more general version of the breeders' equation:

$$R = \left(\frac{\bar{l}_s + \bar{l}_d}{L_s + L_d} \right) \rho(A, x) \sigma_A \tag{4.17}$$

Here, x is the selection scheme measure used to choose the parents to form the next generation. Expressed this way, there are three components of response that the breeder has some control over:

- (i) selection intensity, \bar{l}

- (ii) generation interval, L
- (iii) selection accuracy, ρ

Note that not much can be done with increasing σ_A^2 . Response is increased by decreasing L and increasing ρ and \bar{i} . We have already discussed tradeoffs between L and \bar{i} , and there are similar tradeoffs between L and ρ . Clearly, the longer we wait to allow a parent to reproduce, the more accurate we can predict their breeding value, as information from other relatives and from progeny-testing accumulates over time. However, these increases in ρ also result in increases in L . The optimal selection program must balance all of these competing interests.

Example 6. As an example of the tradeoff between accuracy and generation intervals, consider a trait with $h^2 = 0.25$ and selection only on sires. One scheme is to simply select on the sire's phenotype, which results in a sire generation interval of 1.5 years. Alternatively, one might perform progeny testing to improve the accuracy of the selected sires. This results in an increase of the sire generation interval to (say) 2.5 years. Suppose in both cases, the dam interval is steady at 1.5 years.

Since the intensity of selection and additive genetic variation are the same in both schemes, the ratio of response under mass selection to response under progeny testing is just

$$\frac{R(\text{Sire phenotype})}{R(\text{progeny mean})} = \frac{\rho(A, \text{Sire phenotype})/(L_s + L_d)}{\rho(A, \text{progeny mean})/(L_s + L_d)}$$

Here, $\rho(A, \text{Sire phenotype}) = h = \sqrt{0.25} = 0.5$, while (Example 4)

$$\rho(A, \text{progeny mean}) = \sqrt{\frac{n}{n+a}} = \sqrt{\frac{n}{n+15}}$$

as $a = (4 - h^2)/(h^2) = 15$. Hence,

$$\frac{R(\text{Sire phenotype})}{R(\text{progeny mean})} = \frac{0.5/3.0}{\sqrt{\frac{n}{n+15}}/4} = \frac{2}{3} \cdot \sqrt{\frac{n+15}{n}}$$

If (say) $n = 2$ progeny are tested per sire, this ratio is 1.25, with a larger response under sire-only selection. For $n = 4$, the ratio is exactly one, while for a very large number of offspring tested per sire, the ratio approaches $2/3$, or a 1.5-fold increase in the rate of response under progeny testing, despite the increase in sire generation interval.

Equation 4.17 highlights the importance to animal breeding of advances in reproductive technologies such as artificial insemination (AI) and multiple ovulation embryo transplant (MOET) schemes (Chapter XX). The more offspring a parent can produce, the stronger a selection intensity we can apply and still keep a required fixed number of animals in our herd. Hence, AI has resulted in the potential for far greater selection intensities (and unfortunately far more inbreeding) than would be possible under natural insemination. Likewise, MOET schemes to increase the number of offspring from females potentially allow for increases in the selection intensity on dams as well as decreases in the generation interval.

Prelude to the Multivariate Breeders' Equation

Several alternate parameterizations of the breeders' equation are popular in the evolutionary literature, and we introduce them here to motivate their multivariate versions (discussed in Chapters 15, 17). Expressing the heritability in terms of additive genetic and phenotypic variance,

$$R = \sigma_A^2 \sigma_z^{-2} S \quad (4.18a)$$

While this decomposition seems rather trivial, it suggests that the multivariate version of the breeders' equation (under appropriate linearity assumptions) is given by

$$\mathbf{R} = \mathbf{G}\mathbf{P}^{-1}\mathbf{S} \quad (4.18b)$$

where \mathbf{R} is the vector of responses (changes in the mean of each character), \mathbf{S} the vector of selection differentials for each character, and \mathbf{G} and \mathbf{P} are the additive genetic and phenotypic covariance matrices (LW Chapter 21). We will examine this equation, and its consequences, in Chapters 15 and 17.

A second parameterization follows from the Robertson-Price identity, $S = \sigma(z, w)$. Since the slope of the least-squares linear regression of relative fitness on phenotypic value is $\beta = \sigma(z, w)/\sigma_z^2$, it follows that $S = \sigma_z^2 \beta$. The regression slope β is called the **directional selection gradient**, for reasons that will become apparent shortly. Substituting $S = \sigma_z^2 \beta$ into Equation 4.1 gives

$$R = \sigma_A^2 \beta \quad (4.19a)$$

The multiple linear regression of relative fitness w on a vector \mathbf{z} of characters has slope $\beta = \mathbf{P}^{-1}\mathbf{S}$ (LW Equation 8.10c), where $w = 1 + \beta\mathbf{z}^T + e$. Substituting into Equation 4.18b gives

$$\mathbf{R} = \mathbf{G}\beta \quad (4.19b)$$

The importance of the selection gradient is that under appropriate conditions it relates how a change in the trait mean maps into a change in the mean fitness of a population. In particular, if $w(z)$ denotes the expected fitness of an individual with character value z , then when phenotypes are normally distributed, and fitness is frequency-independent (individual fitnesses are not a function of the mean of the

character), Lande (1976) showed that the directional selection gradient satisfies $\beta = \partial \ln \bar{w} / \partial \mu$. Hence we can express the breeders equation as

$$R = \sigma_A^2 \left(\frac{\partial \ln \bar{w}}{\partial \mu} \right) \quad (4.19c)$$

The multivariate version is the **gradient of mean fitness** (Chapter 15) with respect to the vector of character means,

$$\beta = \frac{\partial \ln \bar{w}}{\partial \boldsymbol{\mu}}$$

giving

$$\mathbf{R} = \mathbf{G} \frac{\partial \ln \bar{w}}{\partial \boldsymbol{\mu}} \quad (4.19d)$$

The gradient term represents the changes in character means that produce the maximal change in population fitness, while the actual response involves the product of this vector with the genetic covariance matrix \mathbf{G} . The resulting response vector is generally not parallel to β and hence the genetic covariance structure causes the character means to change in a direction that does not necessarily result in the optimal change in population fitness. We examine these issues in detail in Chapters 15 and 17.

These alternative expressions point out that we can distinguish between **phenotypic selection**, the change in a phenotypic distribution *within* a generation (measured by S or β), and the **evolutionary response to selection**, the transmission of these within-generation changes to the next generation (R). Lande and Arnold (1983) and Arnold and Wade (1984a,b), following Fisher (1930, 1958) and Haldane (1954), have stressed the utility of this approach. Attempts to measure selection by comparing phenotypic distributions across generations are confounded by inheritance, as R depends on β through σ_A^2 (or \mathbf{G} in the multivariate case). For example, if a character has no additive genetic variation ($\sigma_A^2 = 0$), there is no permanent change in the mean across generations regardless of the selection intensity, and a cross-generation comparison would conclude that selection was not operating. Chapters 14 and 16 examine in detail methods for estimating the nature of phenotypic selection in natural populations.

TRUNCATION SELECTION

Truncation selection is by far the commonest form of artificial selection in plant and animal breeding and in laboratory experiments. Under truncation selection, only the largest (or smallest) individuals are allowed to reproduce (Figure 4.2). Truncation selection is usually described by either the percent p of the population saved or the threshold phenotypic value T below (above) which individuals are

culled. The investigator usually sets these in advance of the actual selection. Hence, while S is trivially computed *after* the parents are chosen, we would like to *predict* the expected selection differential given either T or p . Specifically, given either T or p , what is the expected mean of the selected parents? In our discussions of this issue, we will initially assume a large number of individuals are saved, before turning to complications introduced by finite population size.

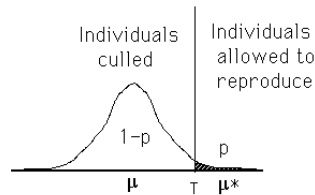


Figure 4.2. Under truncation selection, the uppermost (lowermost) fraction p of a population is selected to reproduce. Alternatively, one could set a threshold level T in advance, above (below) which individuals are allowed to reproduce. To predict response given either p or T , we need to know the mean of the selected tail (μ^*), from which we can compute $S = \mu^* - \mu$ and then apply the breeders' equation.

Selection Intensities and Differentials Under Truncation Selection

Given a threshold cutoff T , the expected mean of the selected adults is given by the conditional mean, $E(z | z \geq T)$. Generally it is assumed that phenotypes are normally distributed, and we use this assumption throughout. With initial mean μ and variance σ^2 , this conditional mean is given by LW Equation 2.14, which gives the expected selection differential as

$$S = \varphi\left(\frac{T - \mu}{\sigma}\right) \frac{\sigma}{p} \tag{4.20}$$

where $p = \Pr(z \geq T)$ is the fraction saved and $\varphi(x) = (2\pi)^{-1/2} e^{-x^2/2}$ is the unit normal density function evaluated at x .

Generally, it is the fraction to be saved p (rather than T) that is preset by the investigator (for example, if we save the uppermost 5 percent, what is the expected S ?). Given p , to apply Equation 4.20, we must first find the threshold value T_p satisfying $\Pr(z \geq T_p) = p$. Notice that T in Equation 4.20 enters only as $(T - \mu)/\sigma$, which transforms T_p to a scale with mean zero and unit variance. Hence,

$$\Pr(z \geq T_p) = \Pr\left(\frac{z - \mu}{\sigma} > \frac{T_p - \mu}{\sigma}\right) = \Pr\left(U > \frac{T_p - \mu}{\sigma}\right) = p$$

where $U \sim N(0, 1)$ denotes a unit normal random variable. Define $z_{[p]}$, the **probit transformation** of p (LW Chapter 11), by

$$\Pr(U < z_{[p]}) = p \quad (4.21a)$$

Hence

$$\Pr(U \geq z_{[1-p]}) = p \quad (4.21b)$$

It immediately follows that $z_{[1-p]} = (T_p - \mu)/\sigma$, and Equation 4.20 gives the expected selection intensity as

$$\bar{z} = \frac{S}{\sigma} = \frac{\varphi(z_{[1-p]})}{p} \quad (4.22a)$$

One can obtain $z_{[1-p]}$, and hence \bar{z} , from standard statistical packages. For example, in **R**, the command `qnorm(1-p)` returns $z_{[1-p]}$, while `dnorm(qnorm(1-p))/p` returns \bar{z} for a pre-assigned p value (e.g., `p <- 0.05`). Alternatively, a number of approximations have been suggested for Equation 4.22a. Assuming normality, Smith (1969) has suggested

$$\bar{z} \simeq 0.8 + 0.41 \ln\left(\frac{1}{p} - 1\right) \quad (4.22b)$$

Simmonds (1977) found that this approximation is generally quite good for $0.004 \leq p \leq 0.75$, and offered alternative approximations for p values outside this range. The most precise approximation is Saxton's (1988), with

$$\bar{z} \simeq \frac{2.97425 - 3.35197p^{0.2} - 1.9319p^{0.4} + 2.3097p^{0.6}}{0.51953 + 0.88768p^{0.2} - 2.38388p^{0.4} + p^{0.6}} \quad (4.22c)$$

Likewise, Montaldo (1997) gave an approximation for the standard truncation value $z = (T - \mu)/\sigma$ in terms of \bar{z} ,

$$z \simeq -1.411053 + 2.077585\bar{z} - 0.454318\bar{z}^2 + 0.097020\bar{z}^3 - 0.008137\bar{z}^4 \quad (4.22d)$$

Example 7. Consider selection on a normally distributed character in which the upper 5% of the population is saved ($p = 0.05$). Here $z_{[1-0.05]} = 1.645$ as $\Pr[U \geq 1.645] = 0.05$. Hence,

$$\bar{z} = \frac{\varphi(1.645)}{0.05} = \frac{0.103}{0.05} \simeq 2.06$$

Applying Equation 4.7 gives the expected response to this amount of selection as $R = h^2 \sigma 2.06$. Smith's approximation gives the selection intensity as

$$\bar{i} \simeq 0.8 + 0.41 \ln\left(\frac{1}{0.5} - 1\right) \simeq 2.01$$

which is quite reasonable. Saxton's approximation gives $\bar{i} \simeq 2.06$.

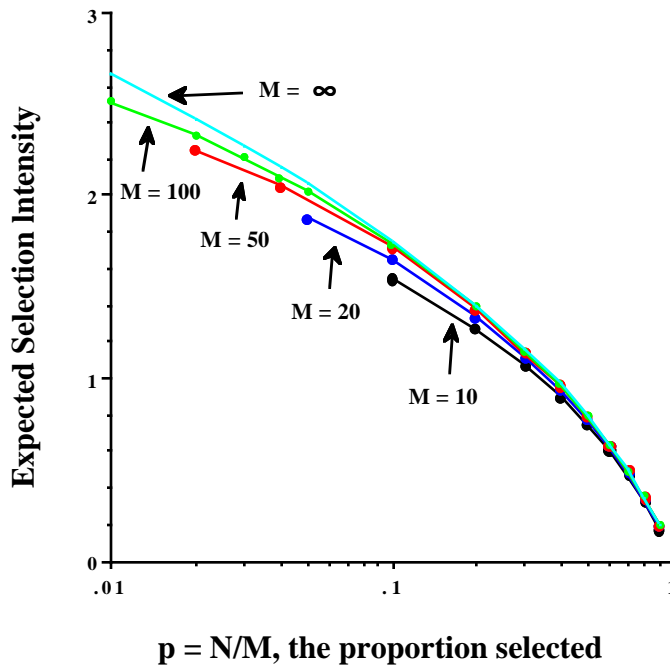


Figure 4.3. The expected selection intensity $E(\bar{i})$ under truncation selection with normally-distributed phenotypes, as a function of the total number of individuals measured M and the fraction of these saved $p = N/M$, N being the number of these adults allowed to reproduce. The curve $M = \infty$ is given by using Equation 4.22a, which is exact if N and M are infinite. The values on the curves for $M = 10, 20, 50,$ and 100 were obtained from the average of the expected values of the N largest unit normal order statistics (Harter 1961). Note that Equation 4.22a is generally a good approximation, unless N is very small.

Correcting the Selection Intensity for Finite Samples

If the number of individuals saved is small, the preceding formulae overestimate the selection differential because of sampling effects (Nordskog and Wyatt 1952, Burrows 1972). To see this, assume M adults are sampled at random from the population and the largest N of these are used to form the new generation, giving $p = N/M$. The expected selection coefficient is computed from the distribution of **order statistics**. Rank the M observed phenotypes as $z_{1,M} \geq z_{2,M} \dots \geq z_{M,M}$ where $z_{k,M}$ is referred to as the k th order statistic when M observations are sampled. The expected selection intensity is given by the expected mean of the N selected parents, which is the average of the first N order statistics,

$$E(\bar{v}) = \frac{1}{\sigma} \left(\frac{1}{N} \sum_{k=1}^N E(z_{k,M}) - \mu \right) = \frac{1}{N} \sum_{k=1}^N E(z'_{k,M})$$

where $z'_{k,M} = (z_{k,M} - \mu)/\sigma$ are the **standardized order statistics**. Properties of order statistics have been worked out for many distributions (Kendall and Stuart 1977, David 1981, Sarhan and Greenberg 1962, Harter 1970a,b). For the unit normal, see Harter (1961) for expected values and Sarhan and Greenberg (1962) for variances and covariances. Figure 4.3 plots exact values for the expected selection intensity for small values of N when phenotypes are normally distributed. Note that finite population size results in Equation 4.22a overestimating the actual selection intensity, although the difference is small unless N is very small.

Burrows (1972) developed a finite-sample approximation for the expected selection intensity for any reasonably well-behaved continuous distribution. Using the standardized variable $y = (z - \mu)/\sigma$ simplifies matters considerably. Letting $\phi(y)$ be the probability density function of the phenotypic distribution, and y_p the truncation point (i.e., $\Pr(y \geq y_p) = p$), Burrows' approximation is

$$E(\bar{v}_{(M,N)}) \simeq \mu_{y_p} - \frac{(M - N)p}{2N(M + 1)\phi(y_p)} \quad (4.23a)$$

where

$$\mu_{y_p} = E(y | y \geq y_p) = \frac{1}{p} \int_{y_p}^{\infty} x \phi(x) dx$$

is the truncated mean, which can be obtained by numerical integration. Since the second term of Equation 4.23a is positive, if M is finite the expected truncated mean overestimates the expected standardized selection differential.

For a unit normal distribution, $\mu_{y_p} = \phi(y_p)/p$, giving

$$\begin{aligned} E(\bar{v}_{(M,N)}) &\simeq \bar{v} - \left[\frac{M - N}{2N(M + 1)} \right] \frac{1}{\bar{v}} \\ &= \bar{v} - \left[\frac{1 - p}{2p(M + 1)} \right] \frac{1}{\bar{v}} \end{aligned} \quad (4.23b)$$

where \bar{v} is given by Equation 4.22a. Lindgren and Nilsson (1985) examined the accuracy of Burrows' approximation. They found the error is rather constant independent of M for $M > 10$, and decreases with N roughly as $1/N^2$. They suggest that Burrows' approximation can be used for all N if an error of 0.025 (less than 5% of the selection intensity) is acceptable, for $N > 2$ if an error less than 0.01 is acceptable, and for $N > 6$ if an error of less than 0.001 is required.

Bulmer (1980) suggests an alternative finite-sample approximation for $E(\bar{v}_{(M,N)})$ when phenotypes are normally distributed, using Equation 4.22a with p replaced by

$$\tilde{p} = \frac{N + 1/2}{M + N/(2M)} \quad (4.23c)$$

Example 8. Consider the expected selection intensity on males when the upper 5% of the sampled males are used to form the next generation and phenotypes are normally distributed. If the number of males sampled is very large, then from Example 7, the expected selection intensity is $\bar{v} \simeq 2.06$. Suppose, however, that only 20 males are sampled so that only the largest male is allowed to reproduce in order to give $p = 0.05$. The expected value for this male is the expected value of the largest order statistic for a sample of size 20. For the unit normal, the expected value of the largest order statistic in a sample of 20 is $\simeq 1.87$ (Harter 1961) and hence $E(\bar{v}_{(20,1)}) \simeq 1.87$. There is considerable spread about this expected value, as the standard deviation of this order statistic is 0.525 (Sarhan and Greenberg 1962). How well do the approximations of $E(\bar{v}_{(20,1)})$ perform? Burrows' approximation gives

$$E(\bar{v}_{(20,1)}) \simeq 2.06 - \frac{(20-1)}{2(20+1)} 2.06 = 2.06 - 0.22 = 1.84$$

while Bulmer's approximation uses

$$\tilde{p} = \frac{1 + 1/2}{20 + 1/40} \simeq 0.075$$

which gives $z_{[1-0.075]} \simeq 1.44$. Since $\varphi(1.44) = 0.1415$,

$$E(\bar{v}_{(20,1)}) \simeq 0.1415/0.075 \simeq 1.89$$

A final correction for finite population size was noted by Rawlings (1976) and (especially) Hill (1976, 1977). If families are sampled, such that n individuals are chosen per family, then the selection intensity is further reduced because the

correlations between family members. In particular, if a total of M individuals are sampled, with n individuals per family then Burrows' correction (Equation 4.23b) is modified to become

$$\bar{v} - \left[\frac{1-p}{2p(M+1)(1-\tau+\tau/n)} \right] \frac{1}{\bar{v}} \quad (4.24)$$

where τ is the intra-class correlation of family members.

Burrows (1975) develops expression of the variance of \bar{v} in finite populations. However, since the distribution of realized differentials is asymmetry (Figure 4.4), the variance alone is not sufficient for computing confidence intervals.

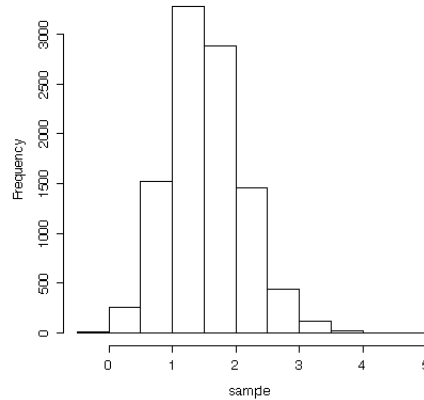


Figure 4.4. The distribution of 10,000 random draws of $\bar{v}_{(10,1)}$, the largest order statistic in a sample of 10. The mean value is 1.54, as opposed to the expected value of $\bar{v} = 1.75$ for $p = 0.1$ in an infinite population. Burrows' approximation gives an expected value of 1.52. Notice that there is a considerable spread of values and that the distribution is not symmetric about the mean, but rather skewed to higher values.

PERMANENT VERSUS TRANSIENT RESPONSE

As was discussed in LW Chapters 7 and 17, the slope of the parent-offspring regression can be inflated by epistasis, genotype \times environment interactions and correlations, and environmental effects shared by parents and their offspring. Hence, even if the parent-offspring regression is linear, the slope can deviate significantly from $h^2/2$, altering the response from that predicted by the breeders' equation. For example, with epistasis and correlation between parental and offspring environmental values,

$$b_{op} = \frac{h^2}{2} + \frac{1}{\sigma_z^2} \left(\frac{\sigma_{AA}^2}{4} + \frac{\sigma_{AAA}^2}{8} + \frac{\sigma_{AAAA}^2}{16} + \dots + \sigma(E_p, E_o) \right) \quad (4.25a)$$

Assuming a linear biparental regression, the response to a single generation of selection becomes

$$R = h^2 S + \frac{S}{\sigma_z^2} \left(\frac{\sigma_{AA}^2}{2} + \frac{\sigma_{AAA}^2}{4} + \frac{\sigma_{AAAA}^2}{8} + \dots + \sigma(E_{fa}, E_o) + \sigma(E_{mo}, E_o) \right) \quad (4.25b)$$

which can deviate significantly from $h^2 S$. Why then do we pay so much attention to h^2 ?

The reason is that we are interested in the **permanent response** to selection. Recall that one of our main assumptions throughout this chapter is that changes in allele frequencies are negligible, hence any changes in genetic variances are due to gametic-phase disequilibrium rather than changes in allele frequencies. Under this assumption, epistasis and/or shared environmental factors inflate the transient response to selection, but once selection stops, their contribution to response decays away. Changes in genotypic frequencies attributable to gametic-phase disequilibrium and environmental correlations are due to nonrandom associations built up by selection. Recombination and randomization of environmental effects causes these correlations to decay. Conversely, changes in allele frequencies are permanent. Once selection is stopped, the new allele frequencies are stable (assuming that our time scale for observing a population is such that drift and mutation have negligible effects). Hence, as will be shown shortly, the permanent response under the conditions leading to Equation 4.25b is $h^2 S$. One exception, discussed in Chapter 6, is when significant inbreeding occurs. In this case, σ_{AA}^2 and other non-additive variance components ($\sigma_{DI}^2, \sigma_{ADI}$) introduced in Chapter 3 can contribute to permanent response.

Response with Epistasis

The response when additive \times additive epistatic variance is present was examined by Griffing (1960a,b) for the infinitesimal model (Chapter 10). Under the assumption that phenotypes are normally distributed and that the effects at any particular locus are very small relative to the total phenotypic variation, the response to one generation of selection is

$$R = S \left(h^2 + \frac{\sigma_{AA}^2}{2\sigma_z^2} \right) \quad (4.26)$$

One might expect that $R(n)$, the cumulative response after n generations of selection, is simply n times the result given by Equation 4.26. However, any increased response due to epistasis is only temporary, reflecting gametic-phase disequilibrium generated by selection. As disequilibrium decays under recombination, so does the component of response due to epistasis. This occurs because the contribution from epistasis is due to favorable *combinations* of alleles at different loci, specifically those alleles that interact epistatically to change the character in the direction favored by selection. Recombination breaks down these combinations, removing the epistatic contribution. Griffing showed that for two linked loci (separated by recombination fraction c), the response when a generation of selection

is followed by τ generations of no selection is

$$S \left(h^2 + (1 - c)^\tau \frac{\sigma_{AA}^2}{2\sigma_z^2} \right) \quad (4.27)$$

which converges to $h^2 S$. Equation 4.27 follows by noting that the probability a gamete containing specific alleles from both loci remains intact following one generation of recombination is $1 - c$. Thus, after τ generations only $(1 - c)^\tau$ of the favorable two-locus combinations selected at $\tau = 0$ remain unaltered by recombination.

Summing Equation 4.27 over t gives the cumulative response after t generations with constant selection differential S as

$$R(t) = t h^2 S + R_{AA}(t) \quad (4.28a)$$

where

$$R_{AA}(t) = S \frac{\sigma_{AA}^2}{2\sigma_z^2} \left(\sum_{i=1}^t (1 - c)^{i-1} \right) = S \left(\frac{1 - (1 - c)^t}{c} \right) \left(\frac{\sigma_{AA}^2}{2\sigma_z^2} \right) \quad (4.28b)$$

denotes the cumulative additive \times additive epistatic contribution. The last equality follows using the partial sum of a geometric series:

$$\sum_{i=0}^n x^i = \frac{1 - x^{n+1}}{1 - x} \quad (4.29)$$

If loci are unlinked ($c = 1/2$), $R_{AA}(t)$ rapidly converges to $S \sigma_{AA}^2 / \sigma_z^2$, while if loci are completely linked ($c = 0$), $R_{AA}(t) = t S \sigma_{AA}^2 / (2\sigma_z^2)$. Hence, with tight linkage, the transient contribution from epistasis can be considerable. With t generations of selection followed by τ generations of no selection, the cumulative response is

$$t h^2 S + (1 - c)^\tau R_{AA}(t) \quad (4.30)$$

which converges to $R = t h^2 S$ for large τ (i.e., many generations after selection is stopped), which is the value predicted from the breeders' equation.

The presence of epistasis can result in a curvilinear selection response if $\sigma_{AA}^2 / \sigma_z^2$ is sufficiently large. However, as Figure 4.5 shows, such curvilinearity is usually difficult to distinguish from a linear response. Further, much of the curvilinearity occurs in the first few generations. With a constant selection differential, the increment to response decreases each generation, eventually converging to $h^2 S$ and hence a linear response from that point on.

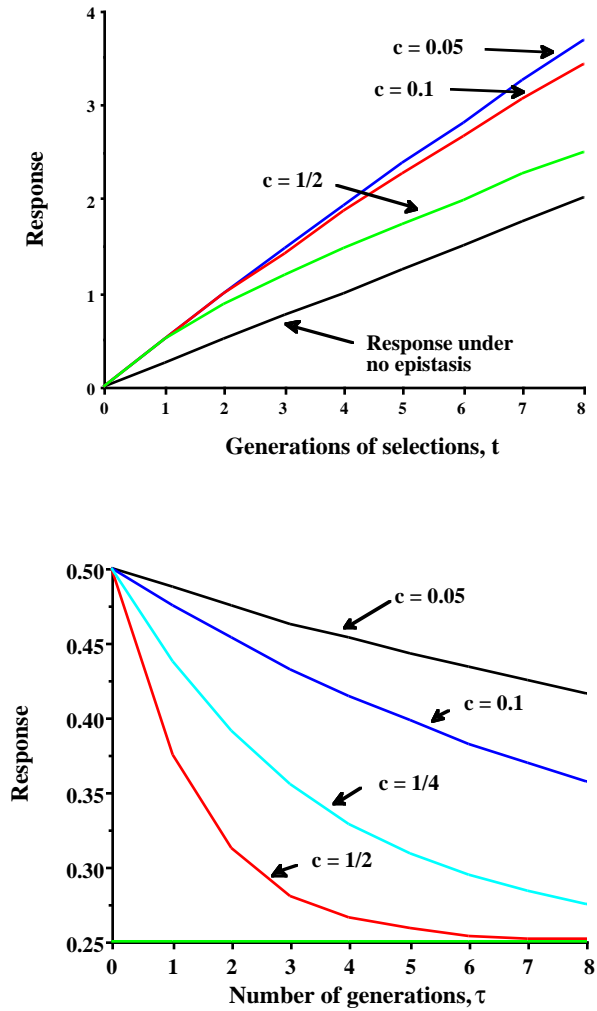


Figure 4.5. The permanent and transient response to selection assuming pairwise epistasis in a diploid, with $h^2 = 1/4$ and $\sigma_{AA}^2/\sigma_z^2 = 1/2$. **Top:** The cumulative response (in units of S) assuming a constant amount of selection for various values of c . Note that even with this large amount of epistasis (σ_{AA}^2 accounting for half the total variance), it is difficult to distinguish the curvilinear response with epistasis from a linear response. **Bottom:** The decay of the response to a single generation of selection due to the decay of the contribution from epistasis. With no epistasis, expected response here is 0.25. Provided $c > 0$, the cumulative response eventually decays to $h^2S = S/4$, the expectation under no epistasis.

Once selection is relaxed, the total response decays back to that predicted from the breeders' equation. Interestingly, this situation mimics the effects of natural selection countering artificial selection, which also results in a decay of the cumulative response once artificial selection stops. Thus, in order to predict the *permanent* response correctly we must know h^2 . If only the parent-offspring slope is estimated, this can overestimate the final amount of response due to the inclusion of σ_{AA}^2 and higher-order epistatic variances.

Griffing's analysis is restricted to two loci, and hence limited to only pair-wise (additive \times additive) epistasis. Equation 4.25 gives the single-generation response for arbitrary levels of additive epistasis, provided the biparental offspring regression is linear. Again assuming the infinitesimal model (and unlinked loci), Bulmer (1980) found the response due to a single generation of selection decays in the next generation to

$$R = S \left(h^2 + \frac{1}{4} \frac{\sigma_{AA}^2}{\sigma_z^2} + \frac{1}{16} \frac{\sigma_{AAA}^2}{\sigma_z^2} + \frac{1}{64} \frac{\sigma_{AAAA}^2}{\sigma_z^2} + \dots \right)$$

which again rapidly converges to $R = h^2 S$ after several generations without selection. For n -locus additive epistasis (e.g., $\sigma_{A\dots A}^2$, where there are n A 's), the per-generation decay rate for unlinked loci is $(1/2)^{n-1}$, the probability that a parental gamete containing specific alleles at n unlinked loci is passed on to an offspring. The probability that such a gamete remains unchanged after t generations is $2^{-t(n-1)}$, which rapidly converges to zero. A final caveat is that these results apply to infinite populations. As we will see in Chapter 12, with finite populations some of the additive epistatic contribution can be permanent.

Selection on Autotetraploids

Polyploidy is very common in plants and can introduce complications in predicting the response to selection. For example, the dynamics of selection response for autotetraploids with dominance is very similar to diploids with epistasis. From LW Equation 7.22 and LW Table 7.5, the autotetraploid parent-offspring covariance when dominance (but no epistasis) is present is

$$\sigma(z_p, z_o) = \frac{\sigma_A^2}{2} + \frac{\sigma_D^2}{6}$$

This also assumes no shared environmental effects, genotype \times environment interactions or correlations.

The inflation in the parent-offspring covariance is due to dominance interactions between the two alleles per locus that each autotetraploid parent passes on to its offspring. Thus, like epistasis in diploids, favorable *combinations* of alleles can be passed down from parent to offspring in polyploids. With equal amounts of selection on both sexes (e.g., selection occurs before pollination), the resulting response (assuming linearity of the parent-offspring regression) is

$$R = S \left(h^2 + \frac{\sigma_D^2}{3\sigma_z^2} \right) \quad (4.31)$$

If selection occurs after pollination, S is replaced throughout the rest of our discussion by $S/2$. Gallais (1975) extended Griffing's (1960a) method (and hence assumed phenotypes are normally distributed with each gene having a very small effect on the character) to obtain the response after t generations of selection with constant differential S as

$$R(t) = th^2S + R_D(t) \quad (4.32a)$$

where

$$R_D(t) = S \frac{3}{2} [1 - (1/3)^t] \frac{\sigma_D^2}{3\sigma_z^2} \quad (4.32b)$$

which converges to $S (\sigma_D^2/2\sigma_z^2)$. Segregation reduces the departure from tetraploid Hardy-Weinberg proportions generated by the selection of favorable combinations of allelic pairs, reducing their contribution to response. The response for t generations of selection followed by τ generations of no selection is

$$th^2S + (1/3)^\tau R_D(t)$$

which again converges to th^2S . In LW Chapter 4, it was shown that in an autotetraploid the difference in the frequency of pairs of alleles from Hardy-Weinberg expectation decays by $1/3$ each generation in the absence of double reduction ($c = 0$), as would occur for a locus completely linked to the centromere. More generally, if c is the per-generation probability of a double reduction, the decay rate of $1/3$ is replaced in the above equations by $(1 - c)/3$. Swanson et al. (1974) found that if some double reductions occur ($c > 0$), the additive variance is slightly inflated over the value expected with no double reductions ($c = 0$), permanently increasing selection response. This results from the slight excess of homozygotes at equilibrium over the Hardy-Weinberg expectation (see LW Chapter 4). Wricke and Weber (1986) discuss additional topics on autotetraploid selection, while single-locus models have been examined by R. Hill (1971). By far the most complete treatment of selection with autopolyploids is the outstanding text by Gallais (2003).

ANCESTRAL REGRESSIONS

A general approach for examining which components of the response are transient is to consider the expected value of an offspring as a function of all its direct relatives that have been under selection. If this **ancestral regression** is linear (as would occur if the joint distribution of the phenotypic values of all relatives is multivariate normal), response can be described by specifying the regression coefficients by an obvious extension of the biparental regression to now include all selected relatives back to the original unselected base population. For example, if selection starts in generation 0, the response in the first generation is $R(1) = 2\beta_{1,0}S_0$,

where $\beta_{1,0}$ is the regression of offspring at generation one on a parent from generation zero (this assumes both parents have the same regression coefficients and selection differentials, an assumption that will be relaxed shortly). Likewise, the total response after two generations, $R(2) = 4\beta_{2,0}S_0 + 2\beta_{2,1}S_1$, depends on the nature of selection on the four grandparents and both parents. Note that this formulation allows the parent-offspring regression to change through time (e.g., $\beta_{2,1}$ need not equal $\beta_{1,0}$), as might happen with inbreeding. Similarly, the response following three generations of selection depends upon the nature of selection on that individual's eight great-grandparents, four grandparents and two parents,

$$R(3) = 8\beta_{3,0}S_0 + 4\beta_{3,1}S_1 + 2\beta_{3,2}S_2$$

Proceeding in this fashion gives the response for generation T as

$$R(T) = \sum_{t=0}^{T-1} \beta_{T,t} (2^{T-t} S_t) \quad (4.33a)$$

where $\beta_{T,t}$ is the regression coefficient for the phenotype of an individual in generation T on one of its relatives in generation $t < T$. With pure selfing each individual has only a single relative in each previous generation, giving the ancestral regression as

$$R(T) = \sum_{t=0}^{T-1} \beta_{T,t} S_t \quad (4.33b)$$

Recall from standard regression theory (LW Chapter 8) that the vector of partial regression coefficients $\beta = \mathbf{V}^{-1} \sigma$, where σ is a vector of covariances between the individuals in generation T with all relatives in previous generations and \mathbf{V} is the phenotypic covariance matrix for the entire collection of individuals. The key here is that the regression coefficients are entirely determined by the covariances between relatives. If we have independence so that the partial regression coefficients reduce to univariate regression coefficients (i.e., $\beta_i = \sigma(y, x_i) / \sigma_{x_i}^2$), then we have

$$R(T) = \sum_{t=0}^{T-1} \frac{\sigma_G(T, t)}{\sigma^2(z_t)} (2^{T-t} S_t) \quad (4.33c)$$

where $\sigma_G(T, t) = \sigma(z_T, z_t)$ is the **cross-generation covariance**, the phenotypic covariance between an individual in generation t and its descendent in generation $T > t$. With selection under pure selfing, each individual has a single ancestor and the 2^{T-t} term in Equation 4.29c is absent.

If different relatives in the same generation experience different amounts of selection, with $S_{k,i}$ being the selection differential on relative i in generation k , then

$$R(T) = \sum_{t=0}^{T-1} \left[\beta_{T,t} \left(\sum_{i=1}^{n(t,T)} S_{t,i} \right) \right] \quad (4.34)$$

where $n(t, T)$ is the number of relatives in generation t that contribute to response in generation T . Note for the case of pure selfing $n(t, T) = 1$. Finally, we can also allow for different regression coefficients on each relative to completely generalize this approach,

$$R(T) = \sum_{t=0}^{T-1} \left(\sum_{i=1}^{n(t,T)} \beta_{T,t,i} S_{t,i} \right) \quad (4.35)$$

where $\beta_{T,t,i}$ is the regression coefficient of the phenotype of an individual in generation T on its i -th relative in generation t .

To apply ancestral regression for predicting response, we require that the regression remains linear and that selection-induced changes in the variances and covariances are negligible. Thus, while we allow changes in $\beta_{T,t}$ due to the particular genetic system being considered (e.g., selfing wherein the additive genetic variance decreases by a predictable amount each generation in the absence of selection) we assume that selection does not confound these changes. Bulmer (1980) shows that under the infinitesimal model the joint distribution of an offspring and all its direct ancestors is multivariate normal and hence the ancestral regression is linear. Since selection does not change allele frequencies under the infinitesimal model (Chapter 10), this might suggest that the regression coefficients $\beta_{T,t}$ are unaffected by selection. The problem, however, is that selection generates gametic-phase disequilibrium that can significantly alter the genotypic moments (Chapter 10). For now, we assume that these changes (over short time scales) are small enough to be neglected.

Example 9: As an application of ancestral regressions, consider additive by additive epistasis. In this case, Cockerham (1984b) found that for two linked loci, the cross-generation covariance is

$$\sigma_G(\tau + t, \tau) = \frac{\sigma_A^2(\tau)}{2^t} + \frac{\sigma_{AA}^2(\tau)}{2} \left(\frac{1-c}{2} \right)^t$$

giving

$$2^t \sigma_G(\tau + t, \tau) = \sigma_A^2(\tau) + (1-c)^t \frac{\sigma_{AA}^2(\tau)}{2}$$

if the genetic variances remain constant, then applying Equation 4.33a we recover Equation 4.30.

The behavior of the regression coefficients over time thus informs us about the permanency of response. Note from Equation 4.33a that unless $2^t \beta_{\tau+t,\tau}$ remains

constant as t increases, the contribution to cumulative response from selection on adults in generation τ changes over time. For example, when loci are strictly additive (no dominance or epistasis), $\sigma_G(\tau+t, \tau) = 2^{-t} \sigma_A^2(\tau)$ and thus $2^t \beta_{\tau+t, \tau} = h_{\tau}^2$, the standard result from the breeders' equation. Note that unless $2^t \sigma_G(\tau+t, \tau)$ remains constant, any response contributed decays. Hence any term of $\sigma_G(\tau+t, \tau)$ that decreases by more than 1/2 each generation contributes only to the transient response. An exception is with pure selfing where the total contribution in generation $t+\tau$ from an ancestor in generation τ is proportional to $\sigma_G(\tau+t, \tau)$, so that any components that decline as τ increases will contribute to the transient response.

SUMMARY: LIMITATIONS OF THE BREEDERS' EQUATION

As many of the previous sections have illustrated, there are a number of situations that can compromise the breeders' equation, even if we are interested only in the single-generation response to selection and can assume a linear parent-offspring regression. One particularly important (and usually unstated) assumption is that we start from an *unselected* base population. If the base population itself has been under selection, decay of transient response components from previous selection compromises the predicted single-generation response. Another troublesome assumption is that our model has accounted for all the selection on the character of interest. This is especially tricky as selection on any character correlated with the one of interest can introduce significant bias. The problem of selection of multiple characters is discussed in Chapters 17–20, but often there is no easy solution, or even any indication of a problem before the experiment begins. Thus, even in the best of situations (linearity and no selection-induced changes in allele and gamete frequencies), there are pitfalls in predicting even a single generation of response from the slope of the parent-offspring regression. Things get worse if the parent-offspring regression is nonlinear, where the single-generation change in the mean can depend on higher order moments of the genotypic distribution, and hence is not predictable from simple variance components (e.g., Equation 9.35b).

Table 4.1 reviews some of the various factors that can compromise the breeders' equation, and the chapters in which these complications are examined in detail. Provided one can assume linearity of the regressions of relatives, many of these complications can be accounted for. The importance of linearity is that if the regression of an individual on all its direct relatives selected in previous generations (back to the original unselected base population) remains linear, response is entirely determined by the covariances between a current individual and these previous relatives (Equation 4.33a).

Even if we have corrected for all of the potential complications listed in Table 4.1, the breeders' equation is expected to be an increasingly poor predictor as selection proceeds. Even a single generation of selection can significantly change

the underlying variance components, which in turn changes the regression coefficients. Further, selection can introduce nonlinearities into an initially linear regression by transforming the starting distribution away from normality (Chapter 10). In the absence of major genes, allele frequency changes over the first few generations of selection are expected to be rather small, but *genotype* frequencies can change dramatically due to selection generating gametic-phase disequilibrium (Chapters 7, 10). Directional selection generates negative disequilibrium, decreasing heritability and hence reducing response. This reduction can be significant if heritability is high. Likewise, selection on the variance itself (through disruptive or stabilizing selection) also creates disequilibrium which changes the genetic variance. Chapter 7 examines such short-term changes in disequilibrium. As selection continues over several generations, allele frequencies themselves start to change, even if all loci have very small effects (Chapter 11). Drift and mutation also become increasingly important and these complications are examined in Chapters 12, 13.

Table 4.1. Summary of various factors that complicate prediction of short-term selection response in the phenotypic mean, even assuming all regressions are linear and that we are considering a single generation of selection from an unselected base population.

G × E interactions (Chapters 17, 20)	Possibility of nonlinear parent-offspring regressions. Possibility of reversed response.
Age-structure (Chapter 6)	Several generations are required to propagate genetic change uniformly through the population.
Epistasis (Chapter 4)	Component of response due to epistasis is transient. Parent-offspring covar. overestimates permanent response.
Correlated environmental effects (Chapter 4)	Contribution from parent-offspring correlation decays away after selection relaxed.
Maternal effects (Chapter 4)	Complicated lags in response — mean changes unpredictably after selection is relaxed. Possibility of reversed response.
Inbreeding (Chapter 6)	Response depends on additional variance components that are difficult to estimate (σ_{DI}^2 , σ_{ADI} , etc). Response has permanent and transient components.
Drift (Chapter 8)	Generates variance in the short-term response.
Gametic-phase disequilibrium (Chapter 7)	Changes additive genetic variance. Directional selection generates negative gametic-phase disequilibrium, reducing h^2 and slowing response.

Assortative Mating (Chapter 7)	Generates gametic-phase disequilibrium which either enhances (positive correlation between mates) or retards (negative correlation between mates) response.
Selection on Correlated Characters (Chapters 17-20)	Response completely unpredictable unless selection on correlated characters accounted for.
Environmental Change (Chapter 5)	A significant change in the environment can obscure the true amount of genetic change.
