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Short-term Changes in the Mean:
1. The Breeder's Equation

Prediction is very difficult, especially if it's about the future. — Niels Bohr

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Selection on quantitative traits, and its consequences, comprises the remainder of this book. We start by discussing the simplest situation — the expected change in the mean of a single character following a single generation of selection. This response is reasonably predictable in a wide variety of settings, using a regression framework and the appropriate covariances between relatives. By contrast, the response after a number of generations is much more unpredictable, as allele-frequency change alters the genetic covariances (and hence the resemblance between relatives) from their initial values. Provided that each locus has only a small effect on the trait, only minor allele-frequency change is expected over the first several generations. In the extreme under the infinitesimal model (the limit of a very large number of loci, each with vanishingly small effect), the additive genic variance (that part of the additive variance independent of any disequilibrium effects) remains essentially unchanged during selection (Chapters 16, 24). The **short-term** response of a trait refers to these early generations where allele-frequency change has a negligible effect on the initial additive variance. Over longer time scales, allele-frequency evolution results in substantial changes in the variance that are extremely difficult to predict. This is the setting for **long-term response**, examined in Chapters 25 - 28.

Selection can occur in any matter of fashions. Our focus in this chapter is **individual** (or **mass**) **selection** under random mating, 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 ranking within a family is discussed in Chapter 21. Chapter 22 discusses the setting where individuals interact in groups (**kin selection** if they are related) and selection may be either on the individual and/or at the group level (**group selection**), while Chapter 23 and 24 examines response in inbred populations. Using additional information, such as the trait value in other relatives and/or the values of other traits in the focal individual, can improve our accuracy in predicting an individual's breeding value and hence increase the response relative to individual selection. This can be done through **index selection**, which leads to BLUP-based selection (Chapters 19, 20, 22; LW Chapter 26), both of which are more fully developed in our final volume. A number of other important selection schemes (such as marker-assisted and genomic selection, selection for outcross performance, and in age-structured populations) are also deferred until our final volume.

There is a huge literature on schemes exploiting special features of specific organisms (such as artificial insemination in animals or complex crosses in selfing plants). See Turner and Young (1969), Pirchner (1983), Ollivier (1988), Weller (1994), Cameron (1997), Simm (1998), and Kinghorn et al. (2000) for applications in animal breeding and Namkoong (1979), Wricke and Weber (1986), Mayo (1987), Hallauer et al. (1988), Stoskopf et al. (1993), Bos and Caligari (1995), Gallais (2003), and Bernardo (2010) for applications in plant breeding.

SINGLE-GENERATION RESPONSE: THE BREEDER'S EQUATION

The Breeder's Equation, a General Approximation for Reponse

Previous chapters developed explicit expressions for a single generation of response based on either specific population-genetic models (Equations 5.23c, 5.27b) or completely general covariance-based expressions based on Price's theorem (Equations 6.12, 6.38, 6.39). These results show that either a large number of underlying loci of small effect and/or a linear parent-offspring regression generally recovers the simple **breeder's equation**

$$R = h^2 S \tag{13.1}$$

plus correction terms that are often small. This approximation is perhaps the most well known expression in quantitative genetics, and its myriad of extensions form the backbone of the quantitative-genetic theory of short-term response. Its actual origin is somewhat unclear, but it was clearly suggested (in multivariate form) in the early writings of Pearson and popularized by Lush (1937). Indeed, Ollivier (2008) makes quite reasonable suggestion it be called the **Lush equation**. 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 (the **selection differential** S) with a measure of how character value is passed across generations (h^2).

As discussed in Chapter 6, a necessary (but not sufficient) condition to recover the breeder's equation is a linear parent-offspring regression, with the phenotypic value z_o of an offspring whose parents have the mean phenotypic value z_{mp} given by

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

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

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

Recall (Equation 6.12) that two other technical restrictions are also required to formally obtain Equation 13.1. First, that the residuals of the parent-offspring and fitness-phenotype regressions are uncorrelated. Second, that the mean does not change in the absence of selection. In our treatment we assume these potential complications either introduce only very small errors, or we explicitly model their effects (e.g., Chapters 15, 20, 22, 23).

The Importance of Linearity

A variety of factors, such as a major gene with dominance, can result in a nonlinear parent-offspring regression (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 13.1 shows, two selected parental populations with the same mean, but different variances, can have different expected responses when this 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 5.27b). While a sufficient condition for linearity is that the joint distribution of breeding and phenotypic values is bivariate normal (LW Chapter 8), selection generally causes the distribution of genotypic values to depart from normality (Chapters 16, 24), creating at least slight departures from linear parent-offspring regressions. Response under strongly non-normal distributions can be very complicated, depending on underlying genetic factors that do not easily translate into standard (and measurable) variance components (Chapter 24).
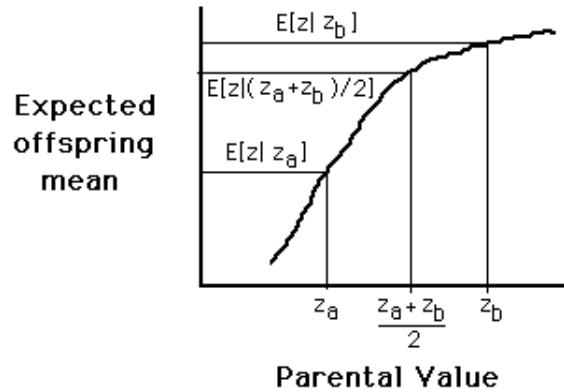
Figure 13.1.   The importance of linearity in the parent-offspring regression. If this regression is nonlinear, different subsets of the population with the same mean can have different offspring means. Suppose equal numbers of parents with values z_a and z_b are chosen. Denoting the expected value of 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 above, can deviate considerably from $(\,E[\,z\,|\,z_a\,] + E[\,z\,|\,z_b\,]\,)\,/\,2$.

Response is the Change in Mean Breeding Value

Under the infinitesmal model and a linear parent-offspring regression, a key concept is that *response 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. Under the infinitesimal model, the expected offspring value is just the average breeding values of its parents (LW Chapter 4).

Trait improvement by artifical selection occurs by choosing parents 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 $h^2 = 1$). Phenotype is an imperfect predictor of breeding value, and therefore the offspring of phenotypically exceptional parents are generally not themselves as exceptional. From standard regression theory (LW Chapter 3), the predicting breeding value $\widehat{A}$ for an individual with phenotypic value z is

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

This since the regression $y = a + bx$ can be expressed as $y - \mu_y = b(x - \mu_x)$, where $b = \sigma(x, y)/\sigma_x^2$. For the regression of A and z, these means are $\mu_A = 0$ and μ_z, while the slope is $\sigma(z, A)/\sigma_z^2 = \sigma_A^2/\sigma_z^2 = h^2$, which follows since

$$\sigma(z, A) = \sigma(G + E, A) = \sigma(A + D + E, A) = \sigma(A, A) = \sigma_A^2.$$

The expected breeding value for a set of selected parents becomes

$$E_s[\widehat{A}] = E_s[h^2(z - \mu_z)] = h^2 E_s[z - \mu_z] = h^2 S$$

where E_s denotes the average value over the selected parents. The change in the mean value of their offspring (relative to the base population) is just the mean parental breeding value,

since (by definition) μ_A in the base population is zero. Thus response equals $h^2 S$ and we recover the breeder's equation. Note that a key assumption made here was that $E_s[h^2] = h^2$, namely that the regression using the selected parents is the same as the regression before selection. Chapter 6 extensively discussed this assumption.

Response Under Sex-Dependent Parent-Offspring Regressions

It is not uncommon for a trait to show different variances between the sexes and/or to have a less than perfect correlation across the sexes. In such cases, the regression coefficients for parent-offspring regressions can vary with the sex of both parents and offspring. 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 straightforward when the biparental regression is linear, i.e.,

$$E(z_o \,|\, z_{fa}, z_{mo}) = \mu_o + b_{o,fa} (z_{fa} - \mu_{fa}) + b_{o,mo} (z_{mo} - \mu_{mo}) \tag{13.2}$$

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

$$\begin{aligned} E_s\big[\, E(z_o \,|\, z_{fa}, z_{mo})\,\big] &= \mu_o + b_{o,fa}\, E_s\big[\,(z_{fa} - \mu_{fa})\,\big] + b_{o,mo}\, E_s\big[\,(z_{mo} - \mu_{mo})\,\big] \\ &= \mu_o + b_{o,fa}\, S_{fa} + b_{o,mo}\, S_{mo} \end{aligned} \tag{13.3}$$

where S_{fa} and S_{mo} are the father and mother directional selection differentials.

Equations 13.2 and 13.3 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 13.3,

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

implying

$$R_{da} = b_{da,fa}\, S_{fa} + b_{da,mo}\, S_{mo} \tag{13.4a}$$

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

$$R_{so} = b_{so,fa}\, S_{fa} + b_{so,mo}\, S_{mo} \tag{13.4b}$$

Example 13.1. 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. Gimelfard and Willis (1994) give other *Drosophila* examples where the regressions differ significantly between sons and daughters. Suppose that different amounts of selection are applied to fathers and mothers, with selected fathers showing an increase of two bristles, while selected mothers show a decrease of one. 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 13.4a, the expected change in bristle number in females becomes

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

Likewise, from Equation 13.4b, the expected change in males is

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

This expected response of a decrease in males and an increase in females is the exact opposite of the pattern of selection on the sexes.

Equation 13.4 requires 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

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

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, $S = (S_{fa} + S_{mo})/2$, again recovers the breeder's equation

$$R = \frac{h^2}{2}\, S_{fa} + \frac{h^2}{2}\, S_{mo} = h^2\, S \tag{13.5}$$

Equation 13.5 shows how differential selection on parents is incorporated into the breeder's equation. For example, consider selection on dioecious plants. If plants that form the next generation are chosen *after* pollination, fathers (pollen donors) are chosen at random with respect to the character under selection ($S_{fa} = 0$), giving $R = (h^2/2)S_{mo}$. If parents are selected before pollination with equal amounts of selection (S) on both sexes, $R = h^2 S$.

The Selection Intensity, $\overline{\imath}$

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, the selection differentials for these two populations are $S_1 = 2.06\,\sigma_1$ and $S_2 = 1.27\,\sigma_2$, where σ_k^2 is the character variance in population k (Equation 14.3a).

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 selection differential** (or **selection intensity**), which is the selection differential expressed in phenotypic standard deviations,

$$\bar{\imath} = S/\sigma_z \tag{13.6a}$$

The selection intensity accounts for differences in the phenotypic variances, akin to the correlation being a better measure of the strength of association than is the covariance (LW Chapter 3). Substituting $\bar{\imath}\,\sigma_z$ for S gives the selection intensity version of the breeder's equation,

$$R = h^2\,\bar{\imath}\,\sigma_z = \bar{\imath}\,h\,\sigma_A \tag{13.6b}$$

which follows since

$$h^2\sigma_z = \frac{\sigma_A^2}{\sigma_z^2}\sigma_z = \frac{\sigma_A}{\sigma_z}\sigma_A = h\,\sigma_A.$$

Equation 13.6b will prove to be a useful starting point for generalizations (developed below) of the breeder's equation to accommodate more general types of selection.

An equally important advantage of the selection intensity is that the fraction saved p under truncation selection completely determines $\bar{\imath}$ (Equation 14.3a), allowing us to predict the response in future generations without having to know S.

The Robertson-Price Identity, $S = \sigma(w, z)$

As introduced in Chapter 6, the selection differential can also be written as the covariance between relative fitness and trait value,

$$S = \sigma(w, z) \tag{13.7}$$

This is the Robertson-Price identity, first noted by Robertson (1966) and later elaborated on by Price (1970, 1972). Chapter 6 showed how this directly follows from Price's theorem. For an alternative derivation, let z_i, p_i, and w_i be the trait value, frequency before selection, and relative fitness (respectively) of class i. The selection differential is simply the mean after selection minus the mean before,

$$S = \mu_s - \mu = \sum z_i\,w_i\,p_i - \sum z_i\,p_i = E[\,z\,w\,] - E[\,z\,].$$

Since $E[\,w\,] = 1$, we can write this as

$$S = E[\,z\,w\,] - E[\,z\,]\,E[\,w\,] = \sigma(w, z)$$

recovering the Robertson-Price identity.

This identity plays an important role in evolutionary quantitative genetics. Consider the slope of the least-squares linear regression of relative fitness w on phenotypic value z,

$$w = 1 + \beta z + e \tag{13.8a}$$

The interpretation of the slope is that a one unit change in z results in change of β in the relative fitness. From the theory of least-squares regression (LW Chapter 3),

$$\beta = \frac{\sigma(z, w)}{\sigma_z^2} = \frac{S}{\sigma_z^2} \tag{13.8b}$$

Substituting $S = \sigma_z^2 \beta$ into Equation 13.1 gives

$$R = \sigma_A^2 \beta \tag{13.8c}$$

which relates the strength of association β between trait value and fitness with the response.

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 trait 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, differential fertility can be accounted for by using the **effective selection differential**, S_e,

$$S_e = \frac{1}{n_p} \sum_{i=1}^{n_p} \left(\frac{n_i}{\overline{n}} \right) (z_i - \mu_z) \tag{13.9}$$

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

Example 13.2.   Consider a trait with heritability 0.3 and before selection mean 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 $R = 0.3 \cdot 7 = 2.1$. Is the predicted response altered when differential fertility is taken into account? Computing the effective selective differential by weighting the selected parents proportional to the number of offspring they leave gives

i	z_i	n_i	$n_i/\overline{n}$
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

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

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 an overestimation of the expected response.

The derivation of Equation 13.9 follows directly from the Robertson-Price identity. If a total of n individuals are examined, n_p of which are selected as parents, then

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

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

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

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

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

Rearranging recovers Equation 13.9. A number of additional metrics of individual fitness are discussed in Chapter 28.

EXPANDING THE BASIC BREEDER'S EQUATION

Accuracy

The breeder's equation can be extended to the much more general setting of 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 gives

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

implying an expected change in y from selection on x as

$$R_y = \mu_y^{**} - \mu_y = \frac{\sigma(x,y)}{\sigma_x^2}\,(\mu_x^* - \mu_x) = \frac{\sigma(x,y)}{\sigma_x^2}\,S_x = \frac{\sigma(x,y)}{\sigma_x}\,\overline{\imath}_x \tag{13.10}$$

where μ^* and μ^{**} denote the mean following selection within- and between-generations.

Example 13.3.   Consider selection on clones or other pure lines, where 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

$$\sigma(z_o, z_p) = \sigma(G_o + E_o, G_p + E_p) = \sigma(G_o, G_p) = \sigma(G, G)$$

namely 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 20), 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. However, when selection continues for several generations, using clones is expected to be less effective, as selection among clones very rapidly removes genetic variation from the population without any mechanism (other than mutation) to regenerate it. 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. Selection and development of pure lines is examined in Chapter 30.

The selection intensity version of Equation 13.10 can alternately be expressed as

$$R_y = \frac{\sigma_{x,y}}{\sigma_x} \, \bar{\imath}_x = \frac{\sigma_{x,y}}{\sigma_x \, \sigma_y} \, \bar{\imath}_x \, \sigma_y = \bar{\imath}_x \, \sigma_y \, \rho(x, y) \tag{13.11a}$$

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 13.11a in terms of the **relative response**, the change in y in phenotypic standard deviations, gives

$$\frac{R_y}{\sigma_y} = \bar{\imath}_x \, \rho(x, y) \tag{13.11b}$$

Equation 13.11b allows one to compare the relative efficiencies of different selection schemes. Fixing the selection intensity $\bar{\imath}$, 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 selection schemes (x_1 versus x_2) is given by $\rho(x_1, y)/\rho(x_2, y)$, assuming $\bar{\imath}_{x_1} = \bar{\imath}_{x_2}$. Typically y is taken as the breeding value A of our focal trait, so that R_y is the change in breeding value for trait y from selection on x, giving

$$R_A = \bar{\imath}_x \, \rho(x, A) \, \sigma_A \tag{13.11c}$$

Hence, the breeder's equation can be considered as a special case of the more general product:

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

The accuracy of mass selection (estimating an individual's breeding value A using only their phenotypic value z) is

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

which recovers Equation 13.6b. When evaluating alternative selection schemes, h is replaced by the appropriate correlation between the breeding value A of an individual and its measure x used for selection. For example, x could be the family mean of the trait 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 (Chapter 21). Assuming $\bar{\imath}$ 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**, where individuals are choosen based on some index $x = \sum a_i z_i$, a linear combination of several traits in the focal individual and/or trait values in its relatives.

Example 13.4. **Progeny testing** uses the mean of an individual's offspring to predict their breeding value. As we show at the end of the example, for half-sibs, the correlation between the mean $x = \overline{z}$ of n offspring and the breeding value A of the common parent is

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

For large n, the accuracy approaches one. From Equation 13.11c, the resulting response to selection is

$$R = \overline{\imath}\,\rho(\overline{z}, A)\,\sigma_A = \overline{\imath}\sigma_A\sqrt{\frac{n}{n + a}} = \overline{\imath}\sigma_A\sqrt{\frac{h^2 n}{4 + h^2(n - 1)}}$$

The ratio of response for progeny testing (R_{pt}) to mass selection (R_{ms}) becomes

$$\frac{R_{pt}}{R_{ms}} = \frac{\overline{\imath}_{pt}\,\rho(\overline{z}, A)\,\sigma_A}{\overline{\imath}_{ms}\,\rho(z, A)\,\sigma_A} = \left(\frac{\overline{\imath}_{pt}}{\overline{\imath}_{ms}}\right)\frac{1}{h}\sqrt{\frac{h^2 n}{4 + h^2(n - 1)}}$$

$$= \left(\frac{\overline{\imath}_{pt}}{\overline{\imath}_{ms}}\right)\sqrt{\frac{n}{4 + h^2(n - 1)}}$$

The selection intensity under progeny testing is likely to be lower, as it is easier (and cheaper) to score a phenotype than to progeny test. When the intensities are equal, the ratio of response approaches $1/h$ for large n. Progeny testing gives a larger response when $\rho(\overline{z}, A) > \rho(z, A)$, or

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

In particular, $n > 4$, 5, and 7, for $h^2 = 0.1$, 0.25, and 0.5. Finally, the accuracy is obtained as follows. Since the covariance between parent and offspring is $\sigma_A^2/2$,

$$\sigma(\overline{z}, A) = \sigma\left(\frac{1}{n}\sum_{i}^{n} z_i, A\right) = \frac{1}{n}n\sigma(z_i, A) = \sigma_A^2/2$$

The expression for $\sigma^2(\overline{z})$ requires a bit more bookkeeping, as sibs are correlated. Assuming half-sibs and no shared environmental effects, $\sigma(z_i, z_j) = \sigma_A^2/4$ (for $i \neq j$), giving

$$\sigma^2(\overline{z}) = \sigma\left(\frac{1}{n}\sum_{i}^{n} z_i, \frac{1}{n}\sum_{j}^{n} z_j\right) = \frac{1}{n^2}n\sigma(z_i, z_i) + \frac{n(n - 1)}{n^2}\sigma(z_i, z_j)$$

$$= \frac{\sigma_z^2}{n} + \left(1 - \frac{1}{n}\right)\frac{\sigma_A^2}{4} = \frac{\sigma_z^2}{4n}\left(4 + (n - 1)h^2\right)$$

Since $\rho(\overline{z}, A) = \sigma(\overline{z}, A)/\sigma_A\sigma(\overline{z})$, substituting the above results yields

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

where $a = (4 - h^2)/h^2$.

Example 13.5.   Suppose the trait of interest is extremely hard to measure in live individuals (such as meat quality). How can we select on individuals if we have to kill them to measure the trait? Likewise, consider traits expressed in only one sex, such as milk production. How can we select on males if they do not express the trait themselves? One solution to both these problems is **sib selection** (Chapter 21), using sibs of exceptional individuals as the parents forming the next generation. For example, choose brothers based on the milk production of their sisters. Here the selection unit x is the phenotype of a sib, with the correlation between the phenotypic value P_{s1} of one sib and the breeding value A_{s2} of another being

$$\sigma(P_{s1}, A_{s2}) = \begin{cases} \sigma_A^2/2 & \text{for full sibs} \\ \sigma_A^2/4 & \text{for half-sibs} \end{cases}, \quad \text{hence,} \quad \rho(x, A) = \begin{cases} h^2/2 & \text{for full sibs} \\ h^2/4 & \text{for half-sibs} \end{cases}$$

The resulting response to selecting based on the performance of a sib is

$$R = \begin{cases} \bar{\imath}\,(h/2)\,\sigma_A & \text{for full sibs} \\ \bar{\imath}\,(h/4)\,\sigma_A & \text{for half-sibs} \end{cases}$$

Using full sibs gives a response half that of mass selection, while using half-sibs gives only a quarter of the response. In the case of milk production, which is a mixture of individual and sib selection, the expected response is

$$R = (1/2)\,\bar{\imath}\,h\,\sigma_A + (1/2)\,\bar{\imath}\,(h/2)\,\sigma_A = (3/4)\,\bar{\imath}\,h\,\sigma_A$$

where the first term is the response from using superior daughters (individual selection) and the second term the response using the brothers of superior sisters (sib selection). This equation is trivial to modify to allow for different selection intensities in the two sexes. An alternative way to consider the total response is that $\bar{\imath}\,h\,\sigma_A$ is the change in breeding values in the selected mothers and $\bar{\imath}\,(h/2)\,\sigma_A$ the change in breeding values of the fathers, with the change in the offspring mean (the response) just the average of these breeding value changes in both sexes of parents.

Reducing Environmental Noise: Stratified Mass Selection

Accuracy (and hence response) can also be increased by using designs that reduce environmental noise. One approach is Gardner's (1961) method of **stratified mass selection**: a population is stratified into a number of blocks (potentially representing different microenvironments) and selection occurs *within* each block. The motivation behind Gardner's method was to improve individual selection for yield in maize. At the time of his 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 presumably similar environments, Gardner was able to use mass selection to obtain fairly significant gains (about 4% per year).

To obtain the expected response under stratified mass selection, we need to compute the accuracy, which first requires the covariance between within-block deviations and an individual's breeding value. Suppose n individuals are measured within each block, and selection occurs on the deviation from the block mean, e.g., on $z_{ij} - \overline{z}_i$ where z_{ij} is the jth individual from block i and $\overline{z}_i$ 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_i and the residual environmental value e_{ij},

$$z_{ij} = \mu + G_{ij} + bl_i + e_{ij} \tag{13.12a}$$

The total environmental variance equals the variance between blocks σ^2_{bl} plus the within-block variance σ^2_{Wbl} (the variance of the residuals e_{ij}), giving the total variance as

$$\sigma^2_z = \sigma^2_G + \sigma^2_E = \sigma^2_G + \sigma^2_{bl} + \sigma^2_{Wbl} \tag{13.12b}$$

For the jth individual in block i, the covariance between their breeding value and within-block deviation is

$$\sigma(z_{ij} - \overline{z}_i, A_{ij}) = \sigma(z_{ij}, A_{ij}) - \frac{1}{n}\sum_{k=1}^{n} \sigma(z_{ik}, A_{ij}) = \sigma^2_A\left(1 - \frac{1}{n}\right) \simeq \sigma^2_A, \tag{13.13}$$

as the assumption is that individuals within blocks are unrelated and that a large number of individuals are scored within each block. The variance of deviations within a block is $\sigma^2_G + \sigma^2_{Wbl}$, giving the accuracy as

$$\rho(z_{ij} - \overline{z}_i, A_{ij}) = \frac{\sigma^2_A(1 - 1/n)}{\sigma_A\sqrt{\sigma^2_G + \sigma^2_{Wbl}}} = \frac{\sigma_A(1 - 1/n)}{\sqrt{\sigma^2_G + \sigma^2_{Wbl}}}. \tag{13.14a}$$

Applying Equation 13.11c gives the resulting response as

$$R = \overline{\imath}\,\rho(z_{ij} - \overline{z}_i, A_{ij})\,\sigma_A = \frac{\overline{\imath}\,\sigma^2_A(1 - 1/n)}{\sqrt{\sigma^2_G + \sigma^2_{Wbl}}} \simeq \frac{\overline{\imath}\,\sigma^2_A}{\sqrt{\sigma^2_G + \sigma^2_{Wbl}}} \tag{13.14b}$$

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

$$R = \frac{\overline{\imath}\,\sigma^2_A}{\sqrt{\sigma^2_G + \sigma^2_{bl} + \sigma^2_{Wbl}}} \tag{13.14c}$$

The relative efficiency of stratification (assuming the block size is modest to large so that $1 - 1/n \simeq 1$) is

$$\sqrt{\frac{\sigma^2_G + \sigma^2_{bl} + \sigma^2_{Wbl}}{\sigma^2_G + \sigma^2_{Wbl}}} = \sqrt{1 + \frac{\sigma^2_{bl}}{\sigma^2_G + \sigma^2_{Wbl}}} \tag{13.15}$$

The response can be significantly improved by taking blocks into consideration when the between-block variance accounts for a significant fraction of the total variation. Finally, it is worth noting that we are ignoring $G \times E$, in that blocks are assumed to represent a random collection of environments all equally relevant to commercial production. More generally, when examined over a set of larger macroenvironments, methods accounting for $G \times E$ must be employed (Volume 3).

Reducing Environmental Noise: Repeated-Measures Selection

The **repeated-measures** design is a second example of increasing accuracy (and response) by providing some control over environmental noise. Here the character of interest is measured n different times for each individual, and selection occurs on $\overline{z}_i$, the mean value for individual i. For example, one could use the mean value of three litters (as opposed

to simply using the first litter). This is an especially common design in behavioral experiments, wherein a single measure (such as wheel-running speed) may vary greatly within an individual over time.

The model here depends on the *repeatability* (LW Chapter 6) of the character. Decompose the character value for the jth measure of individual i as

$$z_{ij} = G_i + E_i + e_{ij} \tag{13.16a}$$

where G_i and E_i are the genotypic and (permanent) environmental values common to all measures of i, and e_{ij} is the special environmental value restricted to the jth measure of i. The repeatability r is defined as

$$r = \frac{\sigma_G^2 + \sigma_E^2}{\sigma_z^2} = 1 - \frac{\sigma_e^2}{\sigma_z^2} \tag{13.16b}$$

Note that

$$r\sigma_z^2 = \sigma_G^2 + \sigma_E^2 \quad \text{and} \quad (1-r)\sigma_z^2 = \sigma_e^2 \tag{13.16c}$$

To obtain the accuracy in using $\overline{z}_i$ to predict A_i, we need both their covariance and the variance of $\overline{z}_i$. The former is just

$$\sigma(A_i, \overline{z}_i) = \sigma\left(A_i, \frac{1}{n}\sum_{j=1}^{n} z_{ij}\right) = \frac{1}{n}\sum_{j=1}^{n}\sigma(A_i, z_{ij}) = \frac{1}{n}\, n\, \sigma(A_i, A_i) = \sigma_A^2 \tag{13.17a}$$

To obtain the variance of $\overline{z}_i$, since

$$\overline{z}_i = \frac{1}{n}\sum_{j=1}^{n} z_{ij} = G_i + E_i + \frac{1}{n}\sum_{j=1}^{n} e_{ij}, \tag{13.17b}$$

it immediately follows from Equation 13.16c that

$$\sigma^2\left(\overline{z}_i\right) = \sigma_G^2 + \sigma_E^2 + \sigma_e^2/n$$
$$= \sigma_z^2 r + \sigma_z^2\frac{1-r}{n} = \sigma_z^2\left(\frac{1+(n-1)r}{n}\right) \tag{13.17c}$$

The resulting accuracy in using $\overline{z}_i$ to predict A_i becomes

$$\rho(\overline{z}_i, A_i) = \frac{\sigma(A_i, \overline{z}_i)}{\sigma_A\,\sigma(\overline{z}_i)} = \frac{\sigma_A^2}{\sigma_A\sqrt{\sigma_z^2\left(\frac{1+(n-1)r}{n}\right)}} = h\sqrt{\frac{n}{1+(n-1)r}}, \tag{13.18a}$$

giving the response as

$$R = \overline{\imath}\,\rho(\overline{z}_i, A_i)\,\sigma_A = \overline{\imath}\,h\sqrt{\frac{n}{1+(n-1)r}}\,\sigma_A. \tag{13.18b}$$

The ratio of accuracies under repeated-measures vs. mass selection becomes

$$\frac{\rho(\overline{z}_i, A)}{\rho(z, A)} = \sqrt{\frac{n}{1+(n-1)r}}, \tag{13.19}$$

which approaches $1/\sqrt{r}$ for large n. Hence, when repeatability is low ($\sigma_e^2 > \sigma_G^2 + \sigma_E^2$), repeated-measured selection can result in a considerable improvement in response. As with previous examples, one might imagine a lower selection intensity under this design (due to the cost and time of additional measures), but this is easily incorporated into comparisons of different selection strategies.

Example 13.6.   As an example of the consequences of basing selection decisions on single versus multiple measurements, consider the following data set, simulated by assuming a character with $h^2 = 0.1$, $\sigma_z^2 = 100$, $\mu = 50$, and $r = 0.2$. The simulated values for twenty individuals for either an initial measurement $z(1)$ or the average of five measurements $z(5)$ are

i	$z(1)$	$z(5)$	i	$z(1)$	$z(5)$
1	54.97	56.80	11	49.81	48.76
2	64.01	54.51	12	51.92	46.76
3	42.64	52.61	13	43.56	51.79
4	42.70	38.69	14	41.60	47.23
5	61.62	56.42	15	51.80	48.90
6	39.86	47.70	16	52.88	47.21
7	56.54	48.63	17	63.86	54.03
8	35.88	47.26	18	39.76	49.62
9	54.32	53.93	19	36.45	47.78
10	57.85	45.10	20	59.07	51.16

Suppose the uppermost 25 percent (top 5 of the 20) are chosen for selection. Based on the initial measure, individuals 2, 5, 10, 17, and 20 would be chosen, while based on five measures, individuals 1, 2, 5, 9, and 17 would be selected. Using a single (initial) measurement, the overall mean is 50.05, while the mean of selected individuals is 61.28, giving an S of 11.23. Using repeated-measures selection, the overall mean is 49.74, while the mean of selected individuals is 55.14, for an S of 5.39. The smaller value of S under repeated measures under the same selection intensity is a simple consequence of the reduced variance associated with using the mean (repeated measures) versus a single observation. From the breeder's equation, the expected response based on single measures is

$$R = h^2 S = 0.1 \cdot 11.23 = 1.12$$

To express the response given by Equation 13.18b in terms of S, note that here $\rho = \sigma_A^2/(\sigma_A \sigma_{\overline{z}}) = \sigma_A/\sigma_{\overline{z}}$, hence $\overline{\imath} \rho \sigma_A = \overline{\imath} \sigma_A^2/\sigma_{\overline{z}} = (\overline{\imath} \sigma_{\overline{z}}) \sigma_A^2/\sigma_{\overline{z}}^2 = S\sigma_A^2/\sigma_{\overline{z}}^2$, or

$$R = h^2 \left(\frac{n}{1 + (n-1)r} \right) S = 0.1 \cdot 2.78 \cdot 5.39 = 1.50$$

Thus, the reduction in S under repeated measures is more than made up for by increased accuracy, yielding a larger expected response relative to mass-selection. From Equation 13.19, the ratio of the accuracies of the five-measure to single-measure schemes is 1.67, which approaches $1/\sqrt{r} \simeq 2.24$ for large n.

Our analysis of repeated-measures selection assumes that the genetic correlation across individual measurements is one, which is expected for many traits. However, if measures are sufficiently separated in time that age effects are important, or of they represent significantly distinct events (such as litter size at different **parities**, i.e., distinct litters), these correlations

can be less than one and/or heteroscedasticity in the residuals can occur. In such cases, one should treat these measurements as a set of correlated traits and use index selection theory (Volume 3).

Adjustments for Non-overlapping Generations

So far, we have been assuming non-overlapping generations — all parents reproduce in a discrete single generation. Domesticated animals, perennial plants, and many species in nature live, and thus can have offspring over, multiple years. In such cases, generations overlap and the response should be considered in terms of response per unit time (typically years), rather than per generation. To express the breeder's equation in terms of *rate of response*, we first need to compute the **generation intervals** L_x (the average age of parents when progeny are born) for both sexes.

Example 13.7.   Compute the sire L_s and dam L_d generation intervals for the following age structure:

Age at Birth of Progeny

Sires	year 2	year 3	year 4	year 5	Total
Number	60	30	0	0	90

Dams	year 2	year 3	year 4	year 5	Total
Number	400	600	100	40	1140

The resulting sire generation interval is the average age of sires when offspring are born. Here, 2/3 (60/90) of the sires are age two, while 1/3 (30/90) are age three, giving

$$L_s = 2 \cdot \frac{60}{90} + 3 \cdot \frac{30}{90} = \frac{2 \cdot 60 + 3 \cdot 30}{90} = 2.33,$$

Similarly, the dam generation interval is

$$L_d = \frac{2 \cdot 400 + 3 \cdot 600 + 4 \cdot 100 + 5 \cdot 40}{1140} = 2.81.$$

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

$$R_y = \left(\frac{\bar{\imath}_s + \bar{\imath}_d}{L_s + L_d} \right) h^2 \sigma_z = \left(\frac{\bar{\imath}_s + \bar{\imath}_d}{L_s + L_d} \right) h \sigma_A \qquad (13.20)$$

This result (in a slightly different form) is due to Rendel and Robertson (1950), although the basic idea traces to Dickerson and Hazel (1944). Thus, one way to increase the rate of 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 decreases as more parents are chosen) is reduced. Equation 13.20 is an *asymptotic result*, as it takes time for response to propagate through an age-structured population. Our final volume examines the effects of age structure on selection response in greater detail.

Maximizing Response Under the Breeder's Equation

We can combine both the selection accuracy (Equations 13.11c) and generation interval (Equation 13.20) versions to give a more general expression, with the expected rate of response as

$$R = \left(\frac{\bar{\imath}_s + \bar{\imath}_d}{L_s + L_d} \right) \rho(A, x)\, \sigma_A, \tag{13.21}$$

where x is the measure used to choose the parents to form the next generation. Beyond importing new genetic material, there is not much a breeder can do to increase σ_A^2, leaving three components of response that the breeder has some control over (Dickerson and Hazel 1944):

(i) selection intensity, $\bar{\imath}$

(ii) generation interval, L

(iii) selection accuracy, ρ

Response is increased by decreasing L and/or increasing ρ and $\bar{\imath}$. We have already discussed tradeoffs between L and $\bar{\imath}$, and there are similar tradeoffs between L and ρ. Clearly, the longer we wait to allow a parent to reproduce, the more accurately 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. An optimal selection program must balance all of these competing interests.

Example 13.8.   As an example of the tradeoff between accuracy and generation intervals, consider a trait with $h^2 = 0.25$ and selection on only sires (fathers). One scheme is to simply select on the sire's phenotype, which results in a sire generation interval of (say) 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 (mothers) interval is constant at 1.5 years.

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

$$\frac{R(\text{Sire phenotype})}{R(\text{progeny mean})} = \left(\frac{\bar{\imath}_{pt}}{\bar{\imath}_{sp}} \right) \frac{\rho(A, \text{Sire phenotype})/(L_s + L_d)}{\rho(A, \text{progeny mean})/(L_s + L_d)}$$

Here, $\rho(A, \text{Sire phenotype}) = h = \sqrt{0.25} = 0.5$, with generation intervals $L_s + L_d = 1.5 + 1.5 = 3$. With progeny testing, Example 13.4 gave

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

as $a = (4 - h^2)/h^2 = 15$, with a total generation interval of $L_s + L_d = 2.5 + 1.5 = 4$. Hence,

$$\frac{R(\text{Sire phenotype})}{R(\text{progeny mean})} \left(\frac{\bar{\imath}_{sp}}{\bar{\imath}_{pt}} \right) = \frac{0.5/3.0}{\sqrt{\frac{n}{n+15}}/4} = \frac{2}{3} \cdot \sqrt{\frac{n + 15}{n}}$$

For $n = 2$ progeny tested per sire, this ratio is 1.95, giving a much larger rate of response under sire-only selection. For $n = 12$, 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. Thus if $\bar{\imath}_{pt} < 1.5 \cdot \bar{\imath}_{sp}$, mass selection is always better.

Equation 13.21 highlights the importance to animal breeding of advances in reproductive technologies such as **artificial insemination (AI)** and **multiple ovulation embryo transplant (MOET)** schemes (e.g., Woolliams 1989). The more offspring a parent can produce, the stronger the selection intensity that can be applied while still keeping a fixed number of animals in a population. AI has resulted in the potential for far greater sire 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 allow for increases in the selection intensity on dams as well as decreases in the generation interval.

Maximizing the Economic Rate of Response

Example 13.8 hints at another important feature of response – economics. Notice that by scoring more than 12 offspring we can obtain a larger expected rate of response using progeny testing (assuming equal selection intensities). Why not simply score 30 progeny, giving a 122% rate of response relative to simple mass selection? The reason is economics – it costs money to raise all of those progeny! Much of applied breeding is concerned with the *economic* rate of response – trying to maximize the rate of response per unit capital, although this point is often under-appreciated, even by some breeders. Besides improvement in quality and quantity, much selection in animal breeding is for increased efficiency (conversion of resources into desirable traits), and hence greater economic gain at the production level. Weller (1994) presents a nice development of how to incorporate economics into animal breeding.

BLUP Selection

LW Chapter 26 introduced the basic **mixed model** for estimating a vector **a** of breeding values for a set of individuals given some vector **y** of *records* (observations), a relationship matrix **A** connecting individuals with records with individuals whose breeding values are of interest, and a set $\boldsymbol{\beta}$ of fixed effects to estimate,

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{a} + \mathbf{e}, \quad \mathbf{a} \sim MVN(\mathbf{0}, \sigma_A^2 \cdot \mathbf{A}), \quad \mathbf{e} \sim MVN(\mathbf{0}, \sigma_e^2 \cdot \mathbf{I})$$

where the matrices **X** and **Z** are given from the data. Solving the model returns a vector $\widehat{\mathbf{a}}$ of BLUP (best linear unbiased prediction) estimates of the breeding values. Much of modern animal breeding (and some of plant breeding) is based on using these estimates to select those individuals with the highest breeding values for the trait to form the next generation. This is called **BLUP selection**. The expected response is simply given from the difference between the mean breeding value of selected parents and the population from which they were chosen. This is an *extremely* flexible methodology, with all of the above examples being special cases of this general approach. Information for all measured relatives enters through **A**, and multiple records (repeated measurements) from the same individual are easily incorporated, as are additional fixed (and random) effects such as plot, location, or herd effects. Further, the effects of age structure are fully accounted for by the relationship matrix **A**. Chapters 19, 20, and 22 discuss features of BLUP estimation of breeding values, while more technical details (such as maximal avoidance of inbreeding) are deferred until Volume 3.

Mean- Versus Variance-Standardized Response

As was the case with the selection differential S, in order to assess the relative strength of response one needs some sort of standardization. One obvious approach is to express the response in units of phenotypic standard deviations (**variance-standardization**). From Equation 13.6b,

$$\frac{R}{\sigma_z} = h^2\,\bar{\imath} \tag{13.22a}$$

implying that a (scaled) strength of selection $\bar{\imath} = 1/h^2$ is required for a standard deviation of response. If $h^2 = 0.25$, a total selection intensity of $\bar{\imath} = 4$ (roughly back-to-back generations of 5% truncation selection) is required to achieve a total response of one phenotypic standard deviation.

While scaling traits in units of phenotypic standard deviations is extremely common, it can also be rather misleading (Houle 1992, Houle et al. 2011). To see this, imagine two traits, both with a standard deviation of two. Trait one has a mean of 10 and trait two a mean of 100. A response of one standard deviation increases trait one by twenty percent, but trait two by only two percent. From a variance-standardized viewpoint, the response is equal, but as a proportional response of the total mean, trait one has clearly experienced a stronger response.

Houle and colleagues (Houle 1992, Hansen et al 2003, Hansen et al. 2011, Houle et al. 2011) argued that **mean-standardization**, R/μ_z, namely the *proportional amount* of response, is often a more appropriate standardized measure. Again using Equation 13.6b,

$$\frac{R}{\mu_z} = \bar{\imath}\,h\,\frac{\sigma_A}{\mu_z} = \bar{\imath}\,h\,CV_A \tag{13.22b}$$

where $CV_A = \sigma_A/\mu_z$, the coefficient of additive genetic variation, is Houle's (1992) initial **evolvability** measure, which he argued was a better measure than h^2 of evolutionary potential. Houle (1992) and Hansen et al. (2011) found that h^2 is essentially uncorrelated with evolvability, so that a trait with a lower h^2 could still have high evolvability (the potential for a significant proportional change in the mean), and vice-versa.

Hansen et al. (2003) and Hansen et al. (2011) later suggested that its square, $I_A = (CV_A)^2 = \sigma_A^2/\mu_z^2$, is a more natural measure of evolvability. To see this, consider the Lande equation $R = \sigma_A^2\beta$ (Equation 13.8c), and let $\beta_u = \beta/\mu_z$ be the mean-standardized gradient. The resulting proportional change in the trait is given by

$$\frac{R}{\mu_z} = \frac{\sigma_A^2}{\mu_z}\beta = \left(\frac{\sigma_A^2}{\mu_z^2}\right)\beta_u = I_A\beta_u \tag{13.22c}$$

showing that I_A is the fractional change in the trait given a unit amount of selection ($\beta_u = 1$). For example, if $I_A = 0.03$, then one unit of selection results in a 3% change in the mean trait value. One suggested complication with using evolvability measures is that CV_A and I_A change with the current mean, so that if σ_A^2 remains roughly constant, the evolvability decreases as the trait mean increases, even if the heritability remains unchanged. This concern is entirely a consequence of scaling. Evolvability is a measure of the potential for a proportional increase, and as the mean increases, a larger absolute change is required for the same proportional increase.

THE MULTIVARIATE BREEDER'S EQUATION

Expressing the heritability in terms of additive genetic and phenotypic variances, the breeder's equation can be written as

$$R = \sigma_A^2\,\sigma_z^{-2}\,S \tag{13.23a}$$

While this decomposition seems rather trivial, it suggests (as we formally show in Volume 3) that its multivariate version (under appropriate linearity assumptions) is given by

$$\mathbf{R} = \mathbf{GP}^{-1}\mathbf{S}, \tag{13.23b}$$

where $\mathbf{R}$ and $\mathbf{S}$ are the vectors of responses and selection differentials for each character, while $\mathbf{G}$ and $\mathbf{P}$ are the additive genetic and phenotypic covariance matrices (LW Chapter 21), with

$$P_{ij} = \sigma(z_i, z_j), \qquad \text{and} \qquad G_{ij} = \sigma(A_i, A_j) \tag{13.23c}$$

Here we be briefly consider just a few features of Equation 13.23b, examing its consequences, and applications, at length in Volume 3.

Response With Two Traits

One expectsthat selection is always acting on multiple traits, as even with strong artificial selection on a single character, natural selection is likely operating on other traits as well. What risks do we run by ignoring this and treating selection as a univariate problem? While this is examined much more fully in Chapters 34 - 38, we can gain significant insight by considering the simple case of two traits, both potentially under selection. Equation 13.23b gives the expected vector of responses as

$$\mathbf{R} = \begin{pmatrix} R_1 \\ R_2 \end{pmatrix} = \mathbf{GP}^{-1}\mathbf{S} = \begin{pmatrix} G_{11} & G_{12} \\ G_{12} & G_{22} \end{pmatrix} \begin{pmatrix} P_{11} & P_{12} \\ P_{12} & P_{22} \end{pmatrix}^{-1} \begin{pmatrix} S_1 \\ S_2 \end{pmatrix} \tag{13.24a}$$

From LW Equation 8.11 and recalling for a covariance that $P_{12} = \rho_z\sqrt{P_{11}P_{22}}$, where ρ_z is the phenotypic correlation between the two traits, we have

$$\begin{aligned} \mathbf{P}^{-1}\mathbf{S} &= \frac{1}{P_{11}P_{22} - P_{12}^2} \begin{pmatrix} P_{22} & -P_{12} \\ -P_{12} & P_{11} \end{pmatrix} \begin{pmatrix} S_1 \\ S_2 \end{pmatrix} \\ &= \frac{1}{P_{11}P_{22}(1 - \rho_z^2)} \begin{pmatrix} S_1P_{22} - S_2P_{12} \\ -S_1P_{12} + S_2P_{11} \end{pmatrix} \end{aligned} \tag{13.24b}$$

Substituting into Equation 13.24a and recalling that $h_i^2 = G_{ii}/P_{ii}$, the response in trait 1 becomes

$$\begin{aligned} R_1 &= \frac{1}{P_{11}P_{22}(1 - \rho_z^2)} \begin{pmatrix} G_{11} & G_{12} \end{pmatrix} \begin{pmatrix} S_1P_{22} - S_2P_{12} \\ -S_1P_{12} + S_2P_{11} \end{pmatrix} \\ &= \frac{G_{11}(S_1P_{22} - S_2P_{12}) + G_{12}(-S_1P_{12} + S_2P_{11})}{P_{11}P_{22}(1 - \rho_z^2)} \\ &= \frac{h_1^2 S_1}{(1 - \rho_z^2)} - S_2\frac{G_{11}P_{12}}{P_{11}P_{22}(1 - \rho_z^2)} + \frac{G_{12}(-S_1P_{12} + S_2P_{11})}{P_{11}P_{22}(1 - \rho_z^2)} \end{aligned} \tag{13.24c}$$

with an analogous expression for R_2. The breeder's equation is recovered only when trait one is phenotypically ($P_{12} = \rho_z = 0$) *and* genetically ($G_{12} = 0$) uncorrelated with trait two. This complicated expression masks the rather different roles played by phenotypic and genetic correlations, impacting (respectively) the within- and between-generation changes.

Accounting for Phenotypic Correlations: The Selection Gradient

Recall from Equation 13.8b that the univariate **directional selection gradient** $\beta = S/\sigma_z^2$ is the slope of the linear regression of relative fitness w as a function of phenotypic value z of the trait (Equation 13.8a). The multivariate extension is given by

$$\beta = \mathbf{P}^{-1}\mathbf{S} \tag{13.25a}$$

where the vector $\boldsymbol{\beta}$ contains the coefficients for the multiple linear regression

$$w = 1 + \sum_i \beta_i z_i + e = 1 + \boldsymbol{\beta}\,\mathbf{z}^T + e \tag{13.25b}$$

of relative fitness w on the vector $\mathbf{z}$ of trait values (LW Equation 8.10c). The interpretation of β_i is that it represents the change in relative fitness given a one unit change in trait i while holding all other trait values constant. This measures of the amount of direct selection on this trait, removing any indirect effects from selection on phenotypically correlated traits (Chapter 290). Since $\boldsymbol{\beta} = \mathbf{P}^{-1}\mathbf{S}$, we have $\mathbf{S} = \mathbf{P}\boldsymbol{\beta}$, giving the observed selection differential as

$$S_i = P_{ii}\beta_i + \sum_{k \neq i} P_{ij}\beta_j \tag{13.25c}$$

The *within-generation* change in the mean of trait i following selection thus consists of an effect from direct selection on that trait ($P_{ii}\beta_i$) *plus* the effects of selection on *all* other *phenotypically* correlated traits ($P_{ij}\beta_j \neq 0$). Hence, the sign of S_i tells us nothing about the sign of β_i (the amount of direct selection on that trait), as **correlated selection** can easily overpower the direct effect. The selection gradient presents the correct picture of which traits are under selection *provided* there are no additional traits under direct selection that are phenotypically correlated with our focal vector $\mathbf{z}$ of traits (Chapter 29).

Accounting for Genetic Correlations: The Lande Equation

To see the effects of genetic correlations, substituting $\mathbf{P}^{-1}\mathbf{S} = \boldsymbol{\beta}$ into Equation 13.23b gives the **Lande equation** (Lande 1979),

$$\mathbf{R} = \mathbf{G}\,\boldsymbol{\beta}, \tag{13.26a}$$

which is the multivariate version of Equation 13.8c, $R = \sigma_A^2\beta$. Considering two traits,

$$\mathbf{R} = \begin{pmatrix} R_1 \\ R_2 \end{pmatrix} = \mathbf{G}\boldsymbol{\beta} = \begin{pmatrix} G_{11} & G_{12} \\ G_{12} & G_{22} \end{pmatrix} \begin{pmatrix} \beta_1 \\ \beta_2 \end{pmatrix} \tag{13.26b}$$

for greatly simplified (relative to Equation 13.24c) responses of

$$R_1 = G_{11}\beta_1 + G_{12}\beta_2$$

$$\tag{13.26c}$$

$$R_2 = G_{12}\beta_1 + G_{22}\beta_2$$

The role of genetic correlations (G_{12}) is now obvious, in that direct selection on trait (say) 2 can influence the response in trait 1 *only* when the two traits have a non-zero genetic correlation ($G_{12} \neq 0$). The contribution $G_{ii}\beta_i$ from direct selection is called the **direct response** and the contribution to response on trait i from direct selection on other *genetically* correlated traits ($G_{ij}\beta_j \neq 0$) is called the **correlated response**. If two traits are genetically uncorrelated, selection on one has no impact on the *response* of the other, even if they are phenotypically correlated.

The Lande equation shows that we can distinguish between **phenotypic selection**, the change in a phenotypic distribution *within* a generation (measured by $\boldsymbol{\beta}$), and the **evolutionary response to selection**, the transmission of these within-generation changes to the next generation (measured by $\mathbf{R}$). 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 $\mathbf{R}$ depends on $\boldsymbol{\beta}$ through $\mathbf{G}$. Chapters 28 and 29 examine in detail methods for estimating the nature of phenotypic selection in natural populations.

Selection Gradients and Mean Population Fitness

Under appropriate conditions, the selection gradient $\boldsymbol{\beta}$ relates how a within-generation change in the vector of trait means maps into a change in the mean fitness of a population. 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 statisfies $\beta = \partial \ln \overline{w} / \partial \mu$ (derivation in Example A5.3). Hence we can express the breeder's equation as

$$R = \sigma_A^2 \left(\frac{\partial \ln \overline{w}}{\partial \mu} \right) \tag{13.27a}$$

The multivariate version of this partial is the **gradient of mean fitness** with respect to the vector of character means, the vector of partials of the log of mean fitness $\ln \overline{w}$ with respect to each trait mean under consideration,

$$\boldsymbol{\beta} = \frac{\partial \ln \overline{w}}{\partial \boldsymbol{\mu}}, \tag{13.27b}$$

so that $\beta_i = \partial \ln \overline{w} / \partial \mu_i$ (the change in log mean fitness from a change in the mean of trait i), giving the gradient version of the Lande equation

$$\mathbf{R} = \mathbf{G} \, \frac{\partial \ln \overline{w}}{\partial \boldsymbol{\mu}} \tag{13.27c}$$

The gradient terms represents the changes in character means that produce the maximal local change in population fitness, while the actual response involves the product (or **projection**) of this vector with the genetic covariance matrix $\mathbf{G}$. The resulting response vector is generally not parallel to $\boldsymbol{\beta}$ 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 the implications of genetic constraints imposed by the structure of $\mathbf{G}$ in detail in Volume 3.

Finally, we can connect the somewhat abstract notion of variance in fitness with a measurable quantity, the amount of selection $\boldsymbol{\beta}$ on a vector $\mathbf{z}$ of traits, as follows. Walsh and Blows (2009) show that the variance in w accounted for by selection on $\mathbf{z}$ is

$$\sigma(\mathbf{z}^T, w)\mathbf{G}^{-1}\sigma(\mathbf{z}, w) \tag{13.28a}$$

Recalling Robertson's secondary theorem, $\sigma(\mathbf{z}, w) = \Delta \mathbf{z} = \mathbf{G}\boldsymbol{\beta}$, giving

$$(\mathbf{G}\boldsymbol{\beta})^T \mathbf{G}^{-1}(\mathbf{G}\boldsymbol{\beta}) = \boldsymbol{\beta}^T \mathbf{G} \boldsymbol{\beta} \tag{13.28b}$$

The remaining variance in fitness that remains unaccounted for after the effects of $\mathbf{z}$ is removed becomes

$$\sigma^2(w) - \boldsymbol{\beta}^T \mathbf{G} \boldsymbol{\beta} \tag{13.28c}$$

In theory, if one had an estimate of $\sigma^2(w)$ in hand, the significant of a set $\mathbf{z}$ of traits can be determined. If these account for most of the variation, then their is little need to consider additional traits. If these account for only a small fraction, important traits are missing.

LIMITATIONS OF THE BREEDER'S EQUATION

As we have seen, the basic breeder's equation has many alternative expressions and extensions (summarized in Table 13.1). All are based on Equation 13.1, which assumes a linear midparent-offspring regression with slope h^2. This single-generation prediction holds over multiple generations provided that selection does not result in a significant change in the base-population heritability, a region we call short-term response. Chapter 16 shows that even a single generation of selection will change h^2 through the generation of linkage disequilibrium, but since this straightforward to correct for, we also treat this as a special case of short-term response. The more serious problem is that eventually allele-frequency change alters the genetic variance (long-term response), and these variances changes cannot be predicted without extensive (and essentially unavailable) knowledge about the distribution of allelic effects and their frequencies. However, even over the short-term response time frame, there are a number of complications that compromise the basic breeder's equation (and by extension any of the versions listed in Table 13.1), and we conclude by reviewing these (Table 13.2).

Table 13.1.   Alternate versions and extensions of the basic breeder's equation.

Version	Expression	Equation No
Basic breeder's equation	$R = h^2 S$	13.1
Sex-specific response (sex s)	$R_s = b_{s,fa}\, S_{fa} + b_{s,mo}\, S_{mo}$	13.4a
Selection intensity	$R = h^2\, \bar{\imath}\, \sigma_z = \bar{\imath}\, h\, \sigma_A$	13.6b
Response (trait y, select using x)	$R_y = \dfrac{\sigma(x,y)}{\sigma_x^2}\, S_x = \dfrac{\sigma(x,y)}{\sigma_x}\, \bar{\imath}_x$	13.10
Accuracy (trait y, select using x)	$R_y = \bar{\imath}_x\, \sigma_y\, \rho(x,y)$	13.11a
Accuracy (breeding values)	$R_A = \bar{\imath}_x\, \rho(x,A)\, \sigma_A$	13.11c
Rate of response	$R = \left(\dfrac{\bar{\imath}_s + \bar{\imath}_d}{L_s + L_d} \right) h\sigma_A$	13.20
Rate of response using accuracy	$R = \left(\dfrac{\bar{\imath}_s + \bar{\imath}_d}{L_s + L_d} \right) \rho(A,x)\, \sigma_A$	13.21
Variance-standardized response	$R/\sigma_z = h^2\, \bar{\imath}$	13.22a
Mean-standardized response	$R/\mu_z = \bar{\imath}\, h\, CV_A$	13.22b
	$R/\mu_z = I_A \beta_u$	13.22c
Multivariate breeder's equation	$\mathbf{R} = \mathbf{G}\mathbf{P}^{-1}\mathbf{S}$	13.23b
Lande equation	$R = \sigma_A^2\, \beta$	13.8c
	$R = \sigma_A^2\, \dfrac{\partial \ln \overline{w}}{\partial \mu}$	13.27a
Multivariate Lande equation	$\mathbf{R} = \mathbf{G}\boldsymbol{\beta}$	13.26a
	$\mathbf{R} = \mathbf{G}\, \dfrac{\partial \ln \overline{w}}{\partial \boldsymbol{\mu}}$	13.27c

There are a number of situations that can compromise the breeder's equation, even if we are interested only in the single-generation response to selection and can assume

Table 13.2.   Summary of various factors complicating the prediction of short-term selection response in the phenotypic mean, even assuming all regressions are linear and we are considering a single generation of selection from an unselected base population. Short-term response specifically refers to conditions where the effects of any allele frequency change on the additive variance are negligible. Models of long-term response (Chapters 25 – 27) relax this restriction.

Major gene with dominance (LW Chapter 17)	Can generate a nonlinear parent-offspring regression.
Epistasis (Chapter 15)	Component of response due to epistasis is transient. Parent-offspring covariance overestimates permanent response.
Correlated environmental effects (Chapter 15)	Contribution from parent-offspring correlation decays away after selection relaxed.
Maternal effects (Chapter 15)	Potential for complicated lags in response — mean changes unpredictably after selection is relaxed. Possibility of reversed response.
Gametic-phase disequilibrium (Chapter 16)	Changes the additive genetic variance. Directional selection generates negative gametic-phase disequilibrium, reducing h^2 and slowing response.
Assortative Mating (Chapter 16)	Generates gametic-phase disequilibrium which either enhances (positive correlation between mates) or retards (negative correlation between mates) response.
Environmental Change (Chapters 18 - 20)	A significant change in the environment can obscure the true amount of genetic change.
Drift (Chapters 18, 19)	Generates variance in the short-term response.
Environmental Correlations (Chapter 20)	Enviromental factors can influence both the trait and fitness, confounding both the nature of selection and the true amount of genetic change.
Associative effects (Chapter 22)	Trait influenced by both direct and social components from group members. A decline in the mean social value can swamp an increase in mean direct value. Possibility of reversed response.
Inbreeding (Chapter 23)	Response depends on additional variance components that are difficult to estimate (σ^2_{DI}, σ_{ADI}, etc). Response has permanent and transient components.
Age-structure (Chapter 33)	Several generations are required to propagate genetic change uniformly through the population.
Selection on Correlated Characters (Chapter 34 - 38)	Response completely unpredictable unless selection on correlated characters accounted for. Possibility of reversed response.

G × E Interactions	Possibility of nonlinear parent-offspring regressions.
(Chapters 42, 43)	Correlated characters problem, with traits measured in different environments treated as correlated traits.
	Possibility of reversed response.

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 (Chapter 15). In the Price equation setting (Equation 6.12), this occurs because the mean of the population changes in the *absence* of selection, which occurs as the population attempts to regain Hardy-Weinberg proportions and linkage equilibrium following a perturbation from past selection.

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. This problem is examined in Chapter 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 still 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., Equations 5.23b and 5.27b for population-genetic expressions and Equations 6.12, 6.38, 6.39 for expression based on the Price equation).

Table 13.2 summarizes some of these various factors compromising the breeder's equation, giving the chapters in which these complications are examined in detail. Provided one can assume linearity of the regressions of relatives, we can account for many of these complications. 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 (Chapter 15).

As mentioned at the start of the chapter, even if we have corrected for all of the potential complications listed in Table 13.2, the breeder's equation is expected to be an increasingly poor predictor as selection proceeds. If there are segregating alleles of large effect, 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 24). 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 16, 24). Directional selection generates negative disequilibrium, decreasing heritability and hence reducing response. This reduction can be significant if heritabilty is high. Likewise, selection on the variance itself (through disruptive or stabilizing selection) also creates disequilibrium which changes the genetic variance. Chapter 16 examines the effect of such short-term changes in disequilibrium on the additive genetic variation. An additional complication occurs when there is genetic variance for the amount of environmental variability that a genotype displays, and this is discussed in Chapter 17. As selection continues over several generations, allele frequencies themselves start to change, even if all loci have very small effects (Chapters 25, 26). Drift and mutation also become increasingly important and these complications are examined in Chapters 26–29.

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