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Applications of Index Selection

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Despite the elegance of the multivariate breeder's equation, most artificial selection on multiple traits occurs via a selection index and many problems in evolutionary biology can similarly be best handle through the use of an index. The next several chapters more fully develop specific applications of index selection. Chapter 35 reviews BLUP selection, essentially a very powerful extension of index selection to any known pedigree of individuals, while Chapter 36 examines marker-assisted and genomic selection (the use of an index of molecular markers to aid in breeding). Chapter 37 extends the results from Chapters 11 (maternal effects) and 18 (associative effects, such as group-defined traits) to multiple traits and develops the related topic of multi-level selection. Chapters 38 and 39 concludes by examining selection in the presence of genotype-environment interactions, which can also be treated as a multiple-trait problem. The focus of this chapter is a bit of a mix, covering several different topics, largely related by simply being multiple-trait problems.

The first topic, which consists of the bulk of this chapter, is using index selection to improve a single trait. One can have a number of measures of the same trait in either relatives of a focal individual or as multiple measures of the same trait in a single individual, or both. How does one best use this information? We start by developing the general theory for using an index to improve the response in a single trait (which follows as a simplification of the Smith-Hazel index). We then apply these results to several important cases — a general analysis when either phenotypic or genotypic correlations are zero, improving response using repeated measurements of a characters over time, and using information from relatives to improve response with a special focus on combined selection (the optimal weighting of individual and family information, proving many of the details first presented in Chapter 17). As we will see in Chapter 35, the mixed-model power of BLUP provides a better solution to many of these problems, but index selection is both historically important as well as providing clean analytic results.

In contrast to the first topic, the final three are essentially independent of each other and we try to presen them as such (so that the reader can simply turn the the section of interest without regard to previous material in this chapter). They include selection on a ratio, selection on sex-specific and sexually-dimorphic traits, and finally selection on the environmental variance σ^2_E when it shows heritable variation (expanding upon results from Chapter 13).

IMPROVING THE RESPONSE OF A SINGLE CHARACTER

Recall that the basis of selection in a random-mating population typically revolves around identifying those individuals with the largest breeding values (Chapter 10). Under standard mass selection, the only information used to predict response (which is formally equivalent to predicting breeding value under the standard assumptions leading to the breeder's equation, e.g., Table 10.1) is an individual's phenotypic value. Often considerably more information

relevant to that character is available, such as repeated measures of that trait over time, correlated characters in the same individual, or values from relatives. Incorporating this information into a Smith-Hazel index improves the response over that of simple univariate selection on the character, as suggested by Hazel (1943) and further developed by numerous authors such as Lush (1944, 1947), Rendel (1954), Osborne (1957a,b,c), Jardie (1958), Le Roy (1985), Skjervold and Ødegard (1959), Purser (1960), Young (1961), Searle (1965), and Gjedrem (1967a,b), to name a few. The power of the matrix formulation of index selection theory (Chapter 33) is that all of the results of these authors for particular cases are easily obtainable given we know the appropriate covariances and, more importantly, are easily extendible to more general (essentially arbitrary) cases. All of this is a prelude to BLUP selection (Chapter 35), which easily allows incorporation of any arbitrary set of relative and (estimable) fixed effects.

Turner and Young (1969) coin the useful term of **aids to selection** to describe situations where mass selection (predicting breeding value from a single record per individual) can considerably benefit from incorporating addition information. They highlight three common reasons for using such aids. The first is when greater accuracy is required. If trait heritability is high, the accuracy in predicting an individual's breeding value given a single observation of their phenotype is often sufficient for our needs. However, when the accuracy is low, it can potentially be improved upon by considering other traits within the individual, trait values in relatives, or even repeated observations (records) from the same individual (or, of course, some combination of all of these). The second is to achieve **early selection** – selection earlier in the life cycle than would be possible with simple mass selection. In an age-structured population, early-generation selection can reduce the generation interval, which in turn increases the response per unit of time (Chapters 10, 23). There can also be considerable economic savings by being able to score traits early. Undesirable individuals can be culled early, allowing more resources to be expended on those surviving individuals. This can allow for a greater selection intensity and/or a greater economic rate of return. Finally, in many cases mass selection is simply impractical. Examples include carcass trait where individuals must be sacrificed to score the trait as well as sex-limited traits. It is difficult to select a male for milk or egg production on the basis of his phenotype alone!

General Theory

All the results of the Smith-Hazel index (Chapter 33) apply, but when our interest is the response of only a single character considerable simplification occurs in many of the results. Let z_1 be the character of interest (the **primary character**) and $z_2, \cdots, z_n$ be $n-1$ other **secondary characters** that potentially provide information on the primary character. Since the only response of the primary character is of interest, the vector of economic weights $\mathbf{a}$ has $a_1 = 1$ and all other elements zero. Writing the additive-genetic variance-covariance matrix as $\mathbf{G} = (\mathbf{g}_1, \mathbf{g}_2, \cdot, \mathbf{g}_n)$ where $\mathbf{g}_i^T = (g_{1i}, g_{2i}, \cdots, g_{ni})$ is the vector of additive genetic covariances between character i and all other characters, we have

$$\mathbf{Ga} = (\mathbf{g}_1, \mathbf{g}_2, \cdot, \mathbf{g}_n) \begin{pmatrix} 1 \\ 0 \\ \vdots \\ 0 \end{pmatrix} = \mathbf{g}_1$$

where $\mathbf{g}_1$ is the vector of additive genetic covariances of the primary character with all other characters being considered. For notational ease, we drop the subscript and simply use $\mathbf{g}$ and likewise use g for the additive genetic value of the focal trait (character one). Note that $H = g$, namely the merit function we are attempting to maximize is just the breeding value of trait one. Applying Equation 33.18a, the vector of weights for the Smith-Hazel index simplifies

to

$$\mathbf{b}_s = \mathbf{P}^{-1}\mathbf{G}\mathbf{a} = \mathbf{P}^{-1}\mathbf{g} \tag{34.1a}$$

giving the index as

$$I_s = \mathbf{b}_s^T\mathbf{z} = \mathbf{g}^T\mathbf{P}^{-1}\mathbf{z} \tag{34.1b}$$

Substituting $\mathbf{G}\mathbf{a} = \mathbf{g}$ into Equation 33.19 gives the response as

$$R = \overline{i} \cdot \sqrt{\mathbf{g}^T\mathbf{P}^{-1}\mathbf{g}} \tag{34.1c}$$

Under univariate selection, $R = \overline{i} \cdot h_1^2\,\sigma_{z_1} = \overline{i} \cdot h_1\,\sigma_g$, giving the increase in response using index selection as

$$\frac{\sqrt{\mathbf{g}^T\mathbf{P}^{-1}\mathbf{g}}}{h_1\,\sigma_g} \tag{34.1d}$$

An alternative way to quantify the advantages of an index over univariate selection is to consider how much variation in g is accounted for by the index. Since the correlation between an individual's phenotypic and additive-genetic (breeding) values is $\rho_{g,z_1} = \sigma_{g,z_1}/\sigma_g\sigma_{z_1} = \sigma_g^2/\sigma_g\sigma_{z_1} = h_1$, the squared accuracy (the fraction of variation in the breeding value accounted for by the index) of using only z_1 to predict g is $\rho_{g,z_1}^2 = h_1^2$. Since

$$\sigma_{H,I_s} = \sigma(g, \mathbf{b}_s^T\mathbf{z}) = \mathbf{b}_s^T\sigma(g,\mathbf{z}) = \mathbf{b}_s^T\mathbf{g},$$

the accuracy of the index given by Equation 34.1b in predicting $H = g$ is

$$\rho_{H,I_s} = \sqrt{\frac{\sigma_{H,I_s}^2}{\sigma_H^2 \cdot \sigma_{I_s}^2}} = \sqrt{\frac{(\mathbf{b}_s^T\mathbf{g})^2}{\sigma_g^2 \cdot \mathbf{b}_s^T\mathbf{P}\mathbf{b}_s}} = \sqrt{\frac{\mathbf{g}^T\mathbf{P}^{-1}\mathbf{g}}{\sigma_g^2}} \tag{34.2a}$$

The last step follows by noting that $\mathbf{b}_s^T\mathbf{P}\mathbf{b}_s = \mathbf{g}^T\mathbf{P}^{-1}\mathbf{g}$. Hence, the improvement in accuracy by using an index over mass selection is

$$\frac{\rho_{g,I_s}}{\rho_{g,z_1}} = \sqrt{\frac{\mathbf{g}^T\mathbf{P}^{-1}\mathbf{g}}{h_1^2 \cdot \sigma_g^2}} \tag{34.2b}$$

Equations 34.1 and 34.2 give the general expressions for improving response in a single character using selection indices and can be applied to a very wide variety of situations.

Example 34.1. Robinson et al. (1951) estimated the genotypic and phenotypic covariances between yield and several other characters in maize. Using their estimates, construct the optimal index to improve yield (z_1, measured as pounds of yield per plant) using plant height (z_2) and ears per plant (z_3) as secondary characters. The estimated phenotypic covariance matrix for these characters is

$$\widehat{\mathbf{P}} = \begin{pmatrix} 0.0069 & 0.0968 & 0.0132 \\ 0.0968 & 28.8796 & 0.2313 \\ 0.0132 & 0.2313 & 0.0526 \end{pmatrix}$$

while the vector of estimated additive genotypic covariances between yield and other characters is

$$\widehat{\mathbf{g}} = \begin{pmatrix} 0.0028 \\ 0.0964 \\ 0.0075 \end{pmatrix}$$

For yield, $\sigma_g^2 = 0.0028$ and $h_1^2 = 0.0028/0.0069 \simeq 0.41$, giving $h_1\sigma_g = \sqrt{0.0028 \cdot 0.41} \simeq 0.0339$, and an expected response to selection solely on yield as $R = 0.0339 \cdot \overline{i}$. Robinson et al. note that with the type of plant spacing assumed in their study, pounds of yield per plant is converted into bushels per acre by multiplying yield by 118.3, for a response of $4.01 \cdot \overline{i}$ bushels per acre.

The optimal index incorporating both yield and the two secondary characters is

$$I_s = \widehat{\mathbf{g}}^T \widehat{\mathbf{P}}^{-1} \mathbf{z} = 0.23 \cdot z_1 + 0.002 \cdot z_2 + 0.075 \cdot z_3$$

which has expected response

$$\overline{\imath}\sqrt{\mathbf{g}^T \mathbf{P}^{-1} \mathbf{g}} = \overline{\imath}\sqrt{0.00141} = \overline{\imath} \cdot 0.0375$$

This converts to 4.44 $\cdot\overline{\imath}$ bushels/acre, an 11 percent increase relative to selection on yield only. The squared accuracy of this index is

$$\mathbf{g}^T \mathbf{P}^{-1} \mathbf{g} / \sigma_g^2 = 0.00141/0.0028 \simeq 0.504$$

so that I_s accounts for 50.4 percent of the additive genetic variance in yield, while the phenotype of yield alone accounts for only $h^2 = 0.41$, or 41 percent. Increasing yield is a common use of an indirect index. However, experiments reviewed by Pritchard et al. (1973) shows that usually the index is only slightly better than direct selection and often can be worse (likely due to sampling errors giving the estimated index incorrect weights). Index selection is most superior when environmental effects overwhelm genetic differences.

A key concern in constructing an index is which secondary characters to include. If $\mathbf{g}$ and $\mathbf{P}$ are estimated without error, addition of any correlated (genetic or phenotypic) character always increases the accuracy of the index. However, genetic parameters *are* estimated with error and the inclusion of characters that are actually uncorrelated, but show a estimated correlation due to sampling effects, reduces the efficiency of the index. Sales and Hill (1976) find that the greatest errors occur when the primary character has low heritability, but this is exactly the case where a selection index is potentially the most useful (Gjedrem 1967a). Bouchez and Goffinet (1990) suggest a robust procedure for evaluating which secondary characters to exclude.

More Detailed Analysis of Two Special Cases

First suppose there are no phenotypic correlations between the characters so that $\mathbf{P}$ (and hence $\mathbf{P}^{-1}$) is diagonal. In this case, the ith diagonal element of $\mathbf{P}^{-1}$ is $1/P_{ii} = 1/\sigma_{z_i}^2$, giving

$$\mathbf{g}^T \mathbf{P}^{-1} \mathbf{g} = \sum_{j=1}^{n} \frac{[\sigma(g, g_j)]^2}{\sigma_{z_j}^2} = \left(\frac{\sigma_g^4}{\sigma_{z_1}^2} \right) \left(1 + \sum_{j=2}^{n} \frac{[\sigma(g, g_j)]^2 \, \sigma_{z_1}^2}{\sigma_g^4 \, \sigma_{z_j}^2} \right)$$

Using $\sigma(g, g_j) = \rho_j \sigma_g \sigma_{g_j}$ where ρ_j is the correlation between additive genetic values of character j and the primary character, Equation 34.1c shows that the response can be expressed as

$$R = \overline{\imath} \, h_1 \, \sigma_g \sqrt{1 + \frac{1}{h_1^2} \sum_{j=2}^{n} \rho_j^2 \, h_j^2} \tag{34.3a}$$

Hence the increase in response in z_1 using an index is

$$\sqrt{1 + \frac{1}{h_1^2} \sum_{j=2}^{n} \rho_j^2 \, h_j^2} \tag{34.3b}$$

This is strictly greater than one unless z_1 is genetically uncorrelated with all the other considered characters in which case it equals one. The advantage of index selection increases as either the heritabilities of correlated characters increase or as the heritability of z_1 decreases. Thus, when the heritability of z_1 is low using an index can result in a significantly increased response.

A second special case is when *none* of the secondary characters are genetically correlated with the primary character. Rendel (1954) considered this as a means of using a second character to increase the heritability of the first. Rendel's idea is that a second *phenotypically* correlated character potentially provides information on the environmental value of the primary character, reducing uncertainly as to its genotypic value and as a consequence increasing heritability (also see Purser 1960). Here $\mathbf{g} = \sigma_g^2(1, 0, \cdots, 0)^T$ implying

$$\mathbf{g}^T\mathbf{P}^{-1}\mathbf{g} = \sigma_g^4 \begin{pmatrix} 1 & 0 & \cdots & 0 \end{pmatrix} \mathbf{P}^{-1} \begin{pmatrix} 1 \\ 0 \\ \vdots \\ 0 \end{pmatrix} = \sigma_g^4 P_{11}^{-1}$$

where P_{11}^{-1} denotes the $1,1$ element of $\mathbf{P}^{-1}$. Substituting into Equation 34.1c gives the response as

$$R = \overline{\imath}\, \sigma_g^2 \sqrt{P_{11}^{-1}} = \overline{\imath}\, h_1 \sigma_g \sqrt{\sigma_{z_1}^2 P_{11}^{-1}} \tag{34.4}$$

and hence the increase in response using an index is $\sqrt{\sigma_{z_1}^2 P_{11}^{-1}}$. To see that this expression is greater than or equal to one, we first digress on a useful identity from matrix algebra. Partitioning the phenotypic variance-covariance matrix as

$$\mathbf{P} = \begin{pmatrix} P_{11} & \mathbf{p}^T \\ \mathbf{p} & \mathbf{Q} \end{pmatrix} \quad \text{where} \quad \mathbf{p} = \begin{pmatrix} P_{12} \\ \vdots \\ P_{1n} \end{pmatrix} \quad \text{and} \quad \mathbf{Q} = \begin{pmatrix} P_{22} & \cdots & P_{2n} \\ \vdots & \ddots & \vdots \\ P_{n2} & \cdots & P_{nn} \end{pmatrix}$$

following Cunningham (1969), it can be shown that

$$P_{11}^{-1} = \left(P_{11} - \mathbf{p}^T\mathbf{Q}^{-1}\mathbf{p}\right)^{-1} = \sigma_{z_1}^{-2}\left(1 - \frac{\mathbf{p}^T\mathbf{Q}^{-1}\mathbf{p}}{\sigma_{z_1}^2}\right)^{-1} \tag{34.5}$$

giving the response as

$$R = \overline{\imath}\, h_1 \sigma_g \left(1 - \frac{\mathbf{p}^T\mathbf{Q}^{-1}\mathbf{p}}{\sigma_{z_1}^2}\right)^{-1/2} \tag{34.6a}$$

showing that increase in response using an index is

$$\left(1 - \frac{\mathbf{p}^T\mathbf{Q}^{-1}\mathbf{p}}{\sigma_{z_1}^2}\right)^{-1/2} \tag{34.6b}$$

which is greater than one if the quadratic product term is positive. Since $\mathbf{Q}$ is itself a covariance matrix, it is positive-definite (unless det($\mathbf{Q}$)=0, namely one of the secondary characters can be expressed as a linear combination of the others, in which case it is nonnegative definite). Recall from Appendix 4 that if $\mathbf{Q}$ is positive definite, so is $\mathbf{Q}^{-1}$ and hence the quadratic product $\mathbf{p}^T\mathbf{Q}^{-1}\mathbf{p} > 0$ unless $\mathbf{p} = \mathbf{0}$. This later case occurs when z_1 is phenotypically uncorrelated with all secondary characters being considered, in which case index selection gives the same response as univariate selection.

Wright (1984) suggests that this sort of index can not only correct for environmental effects, but may also account for at least some non-additive genetic effects that might bias estimates of breeding values. For example, if a plant population is a mixture of outcrossing and selfed individuals, then an individual's phenotypic value as a predictor of its breeding value is biased by its amount of inbreeding when non-additive genetic variance is present. Using a second trait, known to be genetically uncorrelated to the focal trait but which displays heterosis (and hence serves as a potential marker for inbreeding), can partial correct for the differential effects of inbreeding among sampled individuals. While intriguing, there appears to be no formal theory on this otherwise interesting suggestion.

Repeated Measures of a Character

Suppose a single character is measured at n different times to give a vector of observations $(z_1, \cdots, z_n)$ for each individual. Under what conditions does the use of such **repeated measures** improve response? The idea is that if some of the environmental effects change from one measurement to the next, multiple measurements average out these effects. The simplest model of environmental effects is that the jth measurement can be decomposed as $z_j = g + e_p + \epsilon_j$ where e_p the permanent environmental effects (which also includes non-additive genetic terms if they are present) and ϵ_j is the transient part of the environment which is assumed to be uncorrelated from one measurement to the next. Thus

$$\sigma(z_k, z_j) = \sigma(g + e_p + \epsilon_k,\, g + e_p + \epsilon_j) = \begin{cases} \sigma_z^2 & \text{for } k = j \\ \\ \sigma_g^2 + \sigma_{e_p}^2 = r \cdot \sigma_z^2 & \text{for } k \neq j \end{cases}$$

where $r = (\sigma_g^2 + \sigma_{e_p}^2)/\sigma_z^2$ is the squared correlation between measurements, the **repeatability** of the character (LW Chapter 6). The covariance in additive genetic values between measurements is $\sigma(g_i, g_j) = \sigma(g, g) = \sigma_g^2$. Hence,

$$\mathbf{g} = \sigma_g^2 \begin{pmatrix} 1 \\ \vdots \\ 1 \end{pmatrix} \qquad \text{and} \qquad \mathbf{P} = \sigma_z^2 \begin{pmatrix} 1 & r & \cdots & r \\ r & 1 & \cdots & r \\ \vdots & \vdots & \ddots & \vdots \\ r & r & \cdots & 1 \end{pmatrix}$$

To compute the vector of weights $\mathbf{b}_s$, first note the following identity: for the $m \times m$ matrix

$$\mathbf{A} = \begin{pmatrix} 1 & a & \cdots & a \\ a & 1 & \cdots & a \\ \vdots & \vdots & \ddots & \vdots \\ a & a & \cdots & 1 \end{pmatrix}, \quad \text{then} \qquad \mathbf{A}_{ij}^{-1} = \begin{cases} \dfrac{1 + (m-2)a}{1 + (m-2)a - (m-1)a^2} & \text{for } i = j \\ \\ \dfrac{-a}{1 + (m-2)a - (m-1)a^2} & \text{for } i \neq j \end{cases} \tag{34.7}$$

Using this identity, a little algebra gives

$$\mathbf{b}_s = \mathbf{P}^{-1}\mathbf{g} = \frac{h^2}{1 + r(n-1)} \begin{pmatrix} 1 \\ \vdots \\ 1 \end{pmatrix} \tag{34.8}$$

Noting that $I_s = \mathbf{b}_s^T \mathbf{z} = c \cdot \overline{z}$, the index can be rescaled to simply $\overline{z}_i$ (the average of all measurements for an individual). Since

$$\mathbf{g}^T \mathbf{P}^{-1} \mathbf{g} = \mathbf{g}^T \mathbf{b}_s = \left(\frac{h^2\, \sigma_g^2}{1 + r(n-1)} \right) \begin{pmatrix} 1 & \cdots & 1 \end{pmatrix} \begin{pmatrix} 1 \\ \vdots \\ 1 \end{pmatrix} = h^2\, \sigma_g^2 \left(\frac{n}{1 + r(n-1)} \right)$$

the squared accuracy of this index in predicting additive-genetic values is

$$\rho^2_{I,g} = \frac{\mathbf{g}^T\mathbf{P}^{-1}\mathbf{g}}{\sigma^2_g} = h^2 \cdot \left(\frac{n}{1+r(n-1)}\right) \tag{34.9a}$$

with resulting response to selection

$$R = \overline{i} \cdot h_1\sigma_g\sqrt{\frac{n}{1+r(n-1)}} \tag{34.9b}$$

as obtained by Berge (1934). The ratio of response under the index to response using a single measurement approaches $r^{-1/2}$ for large n, so that for repeatabilities of $r = 0.1$, 0.25, 0.5, and 0.75, it approaches 3.2, 2, 1.4, and 1.2. Significant gain in response can occur if repeatability is low, while there is little advantage when repeatability is high. Balancing any potential gain in response is an increase in cost and potentially longer breeding time (Turner and Young 1969). More generally, repeated measures can be modified to allow for correlations between transient environment effects by suitably modifying $\mathbf{P}$. In such cases, the index may weight separate measurements differentially so that the index can be significantly different from the simple average value of repeated measures.

USING INFORMATION FROM RELATIVES

Often measurements of the character of interest exist for relatives and this information can easily be incorporating into a selection index to both improve response and increase the accuracy of predicted breeding values. We mention in passing here that although our discussion is restricted to the case where the character of interest is the one measured in relatives, other measured characters in relatives could also be incorporated using standard index theory. The basic theory presented here very generally extends to arbitrary sets of relatives, although more powerful methods for estimating breeding values exist (BLUP and REML, reviewed in LW Chapters 26, 26 and in Chapters 16 and 35). We start by reviewing the general theory and then examining family selection in detail.

General Theory

Since our interest is response in a single character, we build upon the simplifications of the Smith-Hazel index developed in the previous section. One significant difference with using relatives to construct an index is that far fewer parameters have to be estimated. A general index with n secondary characters has $(n+1)(n+4)/2$ parameters to estimate — $(n+1)(n+2)/2$ phenotypic covariances and $n+1$ additive-genetic covariances. If, however, the index uses measures (of the primary trait) from known relatives then only the significant variance components for the character need be estimated, as the elements of $\mathbf{G}$ and $\mathbf{P}$ can then be constructed from the theory of correlation between relatives (LW Table 7.2). For example, if non-additive genetic variance is not significant and genotype-environment interactions and maternal effects can be ignored, only σ^2_z and h^2 need be estimated regardless of how many relatives are measured.

Let z_1 denote the character value measured in the individual of interest and $z_2, \cdots, z_{n+1}$ be measurements of this character in n of its relatives. Since we are only interested in the response in z_1 (i.e., predicting an individual's breeding value for trait one), then (similar to the previous section) only the vector of additive genetic covariances $\mathbf{g}$ between the individual of interest and each of its relatives is required. Under the assumption that the character has the same phenotypic and additive genetic variance in all relatives, it is useful to work with

correlations, rather than covariances. Denote by $\mathbf{P}_\rho$ the matrix of phenotypic correlations between characters, with

$$\mathbf{P} = \begin{pmatrix} \sigma(z_1, z_1) & \cdots & \sigma(z_1, z_{n+1}) \\ \vdots & \ddots & \vdots \\ \sigma(z_{n+1}, z_1) & \cdots & \sigma(z_{n+1}, z_{n+1}) \end{pmatrix} = \sigma_z^2 \cdot \begin{pmatrix} 1 & \cdots & \rho_{z_1, z_{n+1}} \\ \vdots & \ddots & \vdots \\ \rho_{z_{n+1}, z_1} & \cdots & 1 \end{pmatrix} = \sigma_z^2 \cdot \mathbf{P}_\rho \tag{34.10a}$$

Likewise, let $\mathbf{g}_\rho$ denote the vector of additive-genetic correlations between the individual of interest and its relatives, with

$$\mathbf{g} = \begin{pmatrix} \sigma(g, g) \\ \sigma(g, g_2) \\ \vdots \\ \sigma(g, g_{n+1}) \end{pmatrix} = h^2 \sigma_z^2 \cdot \begin{pmatrix} 1 \\ \rho_{g, g_2} \\ \vdots \\ \rho_{g, g_{n+1}} \end{pmatrix} = h^2 \sigma_z^2 \cdot \mathbf{g}_\rho \tag{34.10b}$$

From Equation 34.1a the resulting Smith-Hazel index weights are

$$\mathbf{b}_s = \mathbf{P}^{-1}\mathbf{g} = h^2 \cdot \mathbf{P}_\rho^{-1}\mathbf{g}_\rho \tag{34.11a}$$

giving (from Equation 34.2a) the best linear predictor of the breeding value for the individual of interest as

$$\mathbf{b}_s^T (\mathbf{z} - \boldsymbol{\mu}) = h^2 \cdot \mathbf{g}_\rho^T \mathbf{P}_\rho^{-1} (\mathbf{z} - \boldsymbol{\mu}) \tag{34.11b}$$

From Equation 34.2b the squared accuracy of this index in predicting breeding value is

$$\rho_{g,I}^2 = \frac{\mathbf{g}^T \mathbf{P}^{-1} \mathbf{g}}{\sigma_g^2} = h^2 \cdot \mathbf{g}_\rho^T \mathbf{P}_\rho^{-1} \mathbf{g}_\rho \tag{34.11c}$$

Since the accuracy in predicting breeding value from a single measure of an individual's phenotype is h, the increase in accuracy using information from relatives is given by the quadratic product $\sqrt{\mathbf{g}_\rho^T \mathbf{P}_\rho^{-1} \mathbf{g}_\rho}$. Finally, from Equation 34.1c the expected response to selection on this index is

$$\frac{R}{\bar{\imath}} = \sqrt{\mathbf{g}^T \mathbf{P}^{-1} \mathbf{g}} = h\sigma_g \cdot \sqrt{\mathbf{g}_\rho^T \mathbf{P}_\rho^{-1} \mathbf{g}_\rho} \tag{34.11d}$$

Information From a Single Relative

As our first application, consider the simplest case of a single measurement from an individual z_1 and a single relative z_2. Letting ρ_p and ρ_g be the phenotypic and additive-genetic correlations between the individual and this relative, we have

$$\mathbf{g}_\rho = \begin{pmatrix} 1 \\ \rho_g \end{pmatrix}, \qquad \mathbf{P}_\rho = \begin{pmatrix} 1 & \rho_z \\ \rho_z & 1 \end{pmatrix} \qquad \text{hence} \qquad \mathbf{P}_\rho^{-1} = (1 - \rho^2)^{-1} \begin{pmatrix} 1 & -\rho_z \\ -\rho_z & 1 \end{pmatrix}$$

Applying 34.11a, and rescaling the index so that the weight on z_1 is one gives the Smith-Hazel index for this situation as

$$I_s = z_1 + \left(\frac{\rho_g - \rho_z}{1 - \rho_z \rho_g} \right) z_2 \tag{34.12a}$$

Similarly,

$$\mathbf{g}^T \mathbf{P}^{-1} \mathbf{g} = h^2 \, \sigma_g^2 \, \mathbf{g}_\rho^T \mathbf{P}_\rho^{-1} \mathbf{g}_\rho = h^2 \, \sigma_g^2 \, \left(1 + \frac{(\rho_g - \rho_z)^2}{1 - \rho_z^2} \right) \tag{34.12b}$$

so that the increase in response over simple mass selection on the trait is

$$\frac{\sqrt{\mathbf{g}^T\mathbf{P}^{-1}\mathbf{g}}}{h\cdot\sigma_g} = \sqrt{1+\frac{(\rho_g-\rho_z)^2}{1-\rho_z^2}} \tag{34.12c}$$

Example 34.2. As an example of the application of Equation 34.12, consider the selection response with an optimal index based on an individual and its father. For an individual and its parent, $\rho_g = 1/2$. If we ignored any shared environmental effects, $\rho_z = h^2/2$. From Equation 34.12a, the index weight on the parent (setting the weight on the individual at one) becomes

$$\frac{\rho_g-\rho_z}{1-\rho_z\rho_g} = \frac{(1/2)(1-h^2)}{1-h^2/4} = \frac{2(1-h^2)}{4-h^2}$$

From Equation 34.10c, the increase in response relative to simply selecting using only the phenotype of the individual is

$$\sqrt{1+\frac{(\rho_g-\rho_z)^2}{1-\rho_z^2}} = \sqrt{1+\frac{(1/4)(1-h^2)^2}{1-h^4/4}} = \sqrt{1+\frac{(1-h^2)^2}{4-h^4}}$$

Hence,

h^2	0.05	0.1	0.25	0.5	0.75
Index weight on father	0.481	0.462	0.400	0.286	0.154
Relative response	1.107	1.097	1.069	1.033	1.009

Thus, as h^2 decreases, the weight on the parent increases (to a limit of 0.5). Likewise, the increase in response also increases, reaching a limit of $\sqrt{1+1/4} \sim 1.118$.

Constructing Selection Indices When the Individual Itself is Not Measured

An important class of applications is the construction of indices to predict breeding value when the individual is not (or cannot be) measured. For example, consider a female-limited character. Selection on males would increase response but the character cannot be scored. Information from females relatives can be used to construct an index to predict breeding value in males, and hence allow for selection in males. Another example is when an individual must to sacrificed to measure the character, such selection on internal organs. In such cases information from scored sibs can be used to predict breeding value.

Indirect indices wherein the primary character is not measured in the focal individual are computed using the previous results by now letting $z_1,\cdots,z_n$ denote the value of the character in n scored relatives and using

$$\mathbf{P}_\rho = \begin{pmatrix} 1 & \cdots & \rho_{z_1,z_n} \\ \vdots & \ddots & \vdots \\ \rho_{z_n,z_1} & \cdots & 1 \end{pmatrix} \tag{34.13a}$$

and

$$\mathbf{g}_\rho = \begin{pmatrix} \rho_{g_0,g_1} \\ \vdots \\ \rho_{g_0,g_n} \end{pmatrix} \tag{34.13b}$$

where the jth element in $\mathbf{g}$ is the the additive genetic correlation between the (unmeasured) individual of interest and its jth relative ($1 \leq j \leq n$). The results from Equations 34.11a -d apply using these definitions.

Finally note that a selection index not including our focal trait is the natural generalization of our discussion in Chapter 30 on conditions under which a larger response in a focal trait can be achieved via a correlated response on some other trait, as opposed to direct selection on the trait itself. From Equation 34.11c, we require $\mathbf{g}_\rho^T \mathbf{P}_\rho^{-1} \mathbf{g}_\rho > 1$ in order to have a larger response using an index not containing the trait as opposed to direct mass selection on the focal trait itself (assuming the same selection intensity). Such multiple trait indirect selection indices can indeed result in a larger response, and Gallais (1984) reviews several such examples from plant breeding.

Example 34.3. What is the index for predicting the breeding value in clutch size for a male give his mother's (z_1) and grandmother's (z_2) clutch size? From LW Table 6.3, $\rho_{g_0,g} = 1/2$ and $\rho_{g_0,g} = 1/4$. Assuming no epistasis and that shared environmental effects can be ignored, the phenotypic correlation between mother and grandmother is $h^2/2$. Thus

$$\mathbf{P}_\rho = \begin{pmatrix} 1 & h^2/2 \\ h^2/2 & 1 \end{pmatrix} \qquad \text{and} \qquad \mathbf{g}_\rho = \begin{pmatrix} 1/2 \\ 1/4 \end{pmatrix}$$

giving

$$\mathbf{b}_s = h^2 \mathbf{P}_\rho^{-1} \mathbf{g}_\rho = \left(\frac{h^2}{2(4-h^4)} \right) \cdot \begin{pmatrix} 4-h^2 \\ 1-h^2 \end{pmatrix} \qquad \text{and} \qquad \mathbf{g}_\rho^T \mathbf{P}_\rho^{-1} \mathbf{g}_\rho = \frac{5+2h^2}{16}$$

The increase in accuracy by using this index, $(\mathbf{g}_\rho^T \mathbf{P}_\rho^{-1} \mathbf{g}_\rho)^{1/2}$, ranges from a low of 0.56 when $h^2 \simeq 0$ to a high of 0.66 when $h^2 \simeq 1$, so that (recalling Equation 34.11d) using the values from the mother and grandmother to construct an index is about 60 percent as efficient as knowing an individuals phenotypic value.

Example 34.4. Consider the response under **sib selection**. Here n sibs are measured and based on the mean value of these individuals, the family is either accepted or rejected. If the family is accepted, other (unmeasured) sibs are used as parents to form the next generation. This is a model for selection when an individual must be sacrificed in order to reliably measure character value. Let r denote the additive-genetic correlation between sibs ($r = 1/4$ for half-sibs, $1/2$ for full-sibs) and $t = rh^2 + c^2$ be the phenotypic correlation between sibs (the intraclass correlation coefficient). The c^2 term accounts for any shared environmental family effects and dominance (Equation 34.17a). Under this design,

$$\mathbf{P}_\rho = \begin{pmatrix} 1 & t & \cdots & t \\ t & 1 & \cdots & t \\ \vdots & \vdots & \ddots & \vdots \\ t & t & \cdots & 1 \end{pmatrix} \qquad \text{and} \qquad \mathbf{g}_\rho = r \begin{pmatrix} 1 \\ 1 \\ \vdots \\ 1 \end{pmatrix} \tag{34.14a}$$

Using Equation 34.7 to obtain $\mathbf{P}_\rho^{-1}$ gives (after a little algebra) the index for predicting the breeding value from an individual from the ith family as

$$I = \frac{h^2 \, r}{1+(n-1)t} \sum_{j=1}^{n} (\, z_{ij} - \mu_z \,) = \frac{r \, n}{1+(n-1)t} \, (\, \overline{z}_i - \mu_z \,) \tag{34.14b}$$

where z_{ij} is the value of the jth sib in the ith family and $\overline{z}_i = n^{-1}\sum z_{ij}$ is the average value of the measured sibs for this family. Likewise, the increase in accuracy becomes

$$\sqrt{\mathbf{g}_\rho^T \mathbf{P}_\rho^{-1} \mathbf{g}_\rho} = \sqrt{\frac{n\, r^2}{1+(n-1)t}} = r\sqrt{\frac{n}{1+(n-1)t}} \tag{34.14c}$$

which for large n approaches $r/\sqrt{t}$. Hence, the response to selecting individuals based entirely on the mean of their sibs is

$$\overline{i}\,\sigma_g\, h\, r\sqrt{\frac{n}{1+(n-1)t}} \tag{34.14d}$$

as obtained by Robertson (1955) using a different approach. Note for large family size that both sib and between-family selection (Chapter 17 and next section) give essentially the same response. Sib and between-family selection differ only in that in the latter the individual is also measured. Thus for large family size, little is lost by not being able to measure an individual.

Example 34.5. We have frequently mentioned the **progeny test**, where the breeding value of a sire is estimated from the mean of n of his half-sibs. We can directly use results from Equation 34.4 to examine the effectiveness of this approach. Here, $\mathbf{P}_\rho$ and $\mathbf{g}_\rho$ are given by Equation 34.14a, where $t = h^2/4$ is the phenotypic covariance among the half-sibs (assuming common environmental effects can be ignored), and $r = 1/2$ for the genetic covariance between a parent and its offspring. Equations 34.11c and 34.14c gives the accuracy of progeny testing as

$$h\sqrt{\mathbf{g}_\rho^T \mathbf{P}_\rho^{-1} \mathbf{g}_\rho} = (h/2)\sqrt{\frac{n}{1+(n-1)(h^2/4)}} = \sqrt{\frac{n}{n+a}} \tag{34.15a}$$

where

$$a = \frac{4-h^2}{h^2}.$$

Finally, from Equation 34.14c the response is

$$\overline{i}\,\sigma_g\sqrt{\frac{n}{n+a}} \tag{34.15b}$$

as was found in Example 10.4 by other means. The progeny test has a long history in animal breeding, especially in dairy and (more recently) beef cattle. Lush (1931) considered the number of daugthers (progeny) needed to "prove" a sire, while Robertson (1957) obtained expressions for the optimal allocation of resources when the total number of sibs that can be reared is fixed because of economic or logistical constraints. The tradeoff is that when more sibs per sire are measured, we obtain a greater accuracy. However, more sibs per sire mean fewer sires are examined, and hence the selection intensity is decreased. James (1979) and Miraei Ashtiani and James (1993) extend these results to allow for prior information or a tested population that contains multiple strains (or lines).

WITHIN- AND BETWEEN-FAMILY SELECTION

A particularly common set of relatives to consider are the family members of an individual and often selection is practiced using both individual and family values. For examine, Chapter 17 considers within-in family selection (individuals selected solely on their deviations

from their family mean) and between-family selection (whole families are either saved or culled depending solely on their mean). A number of other family-based selection schemes have been proposed, such as **sib selection** (Example 34.4) and **progeny testing** (Example 34.5). Turner and Young (1969) review applications of these in animal breeding, while Wricke and Weber (1986) review the special types of family selection possible in plants and other organisms with asexual reproduction and/or selfing.

Our concern here is with **combined selection**, which incorporates both within- and between-family information by selecting on the index

$$I = b_1 \cdot (z - \overline{z}_f) + b_2 \cdot \overline{z}_f \tag{34.16a}$$

where $\overline{z}_f$ is the individual's family mean. Since b_1 weights the within-family deviation and b_2 weights the family mean, $(b_1, b_2) = (1, 0)$ corresponds to strict within-family selection, $(b_1, b_2) = (0, 1)$ to strict between-family selection, and $(b_1, b_2) = (1, 1)$ to individual selection. This index can equivalently be expressed as

$$I = b_1 \cdot z + (b_2 - b_1) \cdot \overline{z}_f \tag{34.16b}$$

showing that within- and between-family selection can be simply related to an index combining individual and between-family selection.

Lush's Index

Lush (1947) applied the Smith-Hazel index to obtain the optimal weighs for combined selection. To obtain his solution, consider the indirect index that optimizes the response in z given selection on the correlated characters $z_1 = z - \overline{z}_f$ (the within-family deviation) and $z_2 = \overline{z}_f$ (the family mean). To avoid separate expressions for half- and full-sib families, we express results in the notation of Chapter 17. Let t and r_A denote the phenotypic and additive genetic correlations (respectively) between sibs in an infinite population. These are related (LW Chapters 7, 18) by

$$t = r_A h^2 + c^2 \qquad \text{with} \qquad \frac{c^2}{\sigma_z^2} = \begin{cases} \sigma^2_{Ec(HS)} & \text{for half-sibs} \\ \\ \sigma_D^2/4 + \sigma^2_{Ec(FS)} & \text{for full-sibs} \end{cases} \tag{34.17a}$$

where $Ec(HS)$ and $Ec(FS)$ denote environmental effects common to half-sibs and full-sib families (respectively) and $r_A = 1/4$ for half sibs and $1/2$ for full sibs. In most cases half-sib families are formed by having a common father so that c^2 is expected to be negligible. Conversely, with full-sibs maternal effects can be quite important and hence c^2 considerable. Finally note that $c^2 < 1 - h^2$ so that c^2 is significant only when heritability is low. For a family of n sibs, the phenotypic and additive genetic correlations have to be corrected slightly to account for finite population size, and we use a slight modification of the notation introduced in Chapter 17,

$$t_n = t + \frac{1-t}{n} \qquad \text{and} \qquad r_{A,n} = r_A + \frac{1 - r_A}{n} \tag{34.17b}$$

The modification is that (in Chapter 17) r_A and $r_{A,n}$ were indicated as r and r_n. Here we attach the additona A subscript to stress that the correlation is among breeding values. To obtain the covariances required to construct the Smith-Hazel index, first note that $\sigma_{z_1,z_2} = 0$ as deviations from the mean and the mean itself are independent. For the index, let the "trait" z_1 denote the within-family deviation $z - \overline{z}_f$, while z_2 denotes the family mean $\overline{z}_f$. Recalling Equations 17.9a and 17.10b, $\sigma^2_{z_2} = t_n\, \sigma^2_z$ and $\sigma^2_{z_1} = (1 - t_n)\, \sigma^2_z$ giving the phenotypic correlation matrix as

$$\mathbf{P}_\rho = \begin{pmatrix} 1 - t_n & 0 \\ 0 & t_n \end{pmatrix} \tag{34.18a}$$

Similarly, the vector of genetic correlations of $(z_1, z_2)^T$ with z are

$$\mathbf{g}_\rho = \begin{pmatrix} 1 - r_{A,n} \\ r_{A,n} \end{pmatrix} \tag{34.18b}$$

Applying Equation 34.11a gives the vector of index weights as

$$\mathbf{P}_\rho^{-1}\mathbf{g}_\rho = \begin{pmatrix} \dfrac{1-r}{1-t} \\ \dfrac{1+n(1-r)}{1+n(1-t)} \end{pmatrix} = \begin{pmatrix} \dfrac{1-r}{1-t} \\ \dfrac{r_{A,n}}{t_n} \end{pmatrix} \tag{34.18c}$$

giving the **Lush index** that optimally weights the within- and between-family effects as

$$I = (z - \overline{z}_f) + \left(\frac{r_{A,n}}{t_n}\right)\left(\frac{1-t}{1-r}\right)\overline{z}_f \tag{34.19}$$

We have rescaled the index to emphasize the relative weighting of within-family deviation versus family mean.

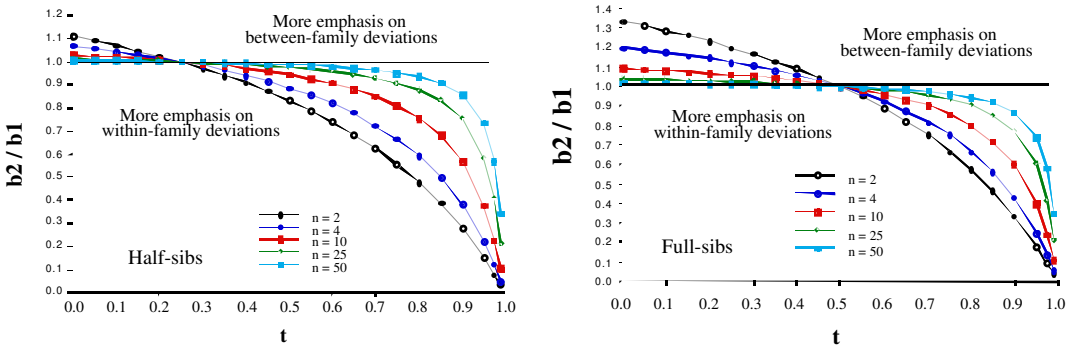

Figure 34.1. The relative weights under the Lush index of family means to within-family deviation (b_2/b_1) as a function of number of sibs n and correlation between sibs t. When $b_2/b_1 > 1$, more weight is placed on family mean (or equivalently, on between-family deviations), while more weight is placed on within-family deviations when $b_2/b_1 < 1$. Note that $b_1 = b_2$ corresponds to individual selection.

Figure 34.1 plots how these relative weights change as a function of t and n. If family size is infinite, within-family deviations and family means receive equal weight, and the Lush index reduces to individual selection (as $I = (z - \overline{z}_f) + \overline{z}_f = z$). For finite n, more weight is placed on within-family deviations when $t > r_A$ (phenotypic similarity between sibs exceeds their additive-genetic similarity) while family means receive more weight when $r_A > t$ (additive-genetic similarity exceeds phenotypic similarity). Significant family environmental effects are required for $t = r_A h^2 + c^2 > r_A$, so that within-family deviations receive more weight only if shared-family environmental effects are very important.

The Lush index can be rearranged to assign weights to individual and family mean values,

$$I = z + \left(\frac{r_A - t}{(1 - r_A)[\,1 + n(1-t)\,]}\right) \cdot \overline{z}_f \tag{34.20}$$

implying that family mean receives negative weight when $t > r_A$, as occurs when common environmental effects are very large. In such cases, much of the between-family differences are environmental rather than genetic and between-family differences are discounted in favor of within-family deviations.

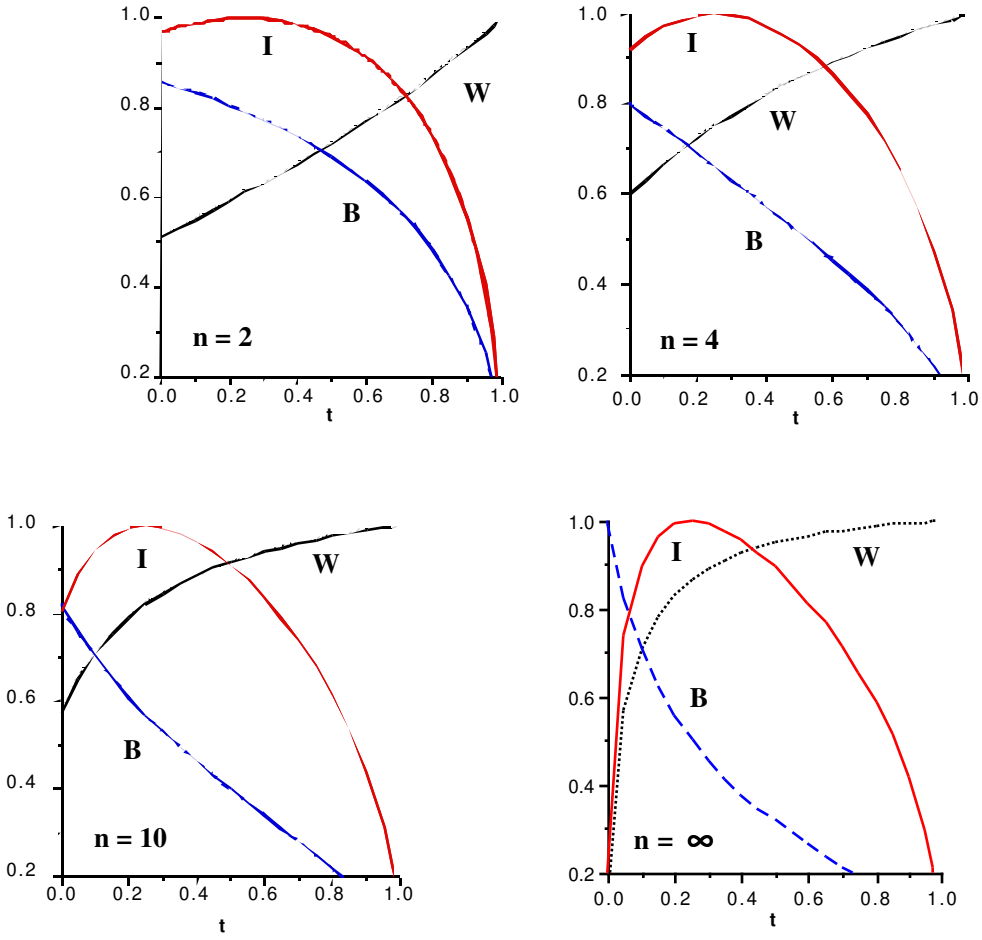

Figure 34.2. Expected single generation response in an infinite population of individual (I), strict within-family (W), and strict between-family (B) selection relative to that of the Lush index (whose response is scaled to give a value of one) for half-sibs as a function of number of sibs n and correlation between sibs t. For half-sibs, it is generally expected that $t = h^2/4$ so that values of $t > 1/4$ occur only in highly usual situations.

To obtain the expected response to selection on the Lush index, note first that

$$\mathbf{g}_\rho^T \mathbf{P}_\rho^{-1} \mathbf{g}_\rho = 1 + \frac{(n-1)(t-r_A)^2}{(1-t)[1+t(n-1)]} \tag{34.21a}$$

Applying Equation 34.11d gives the response in z as

$$\frac{R_z}{\bar{\imath}} = h\,\sigma_g \sqrt{1 + \frac{(n-1)(t-r_A)^2}{(1-t)[1+t(n-1)]}} \tag{34.21b}$$

More generally, consider the response to selection on the index $I = b_1(z - \overline{z}) + b_2 \cdot \overline{z}_f$ for arbitrary b_1 and b_2. Taking the vector of characters as $\mathbf{z} = (z, z - \overline{z}_f, \overline{z}_f)^T$ and substituting $\mathbf{a} = (1, 0, 0)^T$ and $\mathbf{b} = (0, b_1, b_2)^T$ into Equation 33.6 gives the response in z as

$$\frac{R_z}{\overline{t}} = h\,\sigma_g\,\frac{b_1\,(1 - r_{A,n}) + b_2\,r_{A,n}}{\sqrt{b_1^2\,(1 - t_n) + b_2^2\,t_n}} \tag{34.22}$$

Figures 34.2 (half-sibs) and 34.3 (full-sibs) plots of responses of individual ($b_1 = b_2$), strict within-family ($b_1 = 1, b_2 = 0$) and strict between-family section ($b_1 = 0, b_2 = 1$) relative to the response under the Lush index. Note that r_A must be significantly different from t (additive-genetic similarity is much different from phenotypic similarity) for the index to be significantly superior to individual selection.

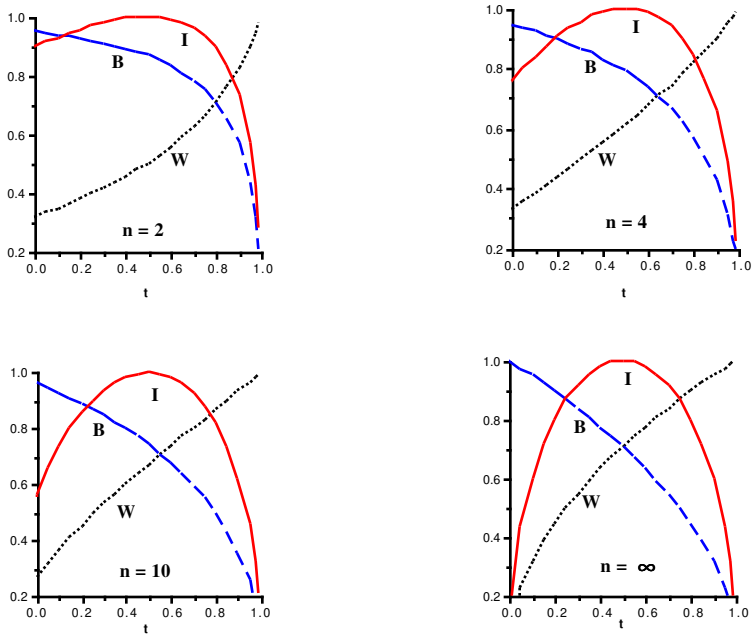

Figure 34.3. Expected single generation response in an infinite population of individual (I), strict within-family (W), and strict between-family (B) selection relative to that of the Lush index for full-sibs as a function of number of sibs n and correlation between sibs t.

One must be cautious of these comparisons of the relative efficiency of the Lush index as they are potentially misleading for several reasons (Chapter 17). First, they assume selection intensities are the same in all comparisons, as one might (naively) expect if the same fraction of individuals is culled for each method. We have seen that finite population size results in overestimation the expected selection intensity (Chapter 10). A second (and more subtle) source of overestimation is correlations between individuals, as occurs when multiple individuals from the same family are selected. Hill (1976, 1977) and Rawlings (1976) examined this problem, with Hill providing tables of exact values and approximate expressions (which depend on n, t, and the number of families) for the expected selection intensities when individuals are correlated. Meuwissen (1991) extends these results to nested full-half sib family structures. When a small number of families is used, the selection intensity of

the Lush index can be significantly below the value predicted by ignoring within-family correlations. Hence, proper comparisons must first correct for potential differences in the expected selection intensity (Chapter 17).

A second concern is that these comparisons are correct for only a single generation of selection from an unselected base population. Selection generates gametic-phase disequilibrium (Chapters 13, 31) and increases inbreeding (Chapter 26), both of which have a larger effect on between-family selection (Robertson 1961, Burrows 1984, Toro et al. 1988). Gametic-phase disequilibrium reduces between-family additive genetic variance while leaving within-family additive variance unchanged (Chapter 13), while selection entirely within a family results in less inbreeding (and hence less reduction in additive variance) than selection entirely between families (Chapter 26). As selection proceeds both these forces increase the importance of within-family effects relative to between-family effects, so that individual value becomes weighted more and family mean less. Wray and Hill (1989) note that while the relative efficiency of combined selection over individual selection may be greatly diminished by gametic-phase disequilibrium, the relative rankings of the methods still hold. Given that inbreeding is greater when more weight is placed on between-family differences, there has been interest in the "optimal" family weights to maximize response while minimizing inbreeding (e.g., Lindgren et al. 1993, Wei 1995). This is an important topic which is examined in detail in Chapter 35.

A final concern is that, as with any index, population parameters have to be correctly estimated or the index constructed from these estimates has incorrect weights and is less than optimal. Fortunately, for the Lush index only the intraclass correlation t must be estimated, and Sales and Hill (1976) have shown that the efficiency of combined selection is quite robust to estimation errors in t (as initially suggested by Lush 1947).

Based on these concerns, it is not surprising that experimental verification of the advantage of the Lush index over individual or family selection is mixed. McBride and Robertson (1963) and Avalos and Hill (1981) found that combined selection gave a larger response than individual selection for abdominal bristles in *Drosophila melanogaster*. More conclusive results for selection on the same character were those of James (cited in Frankham 1982), who found that the observed increase in response under combined selection was $133 \pm 9.7\%$ and $111 \pm 7\%$ in two replicates, very consistent with the expected increase of 121%. Experiments using egg production in poultry was less conclusive, with Kinney et al. (1970) finding that individual selection gave a larger (but not significant) response than combined selection, while Garwood and Lowe (1981) found that combined selection gave a larger response (again not significant) that family selection. Larval and pupal weight in *Tribolium* showed similar mixed results, with Wilson (1974) finding that individual selection gave the largest response, while Campo and Tagarro (1977) did not find any significant differences (combined selection gave a larger response in a replicate with large family size, while individual selection showed the larger response in a replicate with small family size).

Osborne's Index

Finally, a more general combined index was considered by Osborne (1957b, c) which incorporates information from both full- and half-sib families. Osborne assumed the classic full-/ half-sib hierarchical design (LW Chapter 18) wherein a sire is mated to d dams, each of which has n sibs. Under this design each of the d families consists of n full sibs which are also half-sibs with respect to offspring from the other dams mated to the same sire. The resulting index to maximize response in z is constructed by considered three correlated characters: $z_1 = z - \overline{z}_{FS}$ (the deviation within full-sib families), $z_2 = \overline{z}_{FS} - \overline{z}_{HS}$ (the deviation between different full sib families from the same size) and $z_3 = \overline{z}_{HS}$ where $\overline{z}_{FS}$ is the mean of that individual's full-sib family (all offspring from the same dam) and $\overline{z}_{HS}$ the half-sib mean of the individual (the mean of all offspring from that individual's sire). Denoting the intr-

aclass correlation between half- and full-sibs by t_H and t_F, respectively, the corresponding phenotypic correlation matrix is diagonal with

$$(n\,d)\cdot(\mathbf{P}_\rho)_{ii} = \begin{cases} d(n-1)(1-t_H-t_F) & \text{for } i=1 \\ (d-1)[\,1-t_H+(n-1)t_F\,] & \text{for } i=2 \\ 1-(n-1)t_F+(nd-1)t_H & \text{for } i=3 \end{cases} \tag{34.23a}$$

and the vector of additive genetic correlations with z becomes

$$\mathbf{g}_\rho = (4nd)^{-1}\begin{pmatrix} 2d(n-1) \\ (d-1)(n+2) \\ 2+d+dn \end{pmatrix} \tag{34.23b}$$

Upon rescaling (to give full-sib family deviation weight one), the resulting index becomes

$$(\,z-\overline{z}_{FS}\,)+\frac{(2+n)(1-t_F-t_H)}{2(1+t_F(n-1)-t_H)}\,(\,\overline{z}_{FS}-\overline{z}_{HS}\,)+\frac{[\,2+d(1+n)\,]\,[\,1-t_F-t_H\,]}{2[\,1+t_F(1-n)+t_H(dn-1)\,]}\,\overline{z}_{FS} \tag{34.24a}$$

A bit of algebra shows that $\mathbf{g}_\rho^T\mathbf{P}_\rho^{-1}\mathbf{g}_\rho$ equals

$$\frac{n-1}{4n(1-t_F-t_H)}+\frac{(d-1)(2+n)^2}{16dn(1+t_F(n-1)-t_H)}+\frac{(2+d+dn)^2}{16dn[\,1-t_F(n-1)+t_H(dn-1)\,]} \tag{34.24b}$$

Substituting into Equation 34.11d gives the expected response under this index. Osborne (1957b) presents graphs for the relative weights, but under the restrictive assumption of $t = r_A\,h^2$ (no dominance or common familial environmental effects). To construct the Osborne index only two parameters, t_F and t_H, must be estimated. Sales and Hill (1976) show that although the index is more sensitive to poor estimates of t_H than of t_F, it (like the Lush index) is rather robust to errors in either estimated parameter.

The various selection indices developed in this chapter assume defined sets of relatives under balanced samples (i.e., the same number of sibs in each family). This is clearly an idealization of the real world with its highly unbalanced designs and much more diverse sets of relatives. Fortunately, the concept of a selection index can be extended to predict the breeding values for any collection of relatives with a known pedigree (i.e., the relationship matrix **A** among the individuals in question). This is the notion of BLUP (Chapter 16; LW Chapters 26, 27) and selection using BLUPs is the subject of the next chapter.

SELECTION ON A RATIO

Occasionally, it is desirable to select on the ratio of two measured characters. **Feed efficiency**, defined as the ratio of feed intake to growth rate, is a classic example from animal breeding (Lin 1980). There is typically negative selection on this ratio, as the breeder attempts to extract greater growth from smaller feed intake. There are also numerous examples of ratios in plant breeding. One is the **performance index** (Sullivan and Kannenberg 1987), the ratio of grain yield to percent of grain moisture, which is under positive selection to increase yield while decreasing seed moisture. Other plant breeding examples include the leaf-to-stem ratio (Buxton et al. 1987), the ratio of seed weight to biomass which is also known as the **harvest index** (Sharma and Smith 1986), and nitrogen and water-use efficiency indices (Youngquist et al. 1992, Ehdaie and Waines 1993).

Let $r = z_1/z_2$ be the desired ratio based on characters z_1 and z_2. One approach would simply be to treat this as a new trait and apply the standard machinery of the univariate

breeder's equation (e.g., Chapter 10). The problems with this approach are two-fold. First, this machinery makes assumptions of normality that are not appropriate for a ratio. If both z_1 and z_2 are normally-distributed, their ratio is not, rather it is the dreaded Cauchy, a pathological distribution with no defined mean and an infinite variance. The bounded (i.e., finite) range of biological systems avoids some of the more unpleasant aspects of the Cauchy, but the result is still a very heavy-tailed distribution. Computer simulations by Rowe (1995, 1996) show that using standard machinery underestimates the expected gain when selecting to increase the ratio and overestimates the gain when selecting to decrease it.

The second issue is that if we know the individual components that comprise the ratio, we can do better by selecting on them than we can by directly selecting on the ratio, as direct selection on r is less efficient than selection on an index based on z_1 and z_2 (Gunsett 1984, 1986, 1987; Mather et al. 1988; Campo and Rodríguez 1990). Given these issues, three general approaches have been suggested selecting on a ratio. First, Turner (1959) suggested taking logs to give the linear index $I = y_1 - y_2$ using the new characters y_1 and y_2 where $y_i = \ln(z_i)$ and gives expressions for the heritability of a ratio in this case. The downside to this approach it that it requires obtaining estimates of the phenotypic and additive-genetic covariance matrices for the transformed vector $\mathbf{y}$. Further note that I is really the merit function, and hence not the optimal weights on which to select, which are given by the Smith-Hazel index expressed in terms of the genetic and phenotypic covariance matrices of $\mathbf{y}$ and with weights $\mathbf{a}^T = (1, -1)$. The second class of approaches are either linear selection indices or combinations of linear indices, while the final approach is selecting on the ratio directly, but predicting response by following the changes in component means. We examine each of these in turn.

Since the merit function is nonlinear, several of the concerns raised in Chapter 33 need to be addressed before proceeding. First, how does the function change as a result of changes in the means of the components? The expected value of r can be expressed as

$$E[r] = E\left[\frac{z_1}{z_2}\right] = \frac{E[z_1]}{E[z_2]} - \frac{\sigma(z_1/z_2, z_2)}{E[z_2]}, \tag{34.25a}$$

as given by Lin (1980). This immediately follows, upon rearrangement, from the definition of the covariance between z_1/z_2 and z_2,

$$\begin{aligned}\sigma(z_1/z_2, z_2) &= E[(z_1/z_2) \cdot z_2] - E[z_1/z_2] \cdot E[z_2] \\ &= E[z_1] - E[z_1/z_2] \cdot E[z_2]\end{aligned} \tag{34.25b}$$

Hence, the expected value of the ratio is only equal to the ratio of expected values when the second term in Equation 34.25a is negligible. Note that even if z_1 and z_2 are uncorrelated at the start of selection, LD generated by selection can cause them to become correlated during selection, which in turn changes the value of $\sigma(z_1/z_2, z_2)$. When this second term is small, the expected change in the merit function can be approximated by considering the expected change in the ratio given the changes in breeding values,

$$\Delta H = \Delta\left(\frac{g_1}{g_2}\right) \simeq \frac{E[z_1 + \Delta g_1]}{E[z_2 + \Delta g_2]} - \frac{E[z_1]}{E[z_2]} = \frac{\mu_1 + \Delta g_1}{\mu_2 + \Delta g_2} - \frac{\mu_1}{\mu_2} \tag{34.25c}$$

Approximate Linear Indices for Ratio Selection

Chapter 33 noted that while an appropriate linear index usually outperforms a nonlinear index, the issue is how to construct the optimal linear index. When Equation 34.25c is a good

approximation, then again following Lin (1980), the expected change in the merit function can be approximated as

$$\begin{aligned}\Delta H &= \frac{\mu_1 + \Delta g_1}{\mu_2 + \Delta g_2} - \frac{\mu_1}{\mu_2} = \frac{\mu_2 \Delta g_1 - \mu_1 \Delta g_2}{\mu_2(\mu_2 + \Delta g_1)} \\ &= \frac{\mu_2}{\mu_2(\mu_2 + \Delta g_1)} \left(\Delta g_1 - \frac{\mu_1}{\mu_2} \Delta g_2 \right) \end{aligned} \tag{34.26a}$$

Since only the relative weights matter in an index, we can ignore the common term in the last line of Equation 34.26a, giving the linearized merit function as

$$H \simeq g_1 - \frac{\mu_1}{\mu_2} g_2 \tag{34.26b}$$

where μ_i is the current mean of character i, so that the economic weights change each generation to reflect changes in character means. The Smith-Hazel index each generation is constructed by using either $\mathbf{a}^T = (1, -\mu_1/\mu_2)$ or (equivalently) $\mathbf{a}^T = (\mu_2, -\mu_1)$. An advantage of putting this problem into a Smith-Hazel framework is that we can use existing theory to predict the response (e.g., Equation 33.19). Gunsett (1984) also obtained these same weights through a different route, namely by finding the (linear) index of z_1, z_2 that maximizes the correlation with the ratio of breeding values g_1/g_2. Finally, these weights also follow by approximating H by a first-order Taylor series (Equation A5.6), as suggested in Chapter 33. Since

$$\left.\frac{\partial z_1/z_2}{\partial z_1}\right|_{z_1=\mu_1} = \frac{1}{\mu_2}, \quad \text{and} \qquad \left.\frac{\partial z_1/z_2}{\partial z_2}\right|_{z_2=\mu_2} = \frac{-\mu_1}{\mu_2^2}$$

the vector of economic weights again becomes

$$\mu_2 \cdot \mathbf{a} = \begin{pmatrix} 1 \\ -\mu_1/\mu_2 \end{pmatrix}$$

Example 34.6 Consider the ratio of z_1/z_2, where

$$\boldsymbol{\mu} = \begin{pmatrix} 2000 \\ 850 \end{pmatrix}, \qquad \mathbf{P} = \begin{pmatrix} 40000 & 7200 \\ 7200 & 6400 \end{pmatrix}, \qquad \mathbf{G} = \begin{pmatrix} 16000 & 2560 \\ 2560 & 2560 \end{pmatrix}$$

From Equation 34.26b, the resulting vector of weights becomes

$$\mathbf{a} = \begin{pmatrix} 1 \\ -2000/850 \end{pmatrix} = \begin{pmatrix} 1.000 \\ -2.353 \end{pmatrix}$$

Suppose the lower 5% of the population is selected (as would occur when selecting to *decrease* a ratio, such as feed efficiency), so that $\overline{i} = -2.06$. From Equation 33.20, the response in the two components is given by

$$\mathbf{R} = \overline{i} \cdot \frac{\mathbf{G}\mathbf{P}^{-1}\mathbf{G}\mathbf{a}}{\sqrt{\mathbf{a}^T \mathbf{G}\mathbf{P}^{-1}\mathbf{G}\mathbf{a}}} = \begin{pmatrix} -100.08 \\ 35.32 \end{pmatrix}$$

Approximating the mean of the ratio $E[r]$ by the ratio of the means (Equation 34.25c), the response in the ratio under this index becomes

$$\Delta r \simeq \frac{2000 - 100.08}{850 + 35.32} - \frac{2000}{850} = 2.146 - 2.353 = -0.207$$

Other Linear-based Indicies for Ratio Selection

An alternative approach considered by Famula (1990) and Campo and Rodríguez (1990) is motivated by Equation 34.25c. The idea is to construct a nonlinear index I_r consisting of the ratio of two linear indices,

$$I_r = \frac{I_1}{I_2} = \frac{\mathbf{b}_1^T(\mathbf{z} - \boldsymbol{\mu})}{\mathbf{b}_2^T(\mathbf{z} - \boldsymbol{\mu})} \tag{34.27a}$$

where I_i is the index that gives the best linear predictor of the breeding value of character i using information from both z_1 and z_2. One then selects using the I_r values of each individual. This should be an improvement in predicting the value of g_i over that predicted just using the value of z_i alone unless both characters are phenotypically and genetically uncorrelated. Applying Equation 34.2a, the weights of these linear indices are given by

$$\mathbf{b}_1 = \begin{pmatrix} \sigma^2_{z_1} & \sigma_{z_1,z_2} \\ \sigma_{z_1,z_2} & \sigma^2_{z_2} \end{pmatrix}^{-1} \begin{pmatrix} \sigma^2_{g_1} \\ \sigma_{g_1,g_2} \end{pmatrix}, \quad \mathbf{b}_2 = \begin{pmatrix} \sigma^2_{z_1} & \sigma_{z_1,z_2} \\ \sigma_{z_1,z_2} & \sigma^2_{z_2} \end{pmatrix}^{-1} \begin{pmatrix} \sigma_{g_1,g_2} \\ \sigma^2_{g_2} \end{pmatrix} \tag{34.27b}$$

The difference between this non-linear index and the Smith-Hazel index constructed using Equation 34.26a is that the latter attempts to predict the ratio directly, while the nonlinear index attempts to predict the denominator and numerator separately. A disadvantage of the nonlinear approach is that existing theory cannot be use to predict response.

Which Method is Best?

Which of the three approaches — Smith-Hazel approximation, ratio of linear indices, direct selection on the ratio — is best? Direct selection on the ratio is not recommended for two reasons. First, the Smith-Hazel approximation generally provides a larger response. Second, the ratio can change in the desired direction for undesirable reasons. For example, ideally feed efficiency is decreased by both lowering the rate of feed intake and increasing the growth rate. However, selection could reduce *both*, giving improvement in feed efficiency but the undesirable result of reduced growth. With a linear index, we can exert more control over the behavior of the components.

This leaves the two linear-index based approaches as useful candidates. While Famula (1990) showed theoretically that there is should be very little difference between these two approaches, this was not observed by Campo and Rodríguez (1990), who selected for increased values of egg mass/adult weight ratios in *Tribolium castaneum*. They found that this ratio did not respond to direct selection (response after three generations was $R = 0.82 \pm 1.56$). Selection on a linear index with economic weights given by Equation 34.26a was effective ($R = 1.92 \pm 0.44$), while the greatest response was observed by selection on the nonlinear index given by Equation 34.27a ($R = 5.94 \pm 1.52$). Hence while selection using either index was more efficient that selecting directly on the character, the nonlinear index produced the largest response.

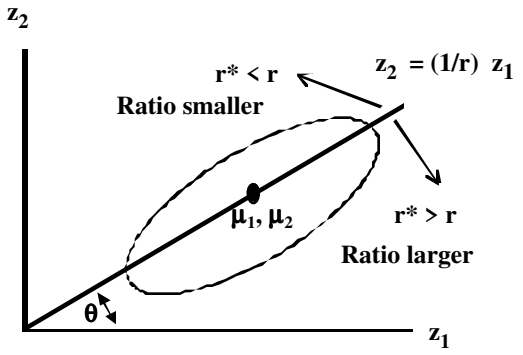

Figure 34.4. Ratio selection when both components are bivariate-normally distributed. The trait of interest is the ratio $r = z_1/z_2$. Values of (z_1, z_2) corresponding to the same ratio r are those that lie along the line $z_2 = (1/r)z_1$, a line through the origin with slope $1/r$. Values above this line have a smaller value for the ratio than r, while values below this line give larger values for the ratio. The easy way to see this is to note that large z_1 and small z_2 yield a large ratio value, while large z_2 and small z_1 give a small ratio value. Thus, if we select individuals above the line passing through the population means, we are selecting for smaller ratios ($r^* < r$), while if we select individuals below this line we are selecting for larger ratios ($r^* > r$). Likewise, changes in the angle θ between this line and the z_1 axis describes the nature of selection. Increasing θ corresponds to selection for a smaller ratio, while decreasing θ corresponds to a larger ratio.

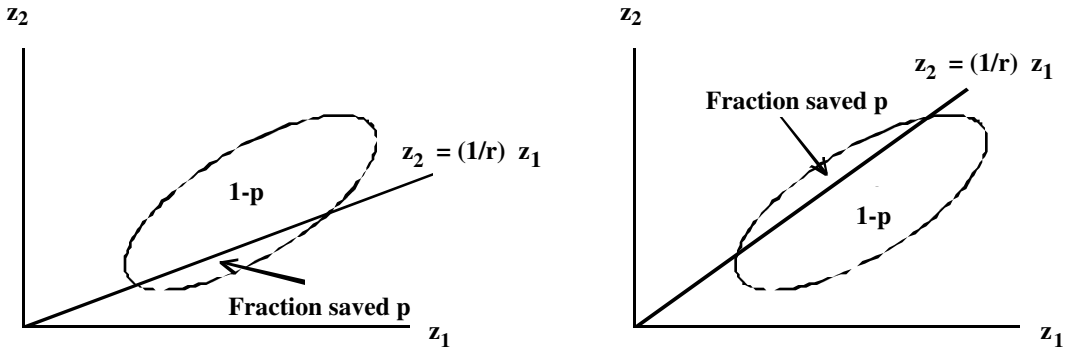

Figure 34.5. The relationship between the threshold ratio score $r_{[p]}$ (simply listed as r in the figure for brevity) and the bivariate distribution of the traits. The problem here is, for a given value of p, to solve for the critical value $r_{[p]}$ such that $\Pr(r \leq r_{[p]}) = p$. For a set cutoff value of r, we have $z_1/z_2 = r$ or $z_2 = (1/r)z_1$, a line passing through the origin with slope $1/r$. **Left:** When selecting to *increase* this ratio (i.e., larger z_1 and smaller z_2), we select those individuals lying *below* this line. Stronger selection decreases the angle between the line and the z_1 axis. **Right:** When selecting to *decrease* this ratio (negative selection), individuals lying *above* the line are selected. Stronger selection increases the angle between this line and the z_1 axis. Note in both cases that by rotating the line (changing the selection intensity) we also change the selection differential unevenly on the two traits. Hence, the selection differential ratio S_1/S_2 for the two traits is not fixed (as would occur with index selection), but rather is a function of the selection intensity.

Selection Directly on a Ratio: Selection Differentials and Response

While selection directly on a ratio is not generally recommended, it is still of interest to examine the behavior of response in such cases. We can approximate the response in the ration using Equation 34.25c, with the vector of responses in each trait given from the breeder's equation $\mathbf{R} = \mathbf{G}\mathbf{P}^{-1}\mathbf{S}$. The issue is obtaining the vector of selection differentials given selection on the ratio, a topic considered by Gunsett (1984) and Mather et al. (1988). These papers assumed selection by truncation selection on either the upper p percent (positive selection to increase the ratio) or the lower p percent (negative selection to decrease the ratio) of measured individuals. Calculation of $\mathbf{S}$ occurs in two stages. The first is obtaining the threshold value $r_{[p]}$ for the ratio that sets the upper (or lower) fraction p of the population, and then with this value of $r_{[p]}$ in hand, obtaining $\mathbf{S}$.

The issue with obtaining the critical value of r given a set amount of truncation selection p is displayed in Figure 34.5. Here, the confidence region for the joint distribution of the z_1, z_2 phenotypes is plotted, and the fraction of individuals whose ratio is great than or equal to $r = z_1/z_2$ is that fraction of the distribution lying *below* the line $z_2 = (1/r)z_1$ (e.g., Figure 34.5 Right). Conversely, if we select for decreased r values we choose individuals laying *above* this line. The key feature of selection, which is hinted at in the figure, is that the selection differentials on the two traits are *very asymmetric*, and the disparity between then is a function of selection intensity. This has two immediate consequences. First, if the selection intensities are different in the two sexes (as often happens with domesticated animals), then the relative amounts of selection on the two components can vary over sexes. This does not happen under linear index selection, as the ratio of the selection weights is unchanged. Note, however (Chapter 33), that when using a linear index to approximate a nonlinear index that the weights can indeed be a function of the selection intensity and hence can change with changes in $\bar{\imath}$. Second, as a consequence of this differential change in the relative amounts of selection, the breeder has much less control over changes in the component traits than would occur when using a linear index.

We now (briefly) turn to the somewhat technical issue of obtaining the critical value $r_{[p]}$ given a fraction p is selected and the translation of this into the vector of selection differentials $\mathbf{S}$. A worked example follows the derivations. We consider the case of negative selection, a decrease in the ratio, as the results for positive selection follows from symmetry. We seek that value $r_{[p]}$ of the ratio such that only p percent of the population have this value (or smaller). By definition, $r_{[p]}$ satisfies

$$\Pr(z_1/z_2 < r_{[p]}) = \Pr(z_1 < r_{[p]}z_2) = \Pr(z_1 - r_{[p]}z_2 < 0) = p \tag{34.28a}$$

Assuming both traits are MVN distributed, then $z_1 + az_2$ is also normal, with mean $\mu_1 + a\mu_2$ and variance $\sigma_1^2 + a^2\sigma_2^2 + 2a\sigma_{1,2}$. Defining $y = z_1 - r_{[p]}z_2$, we have

$$\mu_y = \mu_1 - r_{[p]}\mu_2, \quad \text{and} \quad \sigma_y^2 = \sigma_1^2 + r_{[p]}^2\sigma_2^2 - 2r_{[p]}\sigma_{1,2}$$

Hence, we have

$$U = \frac{y - \mu_y}{\sigma_y}$$

is a unit normal random variable. Hence, we can rewrite 34.28a as

$$\Pr(z_1/z_2 < r_{[p]}) = \Pr(y < 0) = \Pr\left(\frac{y - \mu_y}{\sigma_y} < \frac{-\mu_y}{\sigma_y}\right) = \Pr\left(U < \frac{-\mu_y}{\sigma_y}\right) = p \tag{34.28b}$$

The middle expression follows by subtracting μ_y from sides and then dividing by σ_y. Recalling Equation 10.25a, we defined $z_{[p]}$ as satisfying $\Pr(U < z_{[p]}) = p$. Hence,

$$z_{[p]} = \frac{-\mu_y}{\sigma_y} = \frac{-(\mu_1 - r_{[p]}\mu_2)}{\sqrt{\sigma_1^2 + r_{[p]}^2\sigma_2^2 - 2r_{[p]}\sigma_{1,2}}} \tag{34.29a}$$

Equation 34.29a can be algebraically solved for the threshold value $r_{[p]}$ to give (Mather et al. 1988)

$$r_{[p]} = \frac{\mu_1^2 - z^2\sigma_1^2}{\mu_1\mu_2 - z^2\sigma_{12} + \delta\epsilon\sqrt{(\mu_1\mu_2 - z^2\sigma_{12})^2 - (\mu_1^2 - z^2\sigma_1^2)(\mu_2^2 - z^2\sigma_2^2)}} \tag{34.29b}$$

where we write $z_{[p]}$ simply as z for brevity, and δ and ϵ are indicator variables with

$$\delta = \begin{cases} 1 & \text{if } p < 0.5 \\ -1 & \text{if } p > 0.5 \end{cases}, \qquad \epsilon = \begin{cases} 1 & \text{for negative selection on } r \\ -1 & \text{for positive selection on } r \end{cases} \tag{34.29c}$$

Example 34.7 Suppose we are selecting to decrease a ratio and wish the cuttoff value such that only 5% of the population should have this small a ratio value. Thus, $\Pr(U < z_{[p]}) = 0.05$, or (using the **R** command **`qnorm(0.05)`**), $z_{[p]} = -1.64$. Suppose our two traits are normally distributed with the means and phenotypic covariances as in Example 34.6,

$$\mu_1 = 2000, \quad \mu_2 = 850, \quad \sigma_1^2 = 40000, \quad \sigma_2^2 = 6400, \quad \sigma_{12} = 7200$$

Hence, the starting mean ratio (approximated as the ratio of the means) is 2000/850 = 2.35. Applying Equation 34.29b returns $r_{[0.05]}$ = 1.98. As a check, substitution into Equation 34.29a gives

$$z = \frac{-(2000 - 1.98 \cdot 850)}{\sqrt{40000 + 1.98^2 \cdot 6400 - 2 \cdot 1.98 \cdot 7200}} = -1.64$$

returning (as expected) $z_{[0.05]}$. Hence, for these distributional values, only 5% of the population should have a ratio of 1.98 or less.

Given the critical value $r_{[p]}$ (henceforth simply r for brevity) Mather et al. (1988) obtained expresses for the selection differentials on the component traits by integrating the appropriate truncated slice of the bivariate distribution to obtain the conditional means within the selected region. For the numerator trait (z_1), the resulting differential is

$$S_1 = \frac{\epsilon\,\gamma_1\sigma_1}{p\sqrt{2\pi(1+\alpha_1^2)}}\,\exp\left(-\frac{\beta_1^2}{2(1+\alpha_1^2)}\right) \tag{34.30a}$$

where p is the fraction saved,

$$\alpha_1 = \frac{r\sigma_2\sqrt{1-\rho^2}}{\sigma_1 - r\sigma_2\rho}, \quad \beta_1 = \frac{r\mu_2 - \mu_1}{\sigma_1 - r\sigma_2\rho}, \quad \gamma_1 = \begin{cases} 1 & \text{if } \sigma_1 < r\sigma_2\rho \\ -1 & \text{if } \sigma_1 > r\sigma_2\rho \end{cases} \tag{34.30b}$$

with $r = r_{[p]}$, ρ is the phenotypic correlation, and ϵ as in Equation 34.29c. Similarly,

$$S_2 = \frac{\epsilon\,\gamma_2\sigma_2}{p\sqrt{2\pi(1+\alpha_2^2)}}\,\exp\left(-\frac{\beta_2^2}{2(1+\alpha_2^2)}\right) \tag{34.31a}$$

where

$$\alpha_2 = \frac{\sigma_1\sqrt{1-\rho^2}}{r\sigma_2 - \sigma_1\rho}, \quad \beta_2 = \frac{\mu_1 - r\mu_2}{r\sigma_2 - \sigma_1\rho}, \quad \gamma_2 = \begin{cases} 1 & \text{if } r\sigma_2 > \sigma_1\rho \\ -1 & \text{if } r\sigma_2 < \sigma_1\rho \end{cases} \tag{34.31b}$$

While these equations may look a little busy, an important biological feature follows directly from them, namely that

$$\text{sign}(S_i) = \text{sign}(\gamma_i \cdot \epsilon) \tag{34.32}$$

If the phenotypic correlations are negative ($\rho < 0$), then $\gamma_1 < 0$ and $\gamma_2 > 0$, and the selection differentials on trait means are as expected. When there is selection to reduce the ratio (negative selection, $\epsilon = 1$), then $S_1 < 0$ and $S_2 > 0$, decreasing the mean of the numerator and increasing the mean of the denominator as might be expected. With selection to increase the ratio (negative selection, $\epsilon = -1$), the converse is true (again as expected). However, when the two traits are phenotypically positively correlated, S_1 and S_2 can have the same sign (either both positive or both negative) or can have different signs (Mather et al. 1988; Rowe 1995, 1996). Letting $\phi = \sigma_1/(r_{[p]}\sigma_2)$, then from Equations 34.30b and 34.31b we see that if $\phi < \rho < 1/\phi$ then $\gamma_i = 1$, while if $\phi > \rho > 1/\phi$ then $\gamma_i = -1$ (Figure 34.6). For example, if there is selection to decrease the ratio when $\phi < \rho < 1/\phi$, *both* the numerator and denominator with have positive selection differentials and hence *both means will increase*. The ratio still declines because the denominator means increases more quickly than the numerator mean. Likewise, if $\phi > \rho > 1/\phi$, the means of both traits decrease, but the numerator mean decreases more quickly, decreasing the ratio. Comparative behavior occurs when there is selection to increase the ratio under either of these parameter sets.

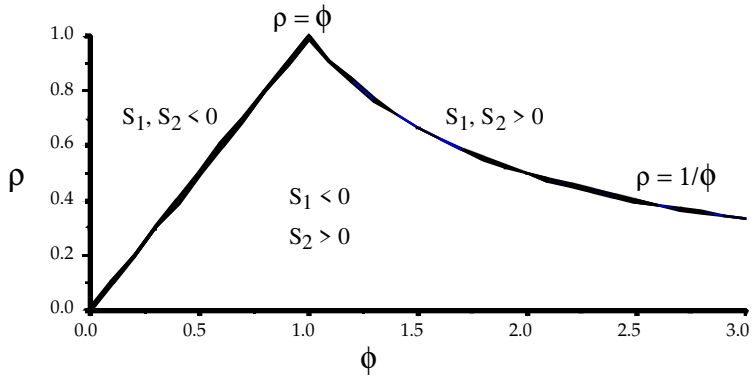

Figure 34.6. When the phenotypic correlation ρ between traits is positive, the signs of the selection differentials for the two components in the ratio can change in unexpected directions. The phase space for $\phi = \sigma_1/(r_{[p]}\sigma_2)$ and ρ given above is for negative selection (selection to reduce the ratio). Note in this case, we typically expect trait one (the numerator) to decrease and trait two (the denominator) to increase. This is precisely what occurs in the middle range of this phase space. However, there are also combinations of ϕ and ρ wherein both traits increase or both traits decrease. In these cases, the ratio still decreases because of differences in the rates of change in the mean. With selection to increase the ratio (positive selection), the signs are reversed above.

Example 34.8 Let's translate the ratio threshold from the last example into the selection differentials on both traits. Applying Equation 34.30 gives

Trait	α	β	γ	S
1	1.101	-2.447	-1	-277.3
2	2.603	4.587	1	59.2

Assuming the same $\mathbf{P}$ and $\mathbf{G}$ matrices as in Example 34.6 and 34.7, applying the multivariate breeder's equation gives the response in the component means as

$$\mathbf{R} = \mathbf{GP}^{-1}\begin{pmatrix} -277.3 \\ 59.2 \end{pmatrix} = \begin{pmatrix} -117.8 \\ 27.1 \end{pmatrix}$$

Using the approximation that the mean ratio is the ratio of the means, the values before and after a single generation of selection become

$$\mu_r \simeq \frac{\mu_1}{\mu_2} = \frac{2000}{850} = 2.353, \qquad \mu_r^* \simeq \frac{\mu_1^*}{\mu_2^*} = \frac{2000 - 117.8}{850 + 27.1} = 2.146$$

Hence, the selection response is $2.353 - 2.146 = -0.207$. Recall from Example 34.6 that this is the same response as that expected (given the appropriate approximations) under a Smith-Hazel index for the ratio. However, there are differences, with a larger change in the numerator trait (117.8 vs. 100.08) and a smaller change in the denominator trait (27.1 vs. 35.32) under direct selection on the ratio versus selection on an index.

Finally, an alternative (but related) approach was suggested by Hühn (1992). From Chapter 30, recall that the correlated response in a variable x given direct selection on another variable r is the change in the breeding value of x caused by selection on r, or

$$\Delta\mu_x = b_{A_x,r} \cdot S_r = \frac{\sigma_{A_x,A_r}}{\sigma_r^2} \cdot S_r = \frac{\sigma_{A_x,A_r}}{\sigma_r}\, \overline{i}_r \tag{34.33}$$

Here $b_{A_x,r}$ denotes the slope of the regression of the breeding value of x on the phenotypic value of r, which is given by their covariance divided by the variance of r. By taking x to be either z_1 or z_2 and $r = z_1/z_2$, then if we can obtain these covariances we can approximate the response. This approach is also an approximation because we are assuming the regression of phenotype in r to breeding value in x is linear and homoscedastic. Assuming z_1, z_2 are jointly multivariate normal, the machinery of LW Appendix 1 (essentially taking the first few terms in the appropriate Taylor series) can be used to approximate these variances and covariances, see Hühn for details.

SELECTION AND SEXUALLY DIMORPHIC TRAITS

A trait can be **sexually dimorphic**, with its mean and/or variance differing over the sexes. In the extreme, some are **sex-specific** or **sex-limited** (e.g., milk production). Trait values in males and females can be treated as correlated characters, with sexual dimorphism generated by an imperfect correlation between the sexes and/or differences in trait variances (see Equation 34.34a). Selection on sexually dimorphic traits is a classic correlated-character problem, as selection on one sex generates a direct response in that sex and a correlated response in the other. This becomes especially interesting in situations where the nature of selection varies over the sexes (particularly when it is antagonistic), and raises a number of interesting questions: Is an observed sexual dimorphism the result of selection for different means in males and females or is it simply a correlated response from direct selection on only one sex? How strongly constrained is the independent evolution of the mean values in the two sexes? These questions, and others, can be addressed by using the multivariate breeder's equation.

A related issue that we will briefly touch on is differential ıtransmission of a trait value depending on the sex of the ıparent. Sexual dimorphism is the differential ıexpression of trait

value depending on the sex of the ıindividual. With sex-specific transmission the individual's sex also influences the transmission of parental value to the offspring, such as occurs when either sex-linked or imprinted autosomal loci influence the trait (LW Chapter 24). Such sex-specific differences in transmission can also be addressed within the framework of sexually dimorphic traits by tracking the transmission from each parent separately.

Components of the Genotype $\times$ Sex Interaction Variance

Sexual dimorphism is simply a genotype $\times$ environment interaction (LW Chapter 24). Restricting attention (for now) to autosomal loci with different effects depending upon the sex in which they reside, a specific genotype might have a value of $A_m + I_m$ in males (the sum of the breeding A and residual I values) and $A_f + I_f$ in females. As a correlated character problem, three quantities are of interest: the additive genetic variances in both sexes ($\sigma^2_{A_m}, \sigma^2_{A_f}$) and the genetic correlation r_A, or covariance $\sigma(A_m, A_f) = r_A \sigma_{A_m} \sigma_{A_f}$, between them. The amount of usable genetic variation for differences between the sexes is given by the genotype $\times$ sex interaction variance, which can be expressed in terms of these components as

$$\sigma^2_{G\times S} = \frac{\left(\sigma_{A_m} - \sigma_{A_f}\right)^2}{2} + \sigma_{A_m}\,\sigma_{A_f}(1 - r_A) \tag{34.34a}$$

$$= \frac{\sigma^2_{A_m} + \sigma^2_{A_f}}{2} - \sigma(A_m, A_f), \tag{34.34b}$$

This simply follows from the G $\times$ E interaction variance for a trait over two environments (Robertson 1959). Equation 34.34a highlights two sources of exploitable between-sex genetic variance. The first, and obvious, is when the genetic correlation r_A between the sexes is less than one. The second is a difference in the genetic variances (**scale effects**), and these can generate usable between-sex genetic variance even when the genetic correlation between the sexes is perfect ($r_A = 1$). Some of the early literature on sexual dimorphism was overly focused on transformations to remove scale effects (e.g., Eisen and Legates 1966, Hanrahan and Eisen 1973), but differences in variance can result in different heritabilities in males and females, and hence differential response even when the sexes are perfectly correlated (Yamada and Scheinberg 1976, Leutenegger and Cheverud 1982). That $\sigma^2_{G\times S}$ measures the amount of usable between-sex differences can be seen by noting that the additive genetic variance for the difference of a genotype expressed in males versus females is just

$$\sigma^2(A_m - A_f) = \sigma^2_{A_m} - 2\sigma(A_m, A_f) + \sigma^2_{A_f} = 2\,\sigma^2_{G\times S,} \tag{34.34c}$$

as noted by Eisen and Legates (1966).

Selection in Sex-limited Traits

Chapter 17 outlined the general approach for selecting on a sex-limited trait. Consider milk production. Mothers can be chosen (i.e., have their breeding values predicted) on the basis of their phenotype, or a more general index based on measured female relatives (for example, by using Equation 34.11). Likewise, the breeding value for the trait in fathers can be estimated from family selection (such as a half-sib daughter design) or again a more general index of measured female relatives. The expected response is simply the average of the parental and maternal breeding values. The generalization of using an index based on all known relatives to predict breeding values in all parents is the basis for BLUP selection, which is discussed in the next chapter.

Differential Selection Across the Sexes

Breeders may impose differential selection across the sexes on a trait, and this may happen in nature as well. There are at least three (non-exclusive) situations for differential selection on the sexes in natural populations (Darwin 1871, Lande 1980, Slatkin 1984, Hedrick and Temeles 1989, Fairbairn 1997). First, there may be ecological reasons, such as reducing competition between the sexes. The **niche variation hypothesis** (e.g., Rothstein 1973, Price 1984) suggests selection pressure for males and females to exploit slightly different niches. Second, males and females may experience differential selection because they have very different reproductive roles. A larger female might be favored by higher fecundity, while a smaller male might be favored by increased dispersal. Finally, there may be **sexual selection** (Darwin 1871; Chapter 44), wherein males either complete amongst themselves for access to mates (**male-male competition**) and/or display traits or behaviors to improve their attractiveness to females (**female choice**). For such traits, there is direct selection only on males, but the trait value in females can also change via a correlated response.

With no genetic variation in sexual dimorphism ($\sigma^2_{G\times S} = 0$) and no sex-specific differences in transmission, the response in a trait is simply $R = h^2 S$, where $S = (S_m + S_f)/2$ is the average selection differential over both sexes (Chapter 10). However, with sexual dimorphism and/or sex-specific differences in transmission, this simple average of the selection coefficients is no longer sufficient, with response depending on four pair-wise regressions of sex of parent on each sex of offspring (Equations 10.4, 34.35).

Sex-specific Transmission Differences

Sex can influence the genetic covariance, and hence the parent-offspring regression, through three different routes. First, consider non-imprinted autosomal loci with sex-specific effects (so that $\sigma^2_{G\times S} \neq 0$). In this case, the sex of an individual influences its genotypic value, and we might expect father-son and mother-daughter genetic covariances to differ, but the two cross-sex genetic covariances (father-daughter, mother-son) to be the same, albeit potentially different from the same-sex covariances. Second, for species in which the male is the heterogametic sex, the male genotype associated with the X chromosome is haploid, while it is diploid in females. Likewise, when females are the heterogametic sex they are haploid (ZW), while males are diploid (ZZ). Again, this results in potentially different father-son, mother-daughter, and cross-sex genetic covariances, although again the two cross-sex (father-daughter, mother-son) covariances are the same (Bohidar 1964, James 1973, Grossman and Eisen 1989; summarized in LW Chapter 24). The final route is when loci influencing a trait show **imprinting** (Spencer 2009, LW Chapter 24), in which case the sex of its *parent*, not the sex of the individual, determines gene expression. For traits influenced by imprinted loci, the father-offspring and mother-offspring covariances can differ (Spencer 2002, Santure and Spencer 2006, Dai and Weeks 2006, Spencer 2009), independent of offspring sex. This results in the cross-sex genetic covariances being potentially different. In any of these three settings, a constant complication when considering paternal- vs. maternal-regressions is inflation of the genetic covariance estimate by material effects. Santure and Spencer (2006) show this is particularly complex when imprinting occurs, and separation of the effects remains a significant challenge. This is especially problematic as maternal effects typically make a transient, rather than permanent, contribution to selection response (Chapter 11), and so separation of the effects is critical to predict the amount of sustainable selection response.

The Joint Response for a Single Dimorphic Trait

Taken together, all of these factors mean that we must consider four different pathways of transmission (father $\rightarrow$ son, father $\rightarrow$ daughter, mother $\rightarrow$ son, mother $\rightarrow$ daughter) to fully account for selection response for a sexual dimorphic trait or a trait with sex-specific transmission. For a single trait, we did just this in Chapter 10 (Equation 10.4, Example 10.1),

where the response in daughters was given by

$$R_{da} = b_{da,fa}\, S_{fa} + b_{da,mo}\, S_{mo} \tag{34.35a}$$

Here $b_{da,fa}$ is the regression coefficient of daughters (da) on their fathers (fa) and $b_{da,mo}$ the mother (mo)-daughter regression coefficient. Likewise, the response in sons (so) is

$$R_{so} = b_{so,fa}\, S_{fa} + b_{so,mo}\, S_{mo} \tag{34.35b}$$

As a prelude to a more general analysis of a vector of sexual dimorphic traits, following Lande (1980) we can place Equations 10.4 and 34.35 into a multivariate breeder's equation framework. This also allows us to express these regression coefficients in terms of genetic and phenotypic variance components.

Since selection in fathers and mothers is based on different individuals, there is no within-generation correlated responses between males and females due to phenotypic correlation. Hence

$$\mathbf{P} = \begin{pmatrix} \sigma^2(z_{fa}) & 0 \\ 0 & \sigma^2(z_{mo}) \end{pmatrix}, \quad \text{so that} \quad \mathbf{P}^{-1} = \begin{pmatrix} \sigma^{-2}(z_{fa}) & 0 \\ 0 & \sigma^{-2}(z_{mo}) \end{pmatrix} \tag{34.36a}$$

A little care is needed with $\mathbf{G}$, as it need not be symmetric (as the cross-sex genetic covariances can differ). While much of our previous discussions have used $\mathbf{G}$ as a variance-covariance matrix of breeding values, a slightly more general definition (that used in Chapter 33) is required here (which reduces to the standard variance-covariance matrix in many cases). Define the elements of $\mathbf{G}$ as the covariance between the phenotypic value z of a parent and the expected value of its offspring, which is simply the expected genotypic value G of a random offspring from that parent. This definition is motivated by the regression of expected offspring value on parental phenotypic value, and gives the elements of $\mathbf{G}$ as

$$G_{ij} = \sigma(G_i, z_j),$$

namely the expected genotypic value for trait i in an offspring of a parent with phenotypic value z for trait j. For a single dimorphic trait, we have

$$\mathbf{G} = \begin{pmatrix} \sigma(G_{so}, z_{fa}) & \sigma(G_{so}, z_{mo}) \\ \sigma(G_{da}, z_{fa}) & \sigma(G_{da}, z_{mo}) \end{pmatrix} \tag{34.36b}$$

Hence,

$$\mathbf{G}\mathbf{P}^{-1} = \begin{pmatrix} \sigma(G_{so}, z_{fa})/\sigma^2(z_{fa}) & \sigma(G_{so}, z_{mo})/\sigma^2(z_{mo}) \\ \sigma(G_{da}, z_{fa})/\sigma^2(z_{fa}) & \sigma(G_{da}, z_{mo})/\sigma^2(z_{mo}) \end{pmatrix} = \begin{pmatrix} b_{so,fa} & b_{so,mo} \\ b_{da,fa} & b_{da,mo} \end{pmatrix} \tag{34.36c}$$

Recalling the multivariate breeder's equation, $\mathbf{R} = \mathbf{G}\mathbf{P}^{-1}\mathbf{S}$, where $\mathbf{R} = (R_{so}, R_{da})^T$, recovers Equation 34.35. One can also use the gradient form of the breeder's equation, $\mathbf{R} = \mathbf{G}\boldsymbol{\beta}$, with $\mathbf{G}$ as defined in Equation 34.36b.

Example 34.9. Pearson and Lee (1903) estimated correlations among height (stature) in fathers and mothers versus their (adult) sons and daughters, a study that was instrumental to Fisher's 1918 paper that marks the founding of quantitative genetics. Rogers and Mukherjee (1992) re-examined these data, converting them to a log scale to remove the correlation

between the mean and variance. The covariance between fathers and sons (on the adjusted log-scale) was 0.809, while the mother-daughter covariance was 0.793. The cross-sex covariance was assumed equal and estimated from the average of the father-daughter and mother-son covariances, giving 0.789. The phenotypic variance of the trait in males and females as 1.575 and 1.567, respectively, giving

$$\mathbf{GP}^{-1} = \begin{pmatrix} 0.809 & 0.789 \\ 0.789 & 0.793 \end{pmatrix} \begin{pmatrix} 1.575 & 0 \\ 0 & 1.567 \end{pmatrix}^{-1} = \begin{pmatrix} 0.514 & 0.504 \\ 0.501 & 0.506 \end{pmatrix}$$

The resulting response equations become

$$R_{so} = 0.514\, S_{fa} + 0.504\, S_{mo}, \quad \text{and} \quad R_{da} = 0.501\, S_{fa} + 0.506\, S_{mo}.$$

To express the elements of $\mathbf{G}$ in terms of genetic variance components, we assume autosomal, non-imprinted loci with differential expression across the sexes underly the trait. Decomposing the genotypic and phenotypic values into breeding values A, interaction effects I, and environmental effects E gives

$$G_{ij} = \sigma(G_i, z_j) = \sigma(A_i + I_i, A_j + I_j + E_j) = \sigma(A_i, A_j) \tag{34.37a}$$

This follows by assuming no genotype-environment covariance and random mating (so that A and I are uncorrelated, however with imprinting these are correlated even under random mating, Spenser 2009). The presence of $A \times A$ epistasis and/or shared environmental values can inflate the response, but (as discussed in Chapter 11), these make transient contributions to the response, while changes in mean breeding value are permanent. Assuming (for now) that the additive genetic variances of the trait are equal in parents and offspring of the same sex (being $\sigma^2(A_m)$ in males, $\sigma^2(A_f)$ in females), then the father-son genetic covariance becomes

$$\sigma(A_{so}, A_{fa}) = \sigma(A_{fa}/2, A_{fa}) = \sigma^2(A_m)/2 \tag{34.37b}$$

This follows since (on average) only half of a parent's breeding value is passed onto their offspring. Likewise, $\sigma(A_{da}, A_{mo}) = \sigma^2(A_f)/2$. For autosomal, non-imprinted loci the cross-sex genetic covariances are equal, with

$$\sigma(A_{so}, A_{mo}) = \sigma(A_{da}, A_{fa}) = \frac{r_A}{2}\, \sigma_{A_m}\, \sigma_{A_f} \tag{34.37c}$$

More generally, the correlation between A_x in an offspring and A_y in its parent is

$$\sigma(A_x, A_y) = \frac{r_{Ax,Ay}}{2}\, \sigma_{A_x}\, \sigma_{A_y}, \tag{34.37d}$$

with Equations 34.37a-c being special cases of this more general form. Substitution into Equation 34.36c yields

$$\begin{aligned} \mathbf{GP}^{-1} &= \frac{1}{2} \begin{pmatrix} \sigma^2_{A_m} & r_A \sigma_{A_m} \sigma_{A_f} \\ r_A \sigma_{A_m} \sigma_{A_f} & \sigma^2_{A_f} \end{pmatrix} \begin{pmatrix} \sigma^2_{z_m} & 0 \\ 0 & \sigma^2_{f_m} \end{pmatrix}^{-1} \\ &= \frac{1}{2} \begin{pmatrix} h^2_m & r_A h_f (\sigma_{A_m}/\sigma_{z_f}) \\ r_A h_m (\sigma_{A_f}/\sigma_{z_m}) & h^2_f \end{pmatrix} \end{aligned} \tag{34.38a}$$

Under the assumption that the phenotypic variances are the same in both sexes, Equation 34.38a reduces to

$$R_{so} = \frac{h_m^2}{2} S_{fa} + \frac{h_m h_f r_A}{2} S_{mo}, \quad R_{da} = \frac{h_m h_f r_A}{2} S_{fa} + \frac{h_f^2}{2} S_{mo} \tag{34.38b}$$

This is the common expression in the literature (e.g., Leutenegger and Cheverud 1982, Fairbairn 1997, Merilä et al. 1998), and shows the influence of both differences in sex-specific heritabilities and the genetic correlation between sexes. Note that even if $r_A = 1$ and the amount of selection is the same in each sex ($S_{fa} = S_{mo} = S$),

$$R_{so} = h_m \left(\frac{h_m + h_f}{2} \right) S \qquad \text{and} \qquad R_{da} = h_f \left(\frac{h_m + h_f}{2} \right) S, \tag{34.38c}$$

so that there can still be a differential response in males and females if the sex-specific heritabilities differ (Yamada and Scheinberg 1976, Leutenegger and Cheverud 1982).

Example 34.10. Merilä et al. (1998) examined sexual dimorphism in body size of collared flycatchers (*Ficedula albicollis*), as measured by tarsus lenght. The genetic correlation between males and females was essentially one, while $h_f^2 = 0.72$ and $h_m^2 = 0.70$. Natural selection was antagonistic, with estimated selection differentials (on survival from fledging to recruitment to the breeding population) during the study period of $S_m = -0.554$ and $S_f = 0.273$. Applying Equaiton 34.38b, the expected response in daughters is

$$R_{da} = -\frac{\sqrt{0.72 \cdot 0.70} \cdot 1}{2} \cdot 0.554 + \frac{0.72}{2} \cdot 0.273 = -0.098$$

To illustrate the constraint imposed by the between-sex genetic correlation, the expected response for $r_A = 0.5$ is

$$R_{da} = -\frac{\sqrt{0.72 \cdot 0.70} \cdot 0.5}{2} \cdot 0.554 + \frac{0.72}{2} \cdot 0.273 = 0,$$

while if trait expression is entirely uncorrelated between the sexes, then

$$R_{da} = h_f^2 \, S_f = 0.72 \cdot 0.273 = 0.197.$$

As this example highlights, the genetic correlation r_A imposes a significant constraint on selection response. However, recall Zeng's (1988) results (Equation 31.39), that ıprovided $\mathbf{G}$ is non-singular (e.g., $r_A < 1$), if there are different optimal values for the two sexes, the population will eventually evolve to them (Lande 1980, Slatkin 1984). The constraint imposed by a high value of r_A is that the time for the population to evolve to the joint equilibrium for the two sexes can be quite considerable. If the environment (and hence potentially the sex-specific optimal values) are changing, the population might evolve too slowly to track them.

Yamada and Scheinberg (1976) consider the more general case when the phenotypic variance differs over sexes. In this case Equation 34.38b becomes

$$R_{so} = \frac{h_m^2}{2} S_{fa} + \frac{r_A}{2} \, h_f \, \frac{\sigma_{A_m}}{\sigma_{z_f}} \, S_{mo} = \frac{h_m^2}{2} S_{fa} + \frac{r_A \, h_m \, h_f}{2} \, \frac{\sigma_{z_m}}{\sigma_{z_f}} \, S_{mo} \tag{34.39a}$$

$$R_{da} = \frac{r_A}{2} \, h_m \, \frac{\sigma_{A_f}}{\sigma_{z_m}} \, S_{fa} + \frac{h_f^2}{2} S_{mo} = \frac{r_A \, h_m \, h_f}{2} \, \frac{\sigma_{z_f}}{\sigma_{z_m}} \, S_{fa} + \frac{h_f^2}{2} S_{mo} \tag{34.39b}$$

Others versions of the joint response (which are special cases of Equation 34.39) were proposed by Eisen and Legates (1966), Griffing (1966a,b), and Frankham (1968a,b). Expressions for joint response when maternal effects are present were given by Eisen and Hanrahan (1972) and Hanrahan and Eisen (1973).

Response with Sex-linkage

Response is the presence of sex-linkage (QTLs on the sex chromosome) can be handled by using expressions for the covariances between relatives under sex-linkage (e.g., LW Equation 24.5b, LW Table 24.1) to fill out the elements of $\mathbf{G}$ in Equation 34.36b. The total response is the sum of the autosomal and sex-linked responses. While straightforward, this approach can obscure some of the important implications of sex-linkage. As discussed in LW Chapter 4, if the allele frequencies at a sex-linked locus differ over the sexes, Hardy-Weinberg is not obtained in a single generation. Rather, male and female allele frequencies show an oscillatory approach to their eventual equilibrium value. Consider a species where the male is the heterogametic sex. The male obtains his X chromosome from his mother, while females receive the same X as in their father and a second X from their mother. If p_m and p_f are the initial allele frequencies at a sex-linked locus in males and females, then under random mating the allele frequencies in both sexes eventually reach an equilibrium value of

$$\widehat{p} = \frac{2p_f + p_m}{3},$$

which follows since 2/3 of the X chromosomes are in females, the rest in males. The frequency of an X-linked allele in males in generation t is simply its frequency in females in the previous generation, while the frequency in females is just the average of both sexes, giving

$$p_m(t) = p_f(t-1), \quad \text{and} \quad p_f(t) = \frac{p_m(t-1) + p_f(t-1)}{2}.$$

The deviation of the female frequency from the equilibrium value $\widehat{p}$ is halved each generation, with (LW Equation 4.2c)

$$p_f(t) - \widehat{p} = \left(-\frac{1}{2}\right)^t (\, p_f - \widehat{p}\,).$$

Hence, if a single generation of selection changes allele frequencies between the sexes (to p_f^* and p_m^*), it takes several generations of random mating for male and female allele frequencies to approach the new equilibrium value $\widehat{p}^* = (2p_f^* + p_m^*)/3$. The exact same argument holds if p_f^* and p_m^* are now the allele frequencies following any number of generations of selection. If $p_f^* \neq p_m^*$, then upon relaxation of selection, the allele frequencies (and hence trait values) will change in males and females as they both equilibrate to the new equilibrium frequency $\widehat{p}^*$. Even if the allele frequency difference at any particular locus is small, the cumulative effect over a modest number of loci can potentially be fairly substantial, resulting in significant fluctuations in the sex-specific means as the loci approach their new equilibrium values (Griffing 1965, Lande 1980).

In a similar fashion to selection generating new disequilibrium while recombination is removing it, under constant selection, the expected change in the means of the two sexes approaches a constant value (Lande 1980), reflecting the effects of random mating trying to equilibrate allele frequencies in both sexes with the generation of new changes in allele frequencies from selection. When selection is stopped, the above comments hold, with potential fluctuations in the means as they approach an equilibrium value, which is set by the sex-specific allele frequencies at the stoppage of selection.

Because of the pattern of sex-chromosome transmission, selection on the homogametic sex results in changes in both the homo- and heterogametic sex in the next generation, while

selection on the heterogametic sex results in only changes in the homogametic sex in the next generation (and then hence in the heterogametic sex in the following generation). For example, selection on XY males changes the frequency of X-linked alleles that are passed onto their daughters. Since they only pass along Y chromosomes to their sons, we must wait until their grandsons to see the effect of selection on their male progeny. Because of this transmission pattern, Beilharz (1960) suggested that, when sex linkage is present, focusing selection on the homogametic sex will result in the largest response. However, Frankham (1968a) found roughly equal response when selection focused only on male or only on females for a trait (abdominal bristles) in *Drosphila* with a strong sex-linked effect (roughly one third of the additive variance was due to sex-linked genes). However, he also found that response was largest in the sex that was selected, consistent with the direct response being greater than the correlated response (Chapter 31). Despite the large fraction of sex-linked variance associated with this trait, Frankham did not see significant fluctuations in the sex-specific means following relaxation of selection.

Sexual Dimorphism: A Correlated or Direct Response?

A response in the between-sex differences in the mean of a trait could be a direct response to differential selection on the two sexes or a correlated response from direct selection on either a single sex or on the average trait value in both sexes. Thus, it is often useful to transform our variables of interest from the response in the means of the two sexes to the response in average trait value

$$R_\mu = \frac{R_m + R_f}{2},$$

and the response in amount of dimorphism (the difference between the sexes)

$$R_\delta = R_m - R_f.$$

Following Rogers and Mukherjee (1992), we can also place the joint evolution of these two traits in a multivariate breeder's framework. Define

$$\mathbf{R}_{\delta,\mu} = \begin{pmatrix} R_\delta \\ R_\mu \end{pmatrix} = \begin{pmatrix} R_m - R_f \\ (R_m + R_f)/2 \end{pmatrix}, \quad \text{and} \quad \mathbf{C} = \begin{pmatrix} 1 & -1 \\ 1/2 & 1/2 \end{pmatrix} \tag{34.40a}$$

Then for $\mathbf{P}$, $\mathbf{G}$, and $\mathbf{R}$ as defined in Equation 34.36, we have

$$\begin{aligned} \mathbf{R}_{\delta,\mu} = \mathbf{CR} &= \mathbf{CG}\left[\mathbf{C}^T(\mathbf{C}^T)^{-1}\right]\mathbf{P}^{-1}\left[\mathbf{C}^{-1}\mathbf{C}\right]\mathbf{S} \\ &= \left[\mathbf{CGC}^T\right]\left[(\mathbf{C}^T)^{-1}\mathbf{P}^{-1}\mathbf{C}^{-1}\right][\mathbf{CS}] \\ &= \widetilde{\mathbf{G}}\widetilde{\mathbf{P}}^{-1}\widetilde{\mathbf{S}} \end{aligned} \tag{34.40b}$$

where

$$\widetilde{\mathbf{G}} = \mathbf{CGC}^T, \quad \widetilde{\mathbf{P}} = \mathbf{CPC}^T, \quad \widetilde{\mathbf{S}} = \mathbf{CS} \tag{34.40c}$$

Example 34.11. From Example 34.9, for human stature the genetic covariance matrix for the traits of sexual dimorphism in stature and average stature becomes

$$\widetilde{\mathbf{G}} = \mathbf{CGC}^T = \begin{pmatrix} 1 & -1 \\ 0.5 & 0.5 \end{pmatrix}\begin{pmatrix} 0.809 & 0.789 \\ 0.789 & 0.793 \end{pmatrix}\begin{pmatrix} 1 & 0.5 \\ -1 & 0.5 \end{pmatrix} = \begin{pmatrix} 0.024 & 0.008 \\ 0.008 & 0.795 \end{pmatrix}$$

If there is only direct selection β on average size, then the correlated response in the amount of sexual dimorphism is $R_\delta = 0.008\,\beta$, while the direct response in average size is $R_\delta = 0.795\,\beta$, a 99-fold difference. A one unit increase in mean size gives a correlated response of a 0.01 unit increase in the difference between males and females. Rogers and Mukherjee (1992) used this observation to suggest that it is unlikely the differences in sexual dimorphism across different human populations are simply a correlated response to direct selection on average size (as had been suggested in the literature).

Sexual Dimorphism in Size: Rensch's Rule

Sexual dimorphism is common in body size, and often denoted as **SSD**, for **sexual size dimorphism**. As with any sexually dimorphic trait, SSD could arise from direct selection to differentially change mean size in the two sexes or it could arise as a correlated response to selection on a single sex. Given our above discussions, when the genetic correlation for body size among the sexes is close to one, the evolution of SSD is very slow, regardless of whether it is a direct or correlated response.

What is intriguing about body size is that some general trends are apparent in animals. As reviewed by Arak (1988), Abouheif and Fairbairn (1997), and Fairbairn (1997), females tend to be larger in most invertebrates, amphibians, and reptiles, while males tend to be larger in many birds and mammals. Further, size dimorphism tends to be more pronounced among polygamous than monogamous species. There are exceptions to these general patterns within each group. A more consistent observation is **Rensch's Rule** (Rensch 1950, 1960): SSD increases with body size for those species in which males are the larger sex (male bias), and decreases with body size for those species with female bias. Fairbairn and Preziosi (1994) and Abouheif and Fairbairn (1997) note that Rensch's rule can be expressed as an allometry, relating the size of males (μ_f) and females (μ_m) among a group of related species by

$$\mu_f = a \cdot \mu_m^b$$

where Rensch's rule implies $b < 1$, and hence a greater evolutionary divergence in male size, independent of which sex is larger. Using corrections for correlations from shared ancestry, Abouheif and Fairbairn (1997) found wide support for Rensch's assertion using a meta-analysis of 21 different animal taxa.

Much of the discussion on the proximate causes for SSD revolves around sexual selection in males and/or fecundity selection in females. Sexual selection by male-male competition may favor larger males (but see Example 34.12), and the strength of sexual selection is expected to be stronger in polygamous species. For many invertebrates, amphibians, and reptiles, fecundity is expected to increase with body size. However, in some cases, fecundity can increase with smaller body size. Downhower (1976) suggested the energetics can determine the nature of selection for reproduction in female birds. If resources must be accumulate directly before reproduction (for example, in a marginal environment following a heavy rain), then smaller size may be favored, as smaller females can accumulate the resources more quickly and hence reproduce earlier. Conversely, when females bring resources (perhaps in the form of fat reserves) with them to a breeding ground, then larger size (and hence more stored resources) could be favored. Price (1984) observed that smaller females in Darwin's finch (*Geospiza fortis*) do indeed have a breeding advantage, being able to more quickly respond to favorable changes in the environment.

Example 34.12. Sźekely et al. (2004) presented an interesting analysis of size dimorphism in shorebirds. This group shows the full range of size dimorphisms, with males ranging from

60% to 170% of female body mass, and mean body size varying almost 80-fold over the group. Rensch's rule exists within this group, and the authors found that two components of sexual selection, the intensity of selection on males and the agility of the male's display, account for the observed pattern. Clutton-Brock (1985) suggested potential size tradeoffs in males under sexual selection. A larger male would be stronger, but less agile. Hence, if display or male/male competition is based on strength, larger male would tend to be favored, but if it is based on agility, smaller males are favored. This is indeed what Sźekely et al. observed, with male biased species showing less agile courtship behavior, and female-biased species displaying more agile courtship behavior. There was also an interaction between these two components, in that for species with low agility courtships, the male bias became increasingly pronounced with the intensity of sexual competition. However, in species with high degrees of agility in courtship, the female size bias was equally pronounced under medium and high levels of sexual competition.

Selection on a Vector of Sexually Dimorphic Traits

Building upon Equation 34.34, now suppose that selection is based on a vectors $\mathbf{z}_{fa}$ and $\mathbf{z}_{mo}$ of (potentially different) traits in fathers and mothers to predict response in vectors of traits $\mathbf{z}_{so}$ and $\mathbf{z}_{da}$ in sons and daughters. The resulting vectors of responses $\mathbf{R}_{so}$ in the sons and $\mathbf{R}_{da}$ in the daughters are

$$\begin{pmatrix} \mathbf{R}_{so} \\ \mathbf{R}_{da} \end{pmatrix} = \begin{pmatrix} \sigma(\mathbf{A}_{so}, \mathbf{z}_{fa}) & \sigma(\mathbf{A}_{so}, \mathbf{z}_{mo}) \\ \sigma(\mathbf{A}_{da}, \mathbf{z}_{fa}) & \sigma(\mathbf{A}_{da}, \mathbf{z}_{mo}) \end{pmatrix} \begin{pmatrix} \mathbf{P}_{\mathbf{z}_{fa}}^{-1} & 0 \\ 0 & \mathbf{P}_{\mathbf{z}_{mo}}^{-1} \end{pmatrix} \begin{pmatrix} \mathbf{S}_{fa} \\ \mathbf{S}_{mo} \end{pmatrix} \tag{34.41a}$$

where $\mathbf{A}_{so}$ and $\mathbf{A}_{da}$ are the vectors of breeding values in sons and daughters (respectively), and $\mathbf{P}_{\mathbf{z}_x}$ is the phenotypic covariance matrix for the traits in sex x. As in Chapter 33, these equations are completely general, allowing for the vector of traits in sons (and/or daughters) to be different from the traits measured in either parent. The resulting response for the vector of traits in sons becomes

$$\begin{aligned} \mathbf{R}_{so} &= \sigma(\mathbf{A}_{so}, \mathbf{z}_{fa})\mathbf{P}_{\mathbf{z}_{fa}}^{-1}\mathbf{S}_{fa} + \sigma(\mathbf{A}_{so}, \mathbf{z}_{mo})\mathbf{P}_{\mathbf{z}_{mo}}^{-1}\mathbf{S}_{mo} \\ &= \sigma(\mathbf{A}_{so}, \mathbf{z}_{fa})\boldsymbol{\beta}_{fa} + \sigma(\mathbf{A}_{so}, \mathbf{z}_{mo})\boldsymbol{\beta}_{mo} \end{aligned} \tag{34.41b}$$

While for daughters, we have

$$\begin{aligned} \mathbf{R}_{da} &= \sigma(\mathbf{A}_{da}, \mathbf{z}_{fa})\mathbf{P}_{\mathbf{z}_{fa}}^{-1}\mathbf{S}_{fa} + \sigma(\mathbf{A}_{da}, \mathbf{z}_{mo})\mathbf{P}_{\mathbf{z}_{mo}}^{-1}\mathbf{S}_{mo} \\ &= \sigma(\mathbf{A}_{da}, \mathbf{z}_{fa})\boldsymbol{\beta}_{fa} + \sigma(\mathbf{A}_{da}, \mathbf{z}_{mo})\boldsymbol{\beta}_{mo} \end{aligned} \tag{34.41c}$$

For (non-imprinted) autosomal loci, the elements in the covariance matrices $\sigma(\mathbf{A}_x, \mathbf{z}_y)$ follow directly from Equation 34.37d. Specially, the ijth element is

$$\sigma(A_{i,x}, z_{j,y}) = \sigma(A_{i,x}, A_{j,y}) = \frac{r_{A_{i,x},A_{j,y}}}{2}\,\sigma_{A_{i,x}}\,\sigma_{A_{j,y}}, \tag{34.4ad}$$

where $A_{i,x}$ is the breeding value of trait i in an offspring of sex x and $A_{j,z}$ is the breeding value of trait j in its parent of sex x.

Example 34.13. Building on Example 34.9, Pearson and Lee (1903) measured span (S) in addition to height (H) in humans, and Rogers and Mukherjee (1992) used this data to obtained

(log-transformed) genetic covariance matrices for the vectors

$$\begin{pmatrix} \mathbf{z}_{so} \\ \mathbf{z}_{da} \end{pmatrix} = \begin{pmatrix} H_{so} \\ S_{so} \\ H_{da} \\ S_{da} \end{pmatrix}, \quad \text{and} \quad \begin{pmatrix} \mathbf{z}_{fa} \\ \mathbf{z}_{mo} \end{pmatrix} = \begin{pmatrix} H_{so} \\ S_{so} \\ H_{da} \\ S_{da} \end{pmatrix}.$$

The structure the genetic covariance matrix considers all combinations of height and span among the two sexes of parents and their offspring. In the matrix below, the element AH_{da}, S_{fa} denotes the covariance between the phenotypic value for span in the father with the breeding value of height in her daughter, with the other entries similarly defined,

$$\mathbf{G} = \begin{pmatrix} AH_{so}, H_{fa} & AH_{so}, S_{fa} & AH_{so}, H_{mo} & AH_{so}, S_{mo} \\ AS_{so}, H_{fa} & AS_{so}, S_{fa} & AS_{so}, H_{mo} & AS_{so}, S_{mo} \\ AH_{da}, H_{fa} & AH_{da}, S_{fa} & AH_{da}, H_{mo} & AH_{da}, S_{mo} \\ AS_{da}, H_{fa} & AS_{da}, S_{fa} & AS_{da}, H_{mo} & AS_{da}, S_{mo} \end{pmatrix}$$

As in Example 34.9, Rogers and Mukherjee assumed that the cross-sex covariances were the same, and used the average of the father-daughter and mother-son values, giving the covariance matrix as

$$\mathbf{G} = \begin{pmatrix} 0.809 & 0.758 & 0.789 & 0.723 \\ 0.785 & 1.168 & 0.771 & 1.161 \\ 0.789 & 0.771 & 0.793 & 0.741 \\ 0.723 & 1.161 & 0.741 & 1.191 \end{pmatrix}$$

Written in gradient form, the expected response becomes

$$\mathbf{R} = \begin{pmatrix} R_{H,so} \\ R_{S,so} \\ R_{H,da} \\ R_{S,da} \end{pmatrix} = \mathbf{G}\boldsymbol{\beta} = \begin{pmatrix} 0.809 & 0.758 & 0.789 & 0.723 \\ 0.785 & 1.168 & 0.771 & 1.161 \\ 0.789 & 0.771 & 0.793 & 0.741 \\ 0.723 & 1.161 & 0.741 & 1.191 \end{pmatrix} \begin{pmatrix} \beta_{H,fa} \\ \beta_{S,fa} \\ \beta_{H,mo} \\ \beta_{S,mo} \end{pmatrix}$$

For example, if there is only selection on the heights of fathers ($\beta_{H,fa} = \beta$), the resulting vector of direct (male stature) and correlated responses (all other combinations) becomes

$$\mathbf{R} = \begin{pmatrix} R_{H,so} \\ R_{S,so} \\ R_{H,da} \\ R_{S,da} \end{pmatrix} = \mathbf{G} \begin{pmatrix} \beta \\ 0 \\ 0 \\ 0 \end{pmatrix} = \beta \begin{pmatrix} 0.809 \\ 0.785 \\ 0.789 \\ 0.723 \end{pmatrix}$$

or correlated response of 97%, 97.5%, and 89% of the direct response for the other trait combinations.

Equation 34.40 for the joint evolution of average size and sexual dimorphism easily extends to a vector of traits,

$$\mathbf{R}_{\delta,\mu} = \begin{pmatrix} \mathbf{R}_{\delta} \\ \mathbf{R}_{\mu} \end{pmatrix} = \begin{pmatrix} \mathbf{R}_m - \mathbf{R}_f \\ (\mathbf{R}_m + \mathbf{R}_f)/2 \end{pmatrix}, \quad \text{with} \quad \mathbf{C} = \begin{pmatrix} \mathbf{I} & -\mathbf{I} \\ \mathbf{I}/2 & \mathbf{I}/2 \end{pmatrix} \tag{34.42}$$

with Equations 34.40b and 34.40c holding with the above definition of $\mathbf{C}$ (Rogers and Mukherjee 1992).

Example 34.14. Consider the joint evolution of average trait value and sexual dimorphism for the traits height and span given in Example 34.13. Here,

$$\mathbf{C} = \begin{pmatrix} 1 & 0 & -1 & 0 \\ 0 & 1 & 0 & -1 \\ 1/2 & 0 & 1/2 & 0 \\ 0 & 1/2 & 0 & 1/2 \end{pmatrix}$$

Using the $\mathbf{G}$ matrix from Example 34.13, Equation 34.40c gives

$$\widetilde{\mathbf{G}} = \mathbf{CGC}^T = \begin{pmatrix} 0.024 & 0.005 & 0.008 & -0.016 \\ 0.032 & 0.037 & 0.046 & -0.012 \\ 0.008 & 0.033 & 0.795 & 0.748 \\ -0.002 & -0.012 & 0.755 & 1.170 \end{pmatrix}$$

If we select on average height only, the resulting vector of responses becomes

$$\mathbf{R}_{\delta,\mu} = \begin{pmatrix} R_{\delta,H} \\ R_{\delta,S} \\ R_{\mu,H} \\ R_{\mu,S} \end{pmatrix} = \begin{pmatrix} 0.024 & 0.005 & 0.008 & -0.016 \\ 0.032 & 0.037 & 0.046 & -0.012 \\ 0.008 & 0.033 & 0.795 & 0.748 \\ -0.002 & -0.012 & 0.755 & 1.170 \end{pmatrix} \begin{pmatrix} 0 \\ 0 \\ \beta \\ 0 \end{pmatrix} = \beta \begin{pmatrix} 0.008 \\ 0.046 \\ 0.795 \\ 0.755 \end{pmatrix}$$

The correlated response in average span ($R_{\mu,S} = 0.755\beta$) is 95% of the direct response in average height ($R_{\mu,H} = 0.795\beta$). The correlated response $R_{\delta,H} = 0.008\beta$ in sexual dimorphism in height is one percent of the gain in average height, while the correlated response $R_{\delta,S} = 0.046\beta$ in span is larger, around six percent of the gain in average height.

SELECTION ON THE ENVIRONMENTAL VARIANCE, σ_E^2

The final section of this chapter uses the machinery of multivariate selection to expand our discussion from Chapter 13 on the consequences of selection when there is heritable variation in σ_E^2. First, we consider the index-selection approach of Mulder et al. (2007) to estimate the joint vector (A_m, A_v) of breeding values for the mean and environmental variance. We then use this method to examine the effects on σ_E^2 from both direct phenotypic selection on a trait and from using schemes for direct selection on A_v using the variation among half-sib families from different sires. Finally, we briefly examine changes in the genetic variance-covariance structure under both the additive and multiplicative models. Given that we rely heavily on models and results introduced in Chapter 13, the reader wish to review this material before proceeding.

The approaches considered here are approximations that rely on various assumptions of normality. Even if the distribution of trait values for a given genotype is indeed normal, the distribution of trait values in the population is a mixture of normals with potentially difference variances, and hence not itself strictly normal (e.g., LW Chapter 13). Under the additive model for environmental variances where $E \sim N(0, \sigma_e^2 + A_V)$, Mulder et al. (2008) found that the excess kurotsis (relative to a normal) is $3\sigma_{A_v}^2/\sigma_z^4$, so that any variation in A_v generates a slightly leptokurtic distribution, with extreme values more likely than under a normal. Likewise, the coefficient of skewness is $3\sigma_{A_m,A_v}/\sigma_z^3$, so that any correlation in breeding values generates asymmetries in the distribution about the mean (in particular, z and z^2 become correlated). Thus, normality of the population distribution of trait values may be a reasonable approximation for values near the mean (e.g., within one or two standard deviations), but it fails when more extreme values are considered. One consequence of this

is that normality may not be an unreasonable assumption for models with relatively weak selection, but under very strong selection (say only the upper one percent is saved) this assumption breaks down.

The Bivariate Mulder-Bijma-Hill Model: Estimation

Building on the additive model (Equation 13.26), Mulder et al. (2007) suggest an approach to estimate the breeding values (A_m, A_v) for an individual simply given its phenotypic value (i.e., not requiring sibs or repeated observations). Their method also generalizes to pedigree information.

Motivated from index selection theory (and supported by simulations), they suggest that the phenotypic value z of an individual is a predictor of the breeding value for trait mean A_m, while z^2 is a predictor for the breeding value A_v for environmental sensitivity. When the correlation r_A between A_m and A_v is zero, they note (through simulations) that the regression of A_m on the phenotypic value z is very close to linear for most of the range of z. The regression of A_v on z^2 is also almost linear. Due to departures from normality, their simulations showed that both relationship becomes somewhat curvilinear for extreme values of z. Hence, $z-\mu_z$ roughly predicts A_m, while $(z-\mu_z)^2 - \mathrm{E}(z-\mu_z)^2$ roughly predicts A_v. If we have only a single observation z for an individual, we can consider the vector

$$\mathbf{z} = \begin{pmatrix} z-\mu_z \\ (z-\mu_z)^2 - \mathrm{E}(z-\mu_z)^2 \end{pmatrix} = \begin{pmatrix} z \\ z^2 - \sigma_z^2 \end{pmatrix} \quad \text{when} \quad \mu_z = 0 \tag{34.43a}$$

as an estimator for the vector of breeding values

$$\mathbf{g} = \begin{pmatrix} A_m \\ A_v \end{pmatrix}. \tag{34.43b}$$

Specifically, Mulder at al. (2007) suggest the regression

$$\mathbf{g} = \mathbf{G}^T \mathbf{P}^{-1} \mathbf{z} \tag{34.43c}$$

where $\mathbf{P} = \sigma(\mathbf{z}, \mathbf{z})$ is the matrix of covariances between the elements of $\mathbf{z}$,

$$\mathbf{P} = \begin{pmatrix} \sigma^2(z) & \sigma\left(z, z^2 - \sigma_z^2\right) \\ \sigma\left(z^2 - \sigma_z^2, z\right) & \sigma^2\left(z^2 - \sigma_z^2\right) \end{pmatrix} = \begin{pmatrix} \sigma_z^2 & 3\sigma_{A_m,A_v} \\ 3\sigma_{A_m,A_v} & 2\sigma_z^4 + 3\sigma_{A_v}^2 \end{pmatrix}, \tag{34.43d}$$

and $\mathbf{G} = \sigma(\mathbf{z}, \mathbf{g})$ is the matrix of covariances between the phenotypic observations $\mathbf{z}$ and the breeding values $\mathbf{g}$,

$$\mathbf{G} = \sigma(\mathbf{z}, \mathbf{g}) = \begin{pmatrix} \sigma(z, A_m) & \sigma(z, A_v) \\ \sigma(z^2, A_m) & \sigma(z^2, A_v) \end{pmatrix} = \begin{pmatrix} \sigma_{A_m}^2 & \sigma_{A_m,A_v} \\ \sigma_{A_m,A_v} & \sigma_{A_v}^2 \end{pmatrix} \tag{34.43e}$$

Note that while $\mathbf{G}$ is symmetric in this case ($\mathbf{G}^T = \mathbf{G}$), we use the transpose notation throughout because we will also consider situations (such as we saw in Chapter 33) where $\mathbf{G}$ is not square, and hence not symmetric. Example 34.15 outlines the derivation of the elements of $\mathbf{P}$ and $\mathbf{G}$.

Example 34.15. The elements in Equations 34.43d and 34.43e follow from the properties of expectations and assumptions of normality. Recall (under the assumption that μ_z is zero) that $z = A_m + E$ where $A_m \sim N\left(0, \sigma_{A_m}^2\right)$ and (under the additive model) $E \sim N\left(0, A_v + \sigma_e^2\right)$.

As in Chapter 13, we use the roman E to denote expectation and the italic E to denote the random environmental variable. For $x \sim N(0, \sigma^2)$, Johnson and Kotz (1970) give the first four moments of x as

$$\mathrm{E}[x] = \mathrm{E}[x^3] = 0, \quad \mathrm{E}[x^2] = \sigma^2, \quad \mathrm{E}[x^4] = \sigma^4 - 3\sigma^2$$

Likewise $\sigma(x, x^2) = 0$, which directly follows as

$$\sigma(x, x^2) = \mathrm{E}(x^3) - \mathrm{E}(x)\mathrm{E}(x^2) = 0 - 0 \cdot \sigma_z^2 = 0$$

These results will prove very useful in computing the elements of $\mathbf{P}$ and $\mathbf{G}$.

First consider $\sigma\left(z, z^2 - \sigma_z^2\right)$, the off-diagonal element in $\mathbf{P}$. Since the covariance of a constant is zero, we have

$$\sigma\left(z, z^2 - \sigma_z^2\right) = \sigma(z, z^2) = \mathrm{E}(z^3) - \mathrm{E}(z)\mathrm{E}(z^2) = \mathrm{E}(z^3) - 0 = \mathrm{E}(z^3)$$

Expanding,

$$\begin{aligned}\mathrm{E}(z^3) = \mathrm{E}[(A_m + E)^3] &= \mathrm{E}(A_m^3 + 3A_m^2E + 3A_mE^2 + E^3) \\ &= 0 + 3\mathrm{E}(A_m^2E) + 3\mathrm{E}(A_mE^2) + 0\end{aligned}$$

Further, $\mathrm{E}(A_m^2E)$ is zero, as A_m^2 is uncorrelated with E. Finally,

$$\mathrm{E}(A_mE^2) = \mathrm{E}[A_m(A_v + \sigma_e^2)] = \mathrm{E}[A_mA_v] + \sigma_e^2\mathrm{E}[A_m] = \sigma_{A_m,A_v} + 0$$

Putting these results together gives

$$\sigma\left(z, z^2 - \sigma_z^2\right) = 3\sigma_{A_m,A_v}$$

Thus z and z^2 are uncorrelated unless there is skew in the distribution, which is generated if A_m and A_v are correlated. Similar gymnastics give the other elements on P, see Mulder et al. (2007) for details.

The elements in $\mathbf{G}$ (Equation 34.43e) follow in a similar fashion. For example, $G_{1,1} = \sigma(z, A_m) = \sigma(A_m + E, A_m) = \sigma_{A_m,A_m} = \sigma^2(A_m)$, while $G_{2,1} = \sigma(z^2, A_m)$, which can be expanded as

$$\sigma(A_m^2 + 2A_mE + E^2, A_m) = \sigma(E^2, A_m) = \sigma(A_v + \sigma_e^2, A_m) = \sigma_{A_v,A_m}$$

The Bivariate Mulder-Bijma-Hill Model: Response in σ_E^2

Since the mean breeding value of a set of offspring is simply the mean breeding value of their parents (Chapter 10), from Equation 34.43c, the expected vector of responses $\mathbf{R}$ is just

$$\mathbf{R} = \boldsymbol{\mu}_{\mathbf{g}^*} - \boldsymbol{\mu}_{\mathbf{g}} = \mathbf{G}^T\mathbf{P}^{-1}\left(\boldsymbol{\mu}_{\mathbf{z}^*} - \boldsymbol{\mu}_{\mathbf{z}}\right) \tag{34.44}$$

where the superscript $*$ indicates the (within-generation) value after selection, while $\boldsymbol{\mu}_{\mathbf{g}}$ and $\boldsymbol{\mu}_{\mathbf{z}}$ are the vectors of mean breeding and phenotypic values (respectively).

Consider truncation selection first, where the uppermost fraction p of the population is saved. Recall (Chapter 10) that when the trait distribution is roughly normal, we can translate

p into a selection differential S (Equation 10.24) or selection intensity $\overline{\imath}$ (Equation 10.26a). Rescaling the pre-selection mean to zero gives the population mean following selection as

$$\mu_{z,s} = \overline{\imath}\,\sigma_z \tag{34.45a}$$

Mulder et al. show that the mean value of z^2 following selection (again assuming normality) is

$$\mu_{z^2,s} = (\overline{\imath}\,x + 1)\sigma_z^2 \tag{34.45b}$$

where x satisfies $\Pr(U > x) = p$ for a unit normal U. Substituting into Equation 34.44 gives the response in A_m, A_v following truncation selection as

$$\begin{aligned}\mathbf{R} = \begin{pmatrix} R_{A_m} \\ R_{A_v} \end{pmatrix} &= \mathbf{G}^T\mathbf{P}^{-1}\begin{pmatrix} \mu_{z,s} - \mu_z \\ \mu_{z^2,s} - \sigma_z^2 - (\mu_{z^2} - \sigma_z^2) \end{pmatrix} \\ &= \begin{pmatrix} \sigma^2_{A_m} & \sigma_{A_m,A_v} \\ \sigma_{A_m,A_v} & \sigma^2_{A_v} \end{pmatrix}\begin{pmatrix} \sigma_z^2 & 3\sigma_{A_m,A_v} \\ 3\sigma_{A_m,A_v} & 2\sigma_z^4 + 3\sigma^2_{A_v} \end{pmatrix}^{-1}\begin{pmatrix} \overline{\imath}\sigma_z \\ \overline{\imath}x_{1-p}\sigma_z^2 \end{pmatrix}\end{aligned} \tag{34.46}$$

Here $R_{A_m} = \Delta\mu_z$ and $R_{A_v} = \Delta\sigma^2_E$. Using the rules of matrix multiplication and writing $\sigma_{A_m,A_v} = r_A\sigma_{A_m}\sigma_{A_v}$ (where r_A is the genetic correlation), recovers Mulder et al. (2007) result,

$$\begin{aligned} R_m &= \left(\frac{\sigma^2_{A_m}(2\sigma_z^4 + 3\sigma^2_{A_v}) - 3r_A^2\sigma^2_{A_m}\sigma^2_{A_v}}{D}\right)\overline{\imath}\,\sigma_z + r_A\left(\frac{(\sigma_z^2 - 3\sigma^2_{A_m})\sigma_{A_m}\sigma_{A_v}}{D}\right)\overline{\imath}\,x\,\sigma_z^2 \\ R_v &= r_A\left(\frac{2\sigma_z^4\,\sigma_{A_m}\sigma_{A_v}}{D}\right)\overline{\imath}\,\sigma_z + \left(\frac{\sigma_z^2\sigma^2_{A_v} - 3r_A^2\sigma^2_{A_m}\sigma^2_{A_v}}{D}\right)\overline{\imath}\,x\,\sigma_z^2 \end{aligned} \tag{34.47}$$

where

$$D = \sigma_z^2(2\sigma_z^4 + 3\sigma^2_{A_v}) - 9r_A^2\sigma^2_{A_m}\sigma^2_{A_v}$$

is the determinant of $\mathbf{P}$. Setting $r_A = 0$ and simplifying recovers Equation 13.31. As shown in Example 34.16, genetic correlations can have a dramatic effect on response in σ^2_E under directional selection on the trait mean.

Example 34.16. To see the effects of genetic correlations between the breeding values for mean and environmental variance, recall Example 13.8. Here, we considered the response in mean and variance following a single generation of truncation selection with $p = 0.1$ for a trait with $h^2_m = 0.3$, $h^2_v = 0.03$, and $\sigma^2_z = 100$. In order to apply Equation 34.47, we need to convert these into variance components. First, $\sigma^2_{A_m} = h^2_m\sigma^2_z = 30$. From Equation 13.27b,

$$0.03 = h^2_v = \frac{\sigma^2_{A_v}}{2\sigma_z^4 + 3\sigma^2_{A_v}} = \frac{\sigma^2_{A_v}}{20000 + 3\sigma^2_{A_v}}$$

Numerically solving gives $\sigma^2_{A_v} = 659.3$. Recall (Example 13.8) that for $r_A = 0$,

$$R_{A_m} = 0.3 \cdot 1.755 \cdot 10 = 5.265, \quad \text{and} \quad R_{A_v} = 0.03 \cdot 1.755 \cdot 1.282 \cdot 100 = 6.750$$

Applying Equation 34.47 with $r_A = 0.5$ gives

$$R_{A_m} = 5.326, \quad \text{and} \quad R_{A_v} = 16.803,$$

while when $r_A = -0.50$,

$$R_{A_m} = 5.180, \quad \text{and} \quad R_{A_v} = -6.124$$

There is a slight increase (1%) in the response in μ_z when A_m and A_v are positively correlated, and a slight decrease (1.6%) when they are negatively correlated, reflecting the indirect response in μ_z contributed from selection directly on A_v. The effect of genetic correlations on σ_E^2 is much more dramatic, more than doubling the response under a positive correlation, and reducing (rather than increasing) the variance when negative correlated.

Mulder et al. show that the approach used for response under directional selection easily extends to stabilizing and disruptive selection under the double-truncation model (Figure 13.1). Under double-truncation stabilizing selection where the upper- and lower-most $p/2$ of the population is culled, assuming z is normally distributed and scaling the mean to zero gives

$$\mu_{z,s} - \mu_z = 0, \quad \text{and} \quad \mu_{z^2,s} - \mu_{z^2} = -\left(\frac{1-p}{p}\,\overline{\imath}'\,x'\right)\sigma_z^2 \tag{34.48a}$$

where $\overline{\imath}'$ and x' are the selection intensity and truncation value corresponding to $p' = (1-p)/2$. Under the normally assumption, there is no direct selection on the mean, and hence μ_z only changes if the breeding values are correlated. In this case, the resulting selection responses become

$$\begin{aligned} R_m &= -r_A\left(\frac{(\sigma_z^2 - 3\sigma_{A_m}^2)\sigma_{A_m}\sigma_{A_v}}{D}\right)\left(\frac{1-p}{p}\,\overline{\imath}'\,x'\right)\sigma_z^2 \\ R_v &= -\left(\frac{\sigma_z^2\sigma_{A_v}^2 - 3r_A^2\sigma_{A_m}^2\sigma_{A_v}^2}{D}\right)\left(\frac{1-p}{p}\,\overline{\imath}'\,x'\right)\sigma_z^2 \end{aligned} \tag{34.48b}$$

If $r_A = 0$, these reduce to

$$R_m = 0, \quad R_v = -h_v^2\,\overline{\imath}'\,x'\,\sigma_z^2 \tag{34.48c}$$

When $r_A \neq 0$, distribution is skewed, and as a result, selection on the variance also results in selection on the mean (see Figure 28.6). Even though the source of skewness is the genetic correlation between A_m and A_v, this effect of the skew putting direct selection pressure on the mean is not accounted for by Equation 34.48b, which only considers the change in the mean as a correlated response of direct selection on the variance, and ignores the additional direct selection created from skew.

Under double-truncation disruptive selection,

$$\mu_{z,s} - \mu_z = 0, \quad \text{and} \quad \mu_{z^2,s} - \mu_{z^2} = \overline{\imath}''\,x''\,\sigma_z^2 \tag{34.49a}$$

where $\overline{\imath}''$ and x'' are the selection intensity and truncation value corresponding to $p'' = p/2$. The resulting response equations become

$$\begin{aligned} R_m &= r_A\left(\frac{(\sigma_z^2 - 3\sigma_{A_m}^2)\sigma_{A_m}\sigma_{A_v}}{D}\right)(\overline{\imath}''\,x'')\,\sigma_z^2 \\ R_v &= \left(\frac{\sigma_z^2\sigma_{A_v}^2 - 3r_A^2\sigma_{A_m}^2\sigma_{A_v}^2}{D}\right)(\overline{\imath}''\,x'')\,\sigma_z^2 \end{aligned} \tag{34.49b}$$

Again if $r_A = 0$, these reduce to

$$R_m = 0, \quad R_v = h_v^2\, \imath''\, x''\, \sigma_z^2 \tag{34.49c}$$

Example 34.17. Stabilizing selection reduces the additive variance $\sigma^2_{A_m}$ in the trait by generating negative disequilibrium (Chapter 13). It also selects for a smaller error variance. What is the relative importance of these two sources of change? Let's return to Example 13.3, with double-truncation stabilizing selection for a trait with $\sigma_z^2 = 100$, $h^2 = 0.5$ and $p = 0.5$ (the upper-most and lower-most 25% of the population is culled). In this case, after one generation of selection the additive variance decreases from 50 to 39.27. What is the expected single-generation reduction in σ_E^2? Here $p' = (1 - 1/2)/2 = 0.25$, giving $x' = 0.675$ and $\overline{\imath}' = 0.636$. Assuming $r_A = 0$ (no genetic correlation) and a standard heritability value of $h_v^2 = 0.03$, the expected reduction in the environmental variance is

$$-h_v^2\, \overline{\imath}'\, x'\, \sigma_z^2 = 0.03 \cdot 0.675 \cdot 0.636 \cdot 100 = 1.29$$

Hence, after one generation the total reduction in variance is 10.73 + 1.43 = 12.02, 89% of which is due to reduction in $\sigma^2_{A_v}$.

While the example illustrates that the reduction in total phenotypic variance from stabilizing selection is largely due to disequilibrium reducing the additive variance $\sigma^2_{A_m}$, rather that σ_E^2, this single-generation result presented is potentially misleading. Most of the reduction in $\sigma^2_{A_m}$ occurs in the first few generations, as the disequilibrium quickly approaches an equilibrium value, which here is -13.3 (Example 13.3). Reduction in σ_E^2, however, continues at (roughly) a linear rate. Hence, after roughly 14 generations, the reduction in σ_E^2 is around 14, on pair with the reduction in $\sigma^2_{A_m}$. The reduction in σ_E^2 eventually itself becomes curvilinear, as the environmental variance must remain positive. At some point the additive model (being a ılocal approximation) breaks down as μ_{A_v} is reduced to the point where there is a significant probability of individuals with a negative environmental variance. A second subtle feature, which we address shortly, is that selection also generates disequilibrium in the additive variance of the environmental sensitivity, so that $\sigma^2_{A_v}$ itself declines, reducing h_v^2 and slowing the response. From Chapter 13, we expect that this decline quickly reaches an equilibrium value.

The above discussion highlights the subtle effects of genetic heterogeneity in σ_E^2 on standard selection-response equations. Under directional or stabilizing selection, negative disequilibrium is generated, reducing the additive variance in trait value. When there is no heritable variation in σ_E^2, the net result is a decline in the heritability. However, with heritable variation, σ_E^2 itself changes. In the absence of a genetic correlation between A_m and A_v, directional and disruptive selection increase σ_E^2, while stabilizing selection decreases it. Hence, the reduction in h^2 under directional selection may be greater than predicted from the standard (homogenous variance) infinitesimal model (Chapter 13), as the phenotypic variance does not decrease as fast as the additive variance (as decreases in $\sigma^2_{A_m}$ are partly offset by increases in σ_E^2). Conversely, when there is a negative genetic correlation, the error variance decreases under directional selection, and if this rate of decrease is sufficiently large, the heritability can actually increase. Similar arguments hold for stabilizing and disruptive selection. Finally, when the genetic correlation is non-zero, directional selection can give asymmetric responses. Suppose $r_A > 0$. Up-selecting on the trait also increases σ_E^2, while

down-selecting on the trait decreases σ^2_E. Under the infinitesimal model, the reduction in $\sigma^2_{A_m}$ in both direction is the same (given equal amounts of selection). However, the change in σ^2_E is not, and as a result the heritabilties differ in the two directions.

Extensions of the Mulder-Bijma-Hill Model: Accounting for Skew

While the use of this bivariate regression is well-motivated from index selection theory (Chapter 33), the distribution of phenotypic values is skewed when the breeding values are correlated. Mulder et al. found through simulation studies that incorporating a cubic term $(z-\mu_z)^3$ accounts for much of skewness and also some of the non-linearity at extreme values from excess kurotsis. Higher moments of z did not improve fit in the simulations and hence were ignored. Based on these observations, they suggest an index of three functions of the phenotypic value be used to estimate A_m and A_v, now using

$$\mathbf{z} = \begin{pmatrix} z \\ z^2 - \mathrm{E}[\,z^2\,] \\ z^3 - \mathrm{E}[\,z^3\,] \end{pmatrix} = \begin{pmatrix} z \\ z^2 - \sigma^2_z \\ z^3 - 3\sigma_{A_m,A_v} \end{pmatrix} \tag{34.50a}$$

Again (as throughout this section) we have scaled the mean to be zero to simplify the expectations for the quadratic and cubic terms. Recall that Chapter 33 examined cases like this where the elements in the vector of selected traits $\mathbf{z}$ did not match the elements in vector $\mathbf{g}$ of desired breeding values. Using this extended $\mathbf{z}$ vector, estimation of $\mathbf{g}$ again follows from Equation 34.43c, but now $\mathbf{P}$ is a 3 x 3 matrix, with the same 2 x 2 elements as in Equation 34.43d and augmented by

$$P_{13} = P_{31} = 4\sigma^4_z + 2\sigma^2_{A_v}, \quad P_{23} = P_{32} = 27\sigma^2_z\sigma_{A_m,A_v}$$

$$P_{33} = 15\sigma^6_z + 45\sigma^2_z\sigma^2_{A_m}\sigma^2_E + 81\sigma^2_{A_m,A_v} + 45\sigma^2_z\sigma^2_{A_v} \tag{34.50b}$$

These new elements are the phenotypic covariances involving z^3, and are obtained using the approach in Example 34.15. Fortunately, the expression for $\mathbf{G}$ is much more straightforward,

$$\mathbf{G} = \sigma(\mathbf{z},\mathbf{g}) = \begin{pmatrix} \sigma^2_{A_m} & \sigma_{A_m,A_v} \\ \sigma_{A_m,A_v} & \sigma^2_{A_v} \\ 3\sigma^2_z\sigma^2_{A_m} & 3\sigma^2_z\sigma_{A_m,A_v} \end{pmatrix} \tag{34.50c}$$

The response is just

$$\mathbf{R} = \mathbf{G}^T\mathbf{P}^{-1}\left(\boldsymbol{\mu}_{\mathbf{z}_s} - \boldsymbol{\mu}_{\mathbf{z}}\right) = \mathbf{G}^T\mathbf{P}^{-1}\begin{pmatrix} \mu_{z,s} - \mu_z \\ \mu_{z^2,s} - \mu_{z^2} \\ \mu_{z^3,s} - \mu_{z^3} \end{pmatrix} \tag{34.50d}$$

For directional truncation selection, the first two elements are given by Equations 34.45a/b, while

$$\mu_{z^3,s} - \mu_{z^3} = \left(\overline{\imath}\,x^2 + 2\,\overline{\imath}\right)\sigma^3_z \tag{34.51}$$

as obtained by Mulder et al.

Extensions of the Mulder-Bijma-Hill Model: Sire-Selection

Increased uniformity is often desired by breeders, and the economic advantage of improving the mean value of a trait may be offset by decreased uniformity through increases in σ^2_E. Indeed, a breeder may be more interested in uniformity than in the trait mean. A breeder would thus like to have more targeted control over changes in σ^2_E over those provided under individual selection.

One option might be sire selection, where A_m and A_v for a specific sire are estimated from the distribution of their offspring values (see Mulder et al. 2007, 2008 for other schemes). An estimate of A_m is provided from the offspring mean $\overline{z}$, while A_v can be estimated from the within-family variance

$$Var_w = \frac{n}{n-1}\left[\,\overline{z^2} - (\overline{z})^2\,\right]$$

where n is the number of measured sibs and $\overline{z^2}$ is the mean of squared offspring values. For small n, Mulder et al. found that $\overline{z}^2$ also provides additional information on estimating A_v and suggest a regression of $\mathbf{g}^T = (A_m, A_v)$ for a sire on the basis of

$$\mathbf{z} = \begin{pmatrix} \overline{z} - \mathrm{E}(z) \\ (\overline{z} - \mu_z)^2 - \mathrm{E}[(\overline{z} - \mu_z)^2] \\ Var_w - \mathrm{E}(Var_w) \end{pmatrix} \tag{34.52a}$$

To compute the expectations in Equation 34.52a, we again rescale the mean to zero ($\mathrm{E}(z) = \mu_z = 0$). The expected within-family variance is simply the total variance σ_z^2 minus the genetic covariance between sibs, $r_w\sigma^2_{A_m}$, where r_w is the additive-genetic relationship among the sibs (e.g., 1/4 for half-sibs, 1/2 for full-sibs). Finally, since $\mathrm{E}(\,\overline{z}\,) = 0$, $\mathrm{E}(\,\overline{z}^2\,)$ is simply the variance in $\overline{z}$. This has two compoents: the sampling variance for the mean σ_z^2/n plus a correction for the fact that relatives are correlated,

$$\begin{aligned}\sigma^2(\,\overline{z}\,) = \sigma^2\left(\frac{1}{n}\sum_{i=1}^{n} z_i\right) &= \frac{n}{n^2}\sigma_z^2 + \frac{1}{n^2}\sum_{i\neq j}\sigma(z_i, z_j) \\ &= \frac{\sigma_z^2}{n} + \frac{n(n-1)}{n^2}\sigma(z_i, z_j) = \frac{\sigma_z^2}{n} + \frac{n-1}{n}\,r_w\sigma^2_{A_m}\end{aligned}$$

Hence, Equation 34.52a becomes

$$\mathbf{z} = \begin{pmatrix} \overline{z} \\ \overline{z}^2 - n^{-1}\left[\,\sigma_z^2 + r_w(n-1)\sigma^2_{A_m}\,\right] \\ Var_w - \left[\sigma_z^2 - r_w\sigma^2_{A_m}\right] \end{pmatrix} \tag{34.52b}$$

As above, we estimate $\mathbf{g}$ by $\mathbf{G}^T\mathbf{P}^{-1}\mathbf{z}$, where $\mathbf{G} = \sigma(\mathbf{z}, \mathbf{g})$ and $\mathbf{P} = \sigma(\mathbf{z}, \mathbf{z})$ with $\mathbf{g}$ given by Equation 34.43b, and $\mathbf{z}$ by Equation 34.52a. The corresponding $\mathbf{G}$ matrix is

$$\mathbf{G} = r_p\begin{pmatrix} \sigma^2_{A_m} & \sigma_{A_m,A_v} \\ \sigma_{A_m,A_v}/n & \sigma^2_{A_v}/n \\ \sigma_{A_m,A_v} & \sigma^2_{A_v} \end{pmatrix} \tag{34.53a}$$

where r_p is the relationship of the relative to the individuals that comprise the data in $\mathbf{z}$, which is 1/2 for the offspring of a sire. The elements of $\mathbf{P}$ are more complex,

$$P_{11} = \frac{\sigma_z^2 + r_w(n-1)\sigma^2_{A_m}}{n}, \quad P_{12} = P_{21} = \frac{3 + 3r_w(n-1)\sigma(A_m, A_v)}{n^2} \tag{34.53b}$$

$$P_{13} = P_{31} = \frac{3 + r_w(n-3)\sigma(A_m, A_v)}{n}, \quad P_{23} = P_{32} = \frac{3 + r_w(n-3)\sigma^2_{A_v}}{n^2} \tag{34.53c}$$

$$P_{22} = 2\,P_{11}^2 + \frac{3 + 3r_w(n-1)\sigma^2_{A_v}}{n^3} \tag{34.53d}$$

$$P_{33} = \frac{2(\sigma_z^2 - r_w\sigma_{A_m}^2)^2}{n-1} + \frac{3\sigma_{A_v}^2}{n} + \sigma_{A_v}^2\frac{r_w(n^2-2n+3)}{n(n-1)} \tag{34.53e}$$

as obtained by Mulder et al. (2007).

Example 34.18. Assume the variance component values for the hypothetical trait examined in Example 34.16, namely, $\sigma_z^2 = 100$, $\sigma_{A_m}^2 = 30$, and $\sigma_{A_v}^2 = 660$ (where we have rounded the later for ease of presentation). Further, assume that A_v and A_m are uncorrelated, so that $\sigma_{A_v,A_m} = 0$. Under half-sib sire design with $n = 50$ offspring, each from an unrelated mother, $r_w = 1/4$ and the resulting $\mathbf{G}$ matrix becomes

$$\mathbf{G} = \frac{1}{2}\begin{pmatrix} 30 & 0 \\ 0/50 & 660/50 \\ 0 & 660 \end{pmatrix} = \begin{pmatrix} 15 & 0 \\ 0 & 6.6 \\ 0 & 330 \end{pmatrix}$$

while

$$\mathbf{P} = \begin{pmatrix} 9.350 & 0.001 & 0.060 \\ 0.001 & 175.039 & 3.103 \\ 0.060 & 3.103 & 550.669 \end{pmatrix} \quad \text{and} \quad \mathbf{z} = \begin{pmatrix} \overline{z} \\ \overline{z}^2 - 9.35 \\ Var_w - 92.5 \end{pmatrix}$$

As above, rescaling the trait so that the population mean is zero, the predicted vector $\mathbf{g} = \mathbf{G}^T\mathbf{P}^{-1}\mathbf{z}$ of breeding values becomes

$$\begin{aligned} \begin{pmatrix} A_M \\ A_v \end{pmatrix} &= \begin{pmatrix} 15 & 0 & 0 \\ 0 & 6.6 & 330 \end{pmatrix} \begin{pmatrix} 9.350 & 0.001 & 0.060 \\ 0.001 & 175.039 & 3.103 \\ 0.060 & 3.103 & 550.669 \end{pmatrix}^{-1} \begin{pmatrix} \overline{z} \\ \overline{z}^2 - 9.35 \\ Var_w - 92.5 \end{pmatrix} \\ &= \begin{pmatrix} 1.604 & 0.000 & 0.000 \\ -0.004 & 0.027 & 0.599 \end{pmatrix} \begin{pmatrix} \overline{z} \\ \overline{z}^2 - 9.35 \\ Var_w - 92.5 \end{pmatrix} \end{aligned}$$

For this example, the estimated breeding values for a sire are

$$\begin{aligned} \widehat{A}_m &= 1.604 \cdot \overline{z} \\ \widehat{A}_v &= -0.004 \cdot \overline{z} + 0.027 \cdot (\overline{z}^2 - 9.35) + 0.599 \cdot (Var_w - 92.5) \\ &= -0.004 \cdot \overline{z} + 0.027 \cdot \overline{z}^2 + 0.599 \cdot Var_w - 55.660 \end{aligned}$$

Only the progeny mean contributes to the estimate A_m for the sire, while the bulk of the information for estimating A_v comes from the within-family variance, with the squared mean and mean making only very minor contributions.

As this example illustrates, family-based selection offers a higher level of control over changes in σ_E^2 than does individual (i.e., phenotypic) selection. Phenotypic directional selection can generate potentially undesirable changes in A_v (and hence σ_E^2), even when A_m and A_v are uncorrelated. When individuals are selected the basis of the mean performance of their offspring (as opposed to their own trait value), there is only weak selection on A_v (provided A_m and A_v are uncorrelated). Further, the strength of selection on A_v quickly diminishes as the number of sibs per sire increases (Zhang and Hill 2004, Mulder et al. 2007). Family-based selection is, however, not a panacea, as A_v can still change dramatically as a correlated response when $r_A \neq 0$.

In addition to allowing one to avoid selection on σ^2_E, family-based schemes allow us to directly target it as well. Selection for increased uniformity can be attempted by choosing sires with smaller within-family variances. The effectiveness of this scheme depends, on part, on how close to reality the infinitesimal model is for the particular trait of interest. Under the infinitesimal, all sires have the same genetic segregation variance (Chapters 13, 24). When there are segregating genes of even modest effect, selection on the within-family variance selects for sires with lower amounts of heterozygosity for QTLs influencing the trait, as such individuals have lower segregation variances and hence lower within-family variances. This results in an increase in the amount of inbreeding. Caution is therefore in order when using a sire-selection scheme to reduce the environmental variance. If the selection for more inbred individuals is significant, this may actually ıinflate the environmental variance, given the empirical association between environmental sensitivity and amount of inbreeding see in some traits (Chapter 13).

Index Selection For Joint Changes in the Mean and Environmental Variance

The index selection machinery developed in Chapter 33 can be employed when the breeding objective is to improve both the mean and uniformity of a trait. Suppose the goal is to maximize the response of some linear combination H of the traits,

$$H = \mu_z + a\sigma^2_z \tag{34.54a}$$

where a is the relative weight on the variance. Under the additive variance model (Equation 13.26b), changes in both trait mean and variance are linear functions of changes in breeding values, so that this breeding objective is equivalent to

$$H = A_m + aA_v = \mathbf{a}^T\mathbf{g} \tag{34.54b}$$

where $\mathbf{a}^T = (1, a)$. Technically, Equation 34.54b is an approximation of Equation 34.54a, as it ignores the change in σ^2_z from any changes in $\sigma^2_{A_m}$ from disequilibrium generated by selection. If desired, these can also be incorporated using the machinery developed here and in Chapter 13.

To maximize response in $H = \mathbf{a}^T\mathbf{g}$, the Smith-Hazel index result (Equation 33.18a) states that selection should be on the index $I = \mathbf{b}^T\mathbf{z}$ of trait values $\mathbf{z}$ (such as the sire family information, Equation 34.52a) with the weights given by $\mathbf{b} = \mathbf{P}^{-1}\mathbf{G}^T\mathbf{a}$. This gives the phenotypic index upon which to select as

$$I_s = \mathbf{a}^T\mathbf{G}\mathbf{P}^{-1}\mathbf{z} \tag{34.54c}$$

Example 34.19. Consider the trait whose variance components were given in Example 34.16, $\sigma^2_z = 100$, $\sigma^2_{A_m} = 30$, and $\sigma^2_{A_v} = 660$. Suppose we wish to maximize response in the index

$$H = \mu_z - \sigma^2_z$$

so that we want to increase both the mean and uniformity. We use a sire selection design with $n = 50$ offspring/sire. With this number of sibs/sire, the additional information provided from $\overline{z}^2$ is small, so we construct an index based on just the family mean $\overline{z}$ and variance Var_w,

$$\mathbf{z} = \begin{pmatrix} \overline{z} \\ Var_w \end{pmatrix}, \quad \mathbf{a} = \begin{pmatrix} 1 \\ -1 \end{pmatrix}, \quad \mathbf{G} = r_p \begin{pmatrix} \sigma^2_{A_m} & \sigma_{A_m,A_v} \\ \sigma_{A_m,A_v} & \sigma^2_{A_v} \end{pmatrix} = \begin{pmatrix} 15 & 0 \\ 0 & 165 \end{pmatrix}$$

where the correction term $\sigma_z^2 - r_w\sigma_{A_m}^2$ on Var_w is ignored in $\mathbf{z}$, because it enters as the same constant for all individuals and does not influence the relative ranking of the index values for different individuals. Finally, $\mathbf{P}$ is now 2 x 2 with elements

$$\mathbf{P} = \begin{pmatrix} P_{11} & P_{13} \\ P_{31} & P_{33} \end{pmatrix} = \begin{pmatrix} 9.350 & 0.060 \\ 0.060 & 550.669 \end{pmatrix}$$

where the P_{ij} are given by Equation 34.53. The Smith-Hazel weights for this index are

$$\mathbf{b} = \mathbf{P}^{-1}\mathbf{G}^T\mathbf{a} = \begin{pmatrix} 9.350 & 0.060 \\ 0.060 & 550.669 \end{pmatrix}^{-1} \begin{pmatrix} 15 & 0 \\ 0 & 165 \end{pmatrix} \begin{pmatrix} 1 \\ -1 \end{pmatrix} = \begin{pmatrix} 1.61 \\ -0.30 \end{pmatrix}$$

Since -0.3/1.61 = -0.19, we can rewrite the optimal index on which to selection as $I = \overline{z} - 0.19 \cdot Var_w$.

The machinery of index selection can be used to obtain quantities of potential interest, such as σ_I^2, $\sigma_{A_I}^2$, or h_I^2 (Equation 33.2). We might also be interested in the response in the index (Equation 33.19) or in its individual components (Equation 33.20). Finally, one might wish a restricted selection index, changing the mean while restricting change in A_v to near zero, or vice-versa. The Morely index (Equation 33.36c), which is the two-trait version of the Kempthorne-Nordskog index (Equation 33.36b), can be used for this purpose.

While a powerful set of results are available to us for linear indices, in many settings the merit function H whose response we seek to optimize is nonlinear. This naturally arises when the multiplicative (Equation 13.24) or exponential (Equation 13.25) model is used for variances. It also arises if the profit (merit) function we seek to maximize is quadratic or some other nonlinear function. One such example is offered by Mulder et al. (2008),

$$H = c_1(z-\theta)^2 + c_2 = (z-\theta)^2 + c \tag{34.55}$$

where θ is the optimal trait value, and c_1 and c_2 are profit weights (with $c = c_2/c_1$). Here c_2 is the profit at the optimal, and c_1 measures the penalty for departures from the optimal. Nonlinear indices are very delicate to work with, as optimizing the merit in the parents ıdoes not optimize merit in their offspring (Chapter 33). One can linearize a nonlinear index by using a first-order Taylor series (e.g., Equations 33.43-33.44), but the resulting weight are not constants and must be continually updated. Other machinery for nonlinear indices introduced in Chapter 33 can also be applied. For example, an optimal linear index for a nonlinear merit function can be constructed given the vector $\mathbf{R}$ of desired total response (Equation 33.35a).

Example 34.20. Following Mulder et al. (2008), consider the quadratic merit function given by Equation 34.55. Since $\mathrm{E}(z^2) = \sigma_z^2 + \mu_z^2$, the expected profit $\mathrm{E}(H)$ for a population is

$$\mathrm{E}(H) = \mathrm{E}\left[(z-\theta)^2 + c\right] = \mathrm{E}(z^2) - 2\theta\mathrm{E}(z) + \theta^2 + c = \sigma_z^2 + \mu_z^2 - 2\theta\mu_z + \theta^2 + c$$

From Equation 33.44, the linearized index values are given as the derivatives of $\mathrm{E}(H)$ with respect to μ_z and σ_z^2, giving the merit (profit) weights for the linearized profit function as

$$a_1 = \frac{\partial \mathrm{E}(H)}{\partial \mu_z} = 2(\mu_z - \theta), \quad a_2 = \frac{\partial \mathrm{E}(H)}{\partial \sigma_z^2} = 1$$

The resulting vector $\mathbf{b} = \mathbf{P}^{-1}\mathbf{G}^T\mathbf{a}$ of optimal weights, where $\mathbf{a} = (a_1, a_2)^T$, changes depending on the population mean. When $\mu_z = \theta$, $a_1 = 0$ and all of the weight is placed on the variance.

Changes in the Genetic Variances and Covariances for A_m, A_v

Until now, we have been ignoring any changes in the genetic covariances, treating them as unchanging under selection. Of course, as we say in Chapter 13, selection on the mean value of A_v also changes its variance. Under the infinitesimal model, all changes in $\sigma^2_{A_m}$, $\sigma^2_{A_v}$, and σ_{A_m,A_v} are caused by linkage disequilibrium, and the machinery of Chapter 31 (Equations 31.1-31.4) can be used to following their dynamics. Before selection, the genetic covariance can be written as $\sigma_{ij} = \sigma_{ij}(0) + d_{ij}$, the linkage-equilibrium value $\sigma_{ij}(0)$ plus the current disequilibrium d_{ij}. Selection generates additional equilibrium d^*_{ij} so that the new covariance in the population of chosen parents becomes

$$\sigma^*_{ij} = \sigma_{ij} + d^*_{ij} = \sigma_{ij}(0) + d_{ij} + d^*_{ij}$$

With unlinked loci, offspring retain only half the disequilibrium of their parents (Chapters 13, 24), giving the covariance among the offspring as

$$\sigma'_{ij} = \sigma_{ij}(0) + \frac{d_{ij} + d^*_{ij}}{2}$$

Given our results from Chapter 13, we expect that directional and stabilizing selection on A_v generates negative d, reducing its genetic variance and heritability. Disruptive selection, on the other hand, generates positive d, increasing the genetic variance. Under the infinitesimal model, when selection stops, the mean value of A_v remains unchanged, but the disequilibrium decays and $\sigma^2_{A_v}$ returns to its initial value. What is less clear are the dynamics of the genetic covariance, and what role (if any) this plays in the dynamics of $\sigma^2_{A_v}$. Again, under the infinitesimal, any changes in covariances are due to disequilibrium, which decays away upon relaxation of selection. The joint dynamics of $\sigma^2_{A_m}$, $\sigma^2_{A_v}$, and $\sigma^2_{A_m,A_v}$ under the infinitesimal model have been examined by Gavrilets and Hastings (1994) and Hill and Zhang (2004, 2005), and we consider their results here. As emphasized in Chapter 31, when the infinitesimal model does not hold, genetic variances, and in particular covariances, can be especially fragile, with the later even changing sign. Hence, the infinitesimal results are best thought of as an approximation to the short-term response. This is also in keeping with the notion of the additive model for heritable variance in σ^2_E being a local model that breaks down after sufficient genetic change.

Gavrilets and Hastings (1994) considered weak quadratic selection under the multiplicative model (Equation 13.24) for the environmental variance, using the fitness function

$$W = 1 - s(z - \theta)^2 \tag{34.56a}$$

which accommodates both weak stabilizing ($s > 0$) and disruptive ($s < 0$) selection. Equation 13.29b frames this fitness function in terms of selection on the vector of breeding values. If we rescale the trait for simplicity such that $\theta = 0$ and $\sigma^2_e = 1$, then Equation 13.29b simplifies to

$$W = 1 - s(A^2_m + A^2_v) \tag{34.56b}$$

Under stabilizing selection, both μ_{A_m} and μ_{A_v} are driven towards zero, and the remainder of our analysis assumes both of these means are zero, and hence no directional selection. At this value the mean population fitness becomes

$$\overline{W} = 1 - s(\sigma^2_{A_m} + \sigma^2_{A_v}), \tag{34.56c}$$

From Equation 13.24c, the mean environmental variance becomes

$$\sigma_E^2 = (\mu_{A_v}^2 + \sigma_{A_v}^2)\sigma_e^2 = 0^2 + \sigma_{A_v}^2 \cdot 1 = \sigma_{A_v}^2, \tag{34.57a}$$

giving the average total variance as the sum of the two additive variances,

$$\sigma_z^2 = \sigma_{A_m}^2 + \sigma_E^2 = \sigma_{A_m}^2 + \sigma_{A_v}^2. \tag{34.57b}$$

Gavrilets and Hastings (1994) use Equation 31.3 to obtain the within-generation change d^* generated by selection under this model as

$$d_{A_m}^* = -\frac{2s}{\overline{W}}\left(\sigma_{A_m}^4 + \sigma_{A_m,A_v}^2\right) \tag{34.58a}$$

$$d_{A_v}^* = -\frac{2s}{\overline{W}}\left(\sigma_{A_v}^4 + \sigma_{A_m,A_v}^2\right) \tag{34.58b}$$

$$d_{A_m,A_v}^* = -\frac{2s}{\overline{W}}\,\sigma_{A_m,A_v}\left(\sigma_{A_m}^2 + \sigma_{A_v}^2\right) \tag{34.58c}$$

For stabilizing selection ($s > 0$), negative disequilibrium is generated and both additive variances decrease. Note that since the genetic covariance enters into Equations 34.58a and b as a squared term, any covariance increases the amount of negative disequilibrium generated for the additive variances. When the genetic covariance is initially zero, it remains so. If it is initially non-zero, selection reduces its absolute value.

Hill and Zhang (2004, errata 2005) develop similar expressions for the disequilibrium created under truncation selection when the additive model (Equation 13.26) is used for σ_E^2. The resulting expressions are considerably more complex,

$$d_{A_m}^* = -\overline{\imath}\left((\overline{\imath} - x)\left[\frac{\sigma_{A_m}^2}{\sigma_z} + x\,\frac{\sigma_{A_m,A_v}}{2\sigma_z^2}\right]^2 + \frac{\sigma_{A_m}^2\sigma_{A_m,A_v}}{\sigma_z^3} + 3\,x\frac{\sigma_{A_m,A_v}^2}{4\sigma_z^4}\right) \tag{34.59a}$$

$$d_{A_v}^* = -\overline{\imath}\left((\overline{\imath} - x)\left[\frac{\sigma_{A_m,A_v}}{\sigma_z} + x\,\frac{\sigma_{A_v}^2}{2\sigma_z^2}\right]^2 + \frac{\sigma_{A_v}^2\sigma_{A_m,A_v}}{\sigma_z^3} + 3\,x\frac{\sigma_{A_v}^4}{4\sigma_z^4}\right) \tag{34.59b}$$

$$d_{A_m,A_v}^* = -\overline{\imath}\left((\overline{\imath} - x)\left[\frac{\sigma_{A_m}^2}{\sigma_z} + x\frac{\sigma_{A_m,A_v}}{2\sigma_z^2}\right]\left[\frac{\sigma_{A_m,A_v}}{\sigma_z} + x\,\frac{\sigma_{A_v}^2}{2\sigma_z^2}\right] + \frac{\sigma_{A_m}^2\sigma_{A_v}^2 + \sigma_{A_m,A_v}}{2\sigma_z^3} + 3x\,\frac{\sigma_{A_m,A_v}\sigma_{A_v}^2}{4\sigma_z^4}\right) \tag{34.59c}$$

where $\overline{\imath}$ and x are as in Equation 34.45. Inspection of these equations suggests that most d generated is negative, and this was borne out in the limited amount of simulations presented by Hill and Zhang. In particular, the disequilibrium associated with σ_{A_m,A_v} tends to be negative, even when it is initially zero, resulting in the covariance becoming more negative following selection. One way to conceptualize this negative correlation in breeding values is to recall that selection tends to make fitness components negatively correlated. Under modest selection (the fraction saved $p < 0.5$), larger values of both A_m and A_v improve fitness, and hence these tend to become negatively associated. Conversely, recall from Figure 13.5 that when $p > 0.5$, ılower values of A_v improve fitness under directional truncation selection, and this may lead to a positive association between A_m and A_v. Indeed for sufficiently weak selection ($p > 0.8$), some positive d can be generated for σ_{A_m,A_v}. In many cases, the change in genetic covariance is modest and have only a minor influence on the dynamics of the mean and covariance, but the full dynamics of Equation 34.59 remain unexplored.

What are the consequences of these changes in variances and covariances? When the decline in phenotypic variance is entirely due to the decline in the additive variance (i.e., declines in d), the heritability decreases and the rate of response in the mean slows. Further, d, and hence the genetic variance and h^2, rather quickly reach an equilibrium value (Chapter 13). However, when there is heritable variation in σ^2_E, changes in μ_{A_v} also change the phenotypic variance, and the change in heritability becomes somewhat unpredictable. It may decline faster than expected, slower that expected, or even increase, depending on the rate (and direction) of change in μ_{A_m}. Another consequence of changes in σ^2_z being due to changes in μ_{A_v} is that an equilibrium value for h^2 many not be reached, as the phenotypic variance continues to change with response in μ_{A_v}. Eventually, the additive model breaks down when the change in μ_{A_v} is sufficiently large to generate negative values of σ^2_E.

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