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## Theory of Index Selection

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A common problem in artificial selection is how to select on a multivariate phenotype. In the final analysis, the investigator assigns (either explicitly or implicitly) a weighting scheme to each character, creating a univariate character (an *index*) that is then selected. For example, if the vector  $\mathbf{z}$  of character values is measured in an individual, the most common index is a linear combination  $\sum b_i z_i = \mathbf{b}^T \mathbf{z}$  and most of our discussion focuses on such linear indices. Our treatment starts by reviewing the general theory of selection on a linear index. This is followed by a detailed examination of the Smith-Hazel index and its extensions, the index giving the largest expected response in a specified linear combination of characters. Next, two alternate multivariate selection approaches, tandem selection and independent culling, are examined. We conclude with an extended discussion of improving the response in a single character by using selection indices that incorporate information from other characters and/or relatives.

There is a huge literature on the theory and application of selection indices. General reviews can be found in Turner and Young (1969), Lin (1978), Namkoong (1979), Bulmer (1980), James (1982), Baker (1986), and Van Vleck (1993), while specific applications to plant breeding (and other organisms with asexual reproduction and/or selfing) can be found in Wricke and Weber (1986) and Baker (1986).

### General Theory of Selection on a Linear Index

Consider selection on the univariate character defined by the linear index  $I = \sum b_j z_j = \mathbf{b}^T \mathbf{z}$  where  $\mathbf{z}$  is the vector of phenotypic values in an individual and  $\mathbf{b}$  a vector of weights. Specific linear indices (e.g., the Smith-Hazel, base, and various restricted indices) discussed in detail later follow by specifying  $\mathbf{b}$ , so all results derived here apply equally to these indices. As before, let  $\mathbf{P}$  and  $\mathbf{G}$  denote the phenotypic and additive-genetic covariance matrices. Applying Equation 31.5,

the phenotypic variance of this new synthetic character  $I$  is

$$\sigma_I^2 = \sigma(\mathbf{b}^T \mathbf{z}, \mathbf{b}^T \mathbf{z}) = \mathbf{b}^T \sigma(\mathbf{z}, \mathbf{z}) \mathbf{b} = \mathbf{b}^T \mathbf{P} \mathbf{b} \quad (23.1a)$$

with additive genetic variance

$$\sigma_{A_I}^2 = \sigma_A(\mathbf{b}^T \mathbf{z}, \mathbf{b}^T \mathbf{z}) = \mathbf{b}^T \sigma_A(\mathbf{z}, \mathbf{z}) \mathbf{b} = \mathbf{b}^T \mathbf{G} \mathbf{b} \quad (23.1b)$$

giving the heritability of  $I$  as

$$h_I^2 = \frac{\sigma_{A_I}^2}{\sigma_I^2} = \frac{\mathbf{b}^T \mathbf{G} \mathbf{b}}{\mathbf{b}^T \mathbf{P} \mathbf{b}} \quad (23.1c)$$

as obtained by Lin and Allaire (1977) and Nordskog (1978). If phenotypes  $\mathbf{z}$  and breeding values  $\mathbf{g}$  are jointly multivariate normal, linear combinations of each is also normally distributed (Chapter 31) and hence the univariate breeders' equation holds for response in  $I$ . Thus if  $\bar{v}$  is the selection intensity on  $I$ , Equation 25.8 gives the response in  $I$  as

$$R_I = \bar{v} h_I^2 \sigma_I = \bar{v} \cdot \frac{\mathbf{b}^T \mathbf{G} \mathbf{b}}{\mathbf{b}^T \mathbf{P} \mathbf{b}} \sqrt{\mathbf{b}^T \mathbf{P} \mathbf{b}} = \bar{v} \cdot \frac{\mathbf{b}^T \mathbf{G} \mathbf{b}}{\sqrt{\mathbf{b}^T \mathbf{P} \mathbf{b}}} \quad (23.2)$$

At the risk of mentioning the obvious, we note to the reader that the index  $I$  is a standard univariate character and hence results of previous chapters apply. For example, the variance in expected response can be computed from Hill's theory (Chapter 26) using the additive genetic variance and heritability of the index,  $\sigma_{A_I}^2$  and  $h_I^2$ . Likewise, the realized heritability of the index can be obtained by the methods discussed in Chapter 26, regressing the response in  $I$  on cumulative selection differential.

How does selection on this index change the vector of underlying character means? Under the conditions of the multivariate breeders' equation,  $\Delta \boldsymbol{\mu} = \mathbf{G} \mathbf{P}^{-1} \mathbf{s}$ , so our task is to obtain the vector of directional selection differentials  $\mathbf{s}$  given selection on  $I$ . Consider  $s_j$ , the differential associated with character  $j$ . First note that the correlation between relative fitness  $w$  and the value of character  $j$  can be expressed as  $\rho_{z_j, w} = \rho_{z_j, I} \cdot \rho_{I, w}$ . Expressed in terms of covariances,

$$\frac{\sigma(z_j, w)}{\sigma_w \sigma_{z_j}} = \left( \frac{\sigma(z_j, I)}{\sigma_I \sigma_{z_j}} \right) \left( \frac{\sigma(I, w)}{\sigma_I \sigma_w} \right) \quad (23.3a)$$

Recalling the Price-Robertson formulation (Equation 3.21),  $\sigma(z_j, w) = s_j$  and likewise  $\sigma(I, w) = s_I = \bar{v} \sigma_I$  where  $\bar{v}$  is the selection intensity on the index. Solving for  $\sigma(z_j, w)$  and using these identities gives

$$s_j = \sigma(z_j, w) = \frac{\sigma(z_j, I) \cdot \sigma(I, w)}{\sigma_I^2} = \bar{v} \cdot \frac{\sigma(z_j, I)}{\sigma_I} \quad (23.3b)$$

Finally, note that  $\sigma(z_j, I) = \sigma(z_j, \sum_k b_k z_k) = \sum_k b_k P_{jkI}$ , where  $P_{ij}$  is the  $ij$ -th element of the phenotypic covariance matrix  $\mathbf{P}$ . Hence, the  $j$  selection differential is

$$s_j = \left( \frac{\bar{l}}{\sigma_I} \right) \cdot \sum_k b_k P_{jk} \quad (23.3c)$$

giving the vector of selection differential as

$$\mathbf{s} = \left( \frac{\bar{l}}{\sigma_I} \right) \cdot \mathbf{P}\mathbf{b} \quad (23.3d)$$

and the vector of responses as

$$\Delta\boldsymbol{\mu} = \mathbf{G}\mathbf{P}^{-1}\mathbf{s} = \left( \frac{\bar{l}}{\sigma_I} \right) \cdot \mathbf{G}\mathbf{b} = \bar{l} \cdot \frac{\mathbf{G}\mathbf{b}}{\sqrt{\mathbf{b}^T \mathbf{P}\mathbf{b}}} \quad (23.4)$$

Equation 23.4 shows that the vector of responses  $\Delta\boldsymbol{\mu}$  is unchanged if the index weights are rescaled from  $\mathbf{b}$  to  $c \cdot \mathbf{b}$  as the constant  $c$  cancels out. However the response in the index itself changes as  $\mathbf{b}$  is rescaled. From Equation 23.2 the response in the index using weights  $c \cdot \mathbf{b}$  is  $c$  times the response expected when the index uses  $\mathbf{b}$ .

A related problem is the correlated response in the some other index  $J = \mathbf{a}^T \mathbf{z} = \sum a_j z_j$  when selection occurs on  $I = \mathbf{b}^T \mathbf{z}$ . Applying Equation 23.4, the expected correlated response is

$$R_J = \mathbf{a}^T (\boldsymbol{\mu} + \Delta\boldsymbol{\mu}) - \mathbf{a}^T \boldsymbol{\mu} = \mathbf{a}^T \Delta\boldsymbol{\mu} = \bar{l} \cdot \frac{\mathbf{a}^T \mathbf{G}\mathbf{b}}{\sqrt{\mathbf{b}^T \mathbf{P}\mathbf{b}}} \quad (23.5)$$

While indices have been presented as the objects of selection, often an investigator observes a vector of selection differentials  $\mathbf{s}$  or vector of responses  $\Delta\boldsymbol{\mu}$  and wishes to obtain the linear index that would give the same  $\mathbf{s}$  and/or  $\Delta\boldsymbol{\mu}$ . This approach of constructing a *retrospective index* (or *index in retrospect*) was first suggested by Dickerson et al. (1954). If the vector of selection differentials  $\mathbf{s}$  is observed, Equation 23.3d suggests the retrospective index  $\mathbf{b} = \mathbf{P}^{-1}\mathbf{s}$  (given our previous remarks we ignore the constant  $\bar{l}/\sigma_I$ ). Even when artificial selection occurs using a known index, a retrospective index constructed from the *effective* selection differentials (which measure fertility differences in addition to artificial selection, see Equation 25.8) provides the investigator with a measure of how natural selection interferes with the desired selection scheme. Alternatively, the investigator may not know the within-generation change in  $\mathbf{s}$  but can observe the between-generation change  $\Delta\boldsymbol{\mu}$ . In this case Equation 23.4 (again ignoring the constant  $\bar{l}/\sigma_I$ ) suggests the retrospective index  $\mathbf{b} = \mathbf{G}^{-1}\Delta\boldsymbol{\mu}$ .

**\*Changes in G due to index selection.** Selection on the index  $I$  changes the additive-genetic covariance matrix of the characters underlying  $I$ . To examine

these changes, make the standard assumption of the infinitesimal model so that allele frequency changes can be ignored and all changes genetic variances are due solely to gametic phase disequilibrium. Further assume that phenotypes are multivariate normally distributed so that any linear combination of characters (such as the index  $I$ ) is also normal. Artificial selection on an index almost always occurs by truncation selection, in which case (Table 1 in Chapter 27) the reduction in the phenotypic variance of  $I$  following selection is  $(\sigma_I^2)^* = \kappa \sigma_I^2$ , where  $\kappa - 1 = \bar{i}[\bar{i} - \text{prb}(1 - p)]$  with  $\text{prb}$  the inversion probability transform for a normal random variable and  $p$  the fraction of individuals saved. Under these conditions, several authors (Zeng 1988, Villanueva and Kennedy 1990, Itoh 1991) have shown that the within-generation change in the phenotypic covariance matrix caused by truncation selection on  $I$  is

$$\mathbf{P}^* = \mathbf{P} + \frac{(\kappa - 1)}{\sigma_I^2} (\mathbf{P}\mathbf{b})(\mathbf{P}\mathbf{b})^T \quad (23.6a)$$

giving

$$\mathbf{P}^{-1}(\mathbf{P}^* - \mathbf{P})\mathbf{P}^{-1} = \frac{(\kappa - 1)}{\sigma_I^2} \mathbf{b}\mathbf{b}^T \quad (23.6b)$$

Following Chapter 33, express the additive-genetic and phenotypic covariance matrix at generation  $t$  as  $\mathbf{G}_t = \mathbf{G}_0 + \mathbf{D}_t$  and  $\mathbf{P}_t = \mathbf{P}_0 + \mathbf{D}_t$  where the subscript zero denotes the matrices before selection and  $\mathbf{D}_t$  is the matrix of gametic-phase disequilibrium values, which is obtained by substituting Equation 23.6b into Equation 33.xx and iterating

$$\Delta \mathbf{D}_t = \frac{1}{2} \left[ \left( \frac{\kappa - 1}{\sigma_I^2(t)} \right) (\mathbf{G}_t \mathbf{b})(\mathbf{G}_t \mathbf{b})^T - \mathbf{D}_t \right] \quad (23.7a)$$

where it is generally assumed no disequilibrium is present before selection starts ( $\mathbf{D}_0 = \mathbf{0}$ ).

While the above expression gives the change in the covariance matrices for all characters underlying the index, often the concern is only with changes in the phenotypic and additive genetic variances of the index itself. From Equations 23.1a and b, these are

$$\sigma_I^2(t) = \mathbf{b}^T \mathbf{P}_t \mathbf{b} = \mathbf{b}^T (\mathbf{P}_0 + \mathbf{D}_t) \mathbf{b} = \sigma_I^2(0) + d_I(t) \quad (23.7b)$$

and

$$\sigma_{A_I}^2(t) = \mathbf{b}^T \mathbf{G}_t \mathbf{b} = \mathbf{b}^T (\mathbf{G}_0 + \mathbf{D}_t) \mathbf{b} = \sigma_{A_I}^2(0) + d_I(t) \quad (23.7c)$$

where  $\mathbf{b}^T \mathbf{D}_t \mathbf{b} = d_I(t)$  is the disequilibrium in  $I$ . Applying Equation 23.7a,

$$\begin{aligned} \Delta d_I(t) &= \mathbf{b}^T \Delta \mathbf{D}_t \mathbf{b} = \mathbf{b}^T \left( \frac{1}{2} \left[ \left( \frac{\kappa - 1}{\sigma_I^2(t)} \right) \mathbf{G}_t \mathbf{b} \mathbf{b}^T \mathbf{G}_t - \mathbf{D}_t \right] \right) \mathbf{b} \\ &= \frac{1}{2} \left( \frac{\kappa - 1}{\sigma_I^2(t)} \right) (\mathbf{b}^T \mathbf{G}_t \mathbf{b}) (\mathbf{b}^T \mathbf{G}_t \mathbf{b}) - \frac{1}{2} \mathbf{b}^T \mathbf{D}_t \mathbf{b} \\ &= \frac{\kappa - 1}{2} \cdot h_I^2(t) \cdot \sigma_{A_I}^2(t) - \frac{d_I(t)}{2} \end{aligned} \quad (23.7d)$$

This is identical to Equation 27.11, showing that Bulmer's univariate results also apply to an index under truncation selection even though the index itself is composed of several different characters whose variances and covariances are changing. Hence the equilibrium additive variance  $\tilde{\sigma}_{A_I}^2$  is given by Equation 27.12, as obtained by several workers (Bruns and Harvey 1976, Bennett and Swiger 1980, Gomez-Raya and Burnside 1990, Villanueva and Kennedy 1993). Since  $\tilde{d}_I = \tilde{\sigma}_{A_I}^2 - \sigma_{A_I}^2(0)$ , the equilibrium phenotypic variance and heritability of the index follow as  $\tilde{\sigma}_I^2 = \sigma_I^2(0) + \tilde{d}_I$  and  $\tilde{h}^2 = \tilde{\sigma}_{A_I}^2 / \tilde{\sigma}_I^2$ .

### The Smith-Hazel Index

The standard goal of multiple character selection is to maximize the response in some overall merit based on an index of phenotypic values. Typically, the merit function is taken to be a linear index  $J = \mathbf{a}^T \mathbf{z}$  where the vector of *economic weights*  $\mathbf{a}$  assigns the desirability of relative responses in each character. For example, if a unit response in character one is three times more desirable than a unit response in character two,  $a_1/a_2 = 3$ . Economic weights are either preset by the investigator or estimated by some prediction of an individual's overall merit as a function of  $\mathbf{z}$ . An example of this latter approach is the prediction of individual fitness  $w$  (merit in this case) from the regression of  $w$  on  $\mathbf{z}$  (Chapters 30, 32). Other methods for estimating economic weights are reviewed by Harris (1970), Gjedrem (1972), Melton et al. (1979, but see cautions by Thompson 1980 and Goddard 1983), and Cotterhill and Jackson (1985). If  $g_i$  is the additive genetic value of character  $i$  in the individual being considered, then  $H = \mathbf{a}^T \mathbf{g} = \sum a_i g_i$  is that individual's additive genetic value for merit and  $H - \mu_H = H - \mathbf{a}^T \boldsymbol{\mu}$  its breeding value.  $H$  is often called the *aggregate genetic value* or *genetic merit*, and in almost all situations is unknown and cannot be directly selected. Under the standard assumptions of no complicating factors (genotype-environment interactions, epistasis, etc.) the mean breeding values of a group of parents equals the expected change in the offspring of those parents. The within-generation change in  $H$  thus equals the between-generation change (response) in the merit  $J$ , which is maximized by selecting those individuals with the largest  $H$  values. Our task is thus to find the linear index based on measurable phenotypic values  $I_s = \mathbf{b}_s^T \mathbf{z}$  that has the highest correlation with  $H$ . Because of genetic and phenotypic correlations between characters, the best predictor of the additive genetic value of merit  $H$  is not necessarily (or even usually) the observed phenotypic merit  $J$ .

To obtain this optimal index, first consider the correlation between an arbitrary index  $I = \mathbf{b}^T \mathbf{z}$  and  $H$ , which is  $\rho_{I,H} = \sigma_{H,I} / (\sigma_H \sigma_I)$ . From Equation 31.5

$$\sigma_H^2 = \sigma(\mathbf{a}^T \mathbf{z}, \mathbf{a}^T \mathbf{z}) = \mathbf{a}^T \mathbf{G} \mathbf{a} \quad (23.8)$$

while (Equation 23.1a)  $\sigma_I^2 = \mathbf{b}^T \mathbf{P} \mathbf{b}$ . Likewise,  $\sigma_{H,I} = \mathbf{a}^T \sigma(\mathbf{g}, \mathbf{z}) \mathbf{b} = \mathbf{a}^T \mathbf{G} \mathbf{b}$  which

follows since  $\sigma(\mathbf{g}, \mathbf{z}) = \sigma(\mathbf{g}, \mathbf{g} + \mathbf{e}) = \sigma(\mathbf{g}, \mathbf{g}) = \mathbf{G}$ , giving the correlation between the breeding value of merit  $H$  and a phenotypic index  $I$  as

$$\rho_{H,I} = \frac{\sigma_{H,I}}{\sigma_H \sigma_I} = \frac{\mathbf{a}^T \mathbf{G} \mathbf{b}}{\sqrt{\mathbf{a}^T \mathbf{G} \mathbf{a}} \sqrt{\mathbf{b}^T \mathbf{P} \mathbf{b}}} \quad (23.9)$$

From standard regression theory (Chapter 3), the fraction of variation in  $H$  accounted for by  $I$  is  $\rho_{H,I}^2$  so that Equation 23.9 provides a measure of how well  $I$  predicts  $H$ . To obtain the value of  $\mathbf{b}$  maximizing this correlation, first note the since  $\mathbf{a}$  is a constant we need only maximize

$$\frac{\mathbf{a}^T \mathbf{G} \mathbf{b}}{\sqrt{\mathbf{b}^T \mathbf{P} \mathbf{b}}} \quad (23.10a)$$

Both quadratic products yield a scalar, so that derivatives can be taken by using the standard quotient rule and then applying the methods of Chapter 31. Taking the derivative with respect to  $\mathbf{b}$  and denoting solutions giving a derivative of zero by  $\tilde{\mathbf{b}}$ , gives

$$\left( \tilde{\mathbf{b}}^T \mathbf{P} \tilde{\mathbf{b}} \right) \mathbf{G} \mathbf{a} = \left( \mathbf{a}^T \mathbf{G} \tilde{\mathbf{b}} \right) \mathbf{P} \tilde{\mathbf{b}} \quad (23.10b)$$

Since both  $\tilde{\mathbf{b}}^T \mathbf{P} \tilde{\mathbf{b}}$  and  $\mathbf{a}^T \mathbf{G} \tilde{\mathbf{b}}$  are scalars, solutions are of the form  $\mathbf{P} \tilde{\mathbf{b}} = c \cdot \mathbf{G} \mathbf{a}$ , giving the *Smith-Hazel selection index*

$$I_s = \mathbf{b}_s^T \mathbf{z} = \left( \mathbf{P}^{-1} \mathbf{G} \mathbf{a} \right)^T \mathbf{z} \quad \text{where} \quad \mathbf{b}_s = \mathbf{P}^{-1} \mathbf{G} \mathbf{a} \quad (23.11)$$

Smith (1936), following a suggestion by Fisher to use his recently developed method of discriminant functions (Fisher 1935), obtained this index for the special case of selection on a collection of pure lines. Hazel (1945) extended Smith's results to outbreeding populations by considered the change in breeding value. To get some appreciation of how each character is weighted in the Smith-Hazel index, consider the case when there are no phenotypic or genetic correlations ( $\mathbf{P}$  and  $\mathbf{G}$  are diagonal). Here  $b_i = a_i h_i^2$ , giving the index as  $\sum a_i h_i^2 z_i$  so that characters with both large heritabilities and economic weights receive the most value, while a large heritability or economic weight by itself is not sufficient to insure a large weight. Constructing this index requires three sets of parameters – estimates of  $\mathbf{P}$ ,  $\mathbf{G}$  and  $\mathbf{a}$ . Errors in estimating  $\mathbf{a}$  appear to have only a small effect on the index weighting (reviewed by James 1982), while the consequences of using estimates of  $\mathbf{P}$  and  $\mathbf{G}$  will be discussed shortly.

### Properties of the Smith-Hazel Index

1) *Selection on the Smith-Hazel index provides largest response in merit for a fixed selection intensity  $\bar{i}$ .* Notice from Equation 23.5 that the response in merit given

selection on the index  $\mathbf{b}^T \mathbf{z}$  for a fixed selection intensity  $\bar{i}$  is given by maximizing the same expression as Equation 23.10a, which has solutions  $\mathbf{b} = \mathbf{b}_s$ . Applying Equation 23.5, expected response in merit using the Smith-Hazel index is

$$\begin{aligned} R_H &= \bar{i} \cdot \frac{\mathbf{a}^T \mathbf{G} \mathbf{b}_s}{\sqrt{\mathbf{b}_s^T \mathbf{P} \mathbf{b}_s}} = \bar{i} \cdot \sqrt{\mathbf{a}^T \mathbf{G} \mathbf{b}_s} \\ &= \bar{i} \cdot \sqrt{\mathbf{a}^T \mathbf{G} \mathbf{P}^{-1} \mathbf{G} \mathbf{a}} \end{aligned} \quad (23.12)$$

while from Equation 23.4 the change in the vector of character means is

$$\Delta \boldsymbol{\mu} = \left( \frac{\bar{i}}{\sigma_I} \right) \cdot \mathbf{G} \mathbf{b}_s = \bar{i} \cdot \frac{\mathbf{G} \mathbf{P}^{-1} \mathbf{G} \mathbf{a}}{\sqrt{\mathbf{a}^T \mathbf{G} \mathbf{P}^{-1} \mathbf{G} \mathbf{a}}} \quad (23.13)$$

2) *The Smith-Hazel index is closely related to the least squares regression of breeding value for merit on the vector of phenotypic values  $\mathbf{z}$ .* This regression can be written as  $H = a + \mathbf{b}^T \mathbf{z}$ , where  $\mathbf{b}$  and  $a$  are chosen such that the regression accounts for the largest amount of variation in  $H$ . This occurs when  $\mathbf{b}$  is chosen to maximize the correlation between  $H$  and  $\mathbf{z}$  and when  $a$  satisfies  $E[H] = a + \mathbf{b}^T E[\mathbf{z}]$  (Chapters 3, 7). Given  $\mathbf{b}_s$  maximizes this correlation, the least squares regression is

$$H = a + \mathbf{b}_s^T \mathbf{z} = a + I_s \quad (23.14a)$$

Noting that  $E[H] = \mathbf{a}^T \boldsymbol{\mu}$  and  $E[\mathbf{z}] = \boldsymbol{\mu}$  gives  $a = \mathbf{a}^T \boldsymbol{\mu} - \mathbf{b}_s^T \boldsymbol{\mu}$ , hence

$$H - \boldsymbol{\mu} = \mathbf{b}_s^T (\mathbf{z} - \boldsymbol{\mu}) \quad (23.14b)$$

Since breeding value is the deviation of additive genetic value from the mean, the regression of the breeding value for merit on phenotypic value is

$$\mathbf{b}_s^T (\mathbf{z} - \boldsymbol{\mu}) = I_s - \mathbf{b}_s^T \boldsymbol{\mu} \quad (23.14c)$$

Estimates of breeding value based on least squares regressions are called often best linear predictors (BLPs). Hence, if phenotypic characters are first recoded to have mean zero, the Smith-Hazel index is the BLP of breeding value. The related method of BLUP (best linear unbiased predictor, Chapter 20), provides the best estimate of breeding value when more general pedigree information is available. Similarities and differences of the Smith-Hazel index BLP estimates and BLUP estimates are discussed later in this chapter.

Just how much of the variance in breeding values is explained by the regressions given by Equations 23.14a-c? From standard regression theory the fraction

of variance explained is  $\rho^2(H, a + \mathbf{b}_s^T \mathbf{z}) = \rho^2(H, \mathbf{b}_s^T \mathbf{z}) = \rho^2(H, I_s)$ . Substituting  $\mathbf{b}_s$  into Equation 23.9 gives

$$\rho_{H, I_s} = \frac{\mathbf{a}^T \mathbf{G} \mathbf{P}^{-1} \mathbf{G} \mathbf{a}}{\sqrt{\mathbf{a}^T \mathbf{G} \mathbf{P}^{-1} \mathbf{G} \mathbf{a}} \cdot \sqrt{\mathbf{a}^T \mathbf{G} \mathbf{a}}} = \sqrt{\frac{\mathbf{a}^T \mathbf{G} \mathbf{P}^{-1} \mathbf{G} \mathbf{a}}{\mathbf{a}^T \mathbf{G} \mathbf{a}}} \quad (23.15a)$$

Thus the fraction of the additive genetic variance in merit explained by the Smith-Hazel index is

$$\frac{\mathbf{a}^T \mathbf{G} \mathbf{P}^{-1} \mathbf{G} \mathbf{a}}{\mathbf{a}^T \mathbf{G} \mathbf{a}} \quad (23.15b)$$

leaving a residual (unexplained) variance of  $(1 - \rho^2)\sigma_H^2$  or

$$\left( \frac{\mathbf{a}^T \mathbf{G} \mathbf{P}^{-1} \mathbf{G} \mathbf{a}}{\mathbf{a}^T \mathbf{G} \mathbf{a}} \right) \cdot \mathbf{a}^T \mathbf{G} \mathbf{a} = \mathbf{a}^T \mathbf{G} \mathbf{P}^{-1} \mathbf{G} \mathbf{a} \quad (23.15c)$$

Property 2 does not require assumptions of multivariate normality, but property 1 does. Two other useful properties of the Smith-Hazel index (due to Williams 1962 and Henderson 1963), that also require multivariate normality are

3) *The Smith-Hazel index gives the maximal probability of selecting the individual with the largest breeding value for merit in a sample.*

4) *The Smith-Hazel index gives the maximal probability of selecting the individual with largest breeding value for merit from any pair of individuals. This is a special case of property 3).*

**Other useful results.** Popular expressions in the literature relating to the Smith-Hazel index are

$$\sigma_{H, I_s} = \sigma_{I_s}^2, \quad \rho_{H, I_s} = \frac{\sigma_{I_s}}{\sigma_H}, \quad R_H = \bar{v} \cdot \sigma_{I_s} \quad (23.16a)$$

These are obtained by first noting for  $\mathbf{b}_s = \mathbf{P}^{-1} \mathbf{G} \mathbf{a}$  that

$$\sigma_{I_s}^2 = \mathbf{b}_s^T \mathbf{P} \mathbf{b}_s = \mathbf{a}^T \mathbf{G} \mathbf{P}^{-1} \mathbf{G} \mathbf{a} = \mathbf{a}^T \mathbf{G} \mathbf{b}_s = \sigma_{H, I_s} \quad (23.16b)$$

Substitution into Equations 23.15a and 12 (respectively) gives the last two identities. While these simplifications are useful, care must be taken if index is rescaled. Since  $c \cdot \mathbf{P}^{-1} \mathbf{G} \mathbf{a}$  for any constant  $c$  also satisfies Equation 23.10a, the Smith-Hazel index is not unique and can be rescaled at the investigator's convenience. However, if the investigator uses rescaled weights  $\tilde{\mathbf{b}}_s = c \cdot \mathbf{P}^{-1} \mathbf{G} \mathbf{a}$ , the expression in

Equations 23.16a are incorrect if  $\tilde{\sigma}_{I_s}^2 = \tilde{\mathbf{b}}_s^T \mathbf{P} \tilde{\mathbf{b}}_s$  is used in place of  $\sigma_{I_s}^2 = \mathbf{b}_s^T \mathbf{P} \mathbf{b}_s$ . Since  $\tilde{\sigma}_{I_s}^2 = \sigma_{I_s}^2 / c^2$ , the correct expressions for this rescaled index are

$$\sigma_{H,I_s} = \frac{\tilde{\sigma}_{I_s}^2}{c^2}, \quad \rho_{H,I_s} = \frac{\tilde{\sigma}_{I_s}}{c \cdot \sigma_H}, \quad R_H = \bar{v} \cdot \frac{\tilde{\sigma}_{I_s}}{c} \tag{23.16c}$$

The Smith-Hazel index can easily be extended to the case where  $H$  and  $I_s$  have different number of elements, viz.,

$$H = \sum_{j=1}^n a_j g_j \quad \text{and} \quad I_s = \sum_{k=1}^m b_k z_k$$

Note that it is entirely possible  $H$  and  $I_s$  contain no overlapping characters. Define  $\mathbf{P}$  as the  $m \times m$  phenotypic covariance matrix of  $\mathbf{z}$  and  $\mathbf{G}$  as the  $m \times n$  covariance matrix whose elements  $G_{kj} = \sigma(z_k, g_j)$  for  $1 \leq k \leq m, 1 \leq j \leq n$  are the additive genetic covariances between the phenotypic values of the  $m$  characters comprising  $I_s$  and the additive genetic values of the  $n$  characters comprising  $H$ . Using this definition of  $\mathbf{G}$ , the Smith-Hazel index is again given by  $\mathbf{b}_s = \mathbf{P}^{-1} \mathbf{G} \mathbf{a}$ . Since  $\mathbf{G}$  is not square (and hence not symmetric), the response is given by

$$R_H = \bar{v} \cdot \sqrt{\mathbf{a}^T \mathbf{G}^T \mathbf{P}^{-1} \mathbf{G} \mathbf{a}}$$

When the phenotypic and genetic covariances are estimated in several populations and/or environments (such as different years), the investigator is faced with a decision as how to combine these estimates when constructing an index. At one extreme the index can be computed using pooled covariance matrices to give an *average index*. At the other extreme, separate indices can be constructed for each population/environment, giving *specific indices*. Hanson and Johnson (1957) develop an approach for the optimal response that differentially weights the covariances matrices, yielding what they refer to as a *general index*. Caldwell and Weber (1965), examining response in soybeans over four populations, found that specific indices gave the best overall performance, but that either general or average indices were reasonable substitutes. Clearly, this is an area for both more theoretical and experimental investigation.

**Estimated, base, and Elston indices.** The Smith-Hazel index requires that both the phenotypic and additive-genetic covariance matrices are known. Since these are usually unknown, the *estimated index*  $\hat{I}_s = \hat{\mathbf{P}}^{-1} \hat{\mathbf{G}} \mathbf{a}^T \mathbf{z}$  is constructed using the estimated phenotypic and genetic covariance matrices ( $\hat{\mathbf{P}}$  and  $\hat{\mathbf{G}}$ ). Due to the inaccuracies inherent in estimating these matrices (especially  $\mathbf{G}$ ), this index may be quite different from the correct Smith-Hazel index. This lead Panse (1946), Brim et al. (1959), and Williams (1962a,b) to suggest that the *base index*  $I_b = \sum a_i z_i$ ,

which is independent of  $\mathbf{P}$  and  $\mathbf{G}$ , may in many cases be preferable. The base and Smith-Hazel indices are identical when there are no genetic and phenotypic correlations and all characters have the same heritability. More generally, the two indices are equivalent when  $\mathbf{P}^{-1}\mathbf{G} = c \cdot \mathbf{I}$  or  $\mathbf{P} = c \cdot \mathbf{G}$  for any positive constant  $c$ . Heidhues and Henderson (1962) have proposed the *heritability index* with weights  $b_i = a_i h_i^2$  as an alternative to the base index when confidence in genetic covariance estimates is low. Note from previous discussion that this reduces to the Smith-Hazel index when there are no genetic or phenotypic correlations between characters.

The expected response under the base index relative to the true Smith-Hazel index is given by the correlation between these indices,

$$\begin{aligned} \rho_{I_s, I_b} &= \frac{\sigma(I_s, I_b)}{\sigma_{I_s} \cdot \sigma_{I_b}} = \frac{\sigma(\mathbf{b}_s^T \mathbf{z}, \mathbf{a}^T \mathbf{z})}{\sqrt{\mathbf{b}_s^T \mathbf{P} \mathbf{b}_s \cdot \mathbf{a}^T \mathbf{P} \mathbf{a}}} \\ &= \frac{\mathbf{b}_s^T \mathbf{P} \mathbf{a}}{\sqrt{\mathbf{b}_s^T \mathbf{P} \mathbf{b}_s \cdot \mathbf{a}^T \mathbf{P} \mathbf{a}}} = \frac{\mathbf{a}^T \mathbf{G} \mathbf{a}}{\sqrt{\mathbf{a}^T \mathbf{G} \mathbf{P}^{-1} \mathbf{G} \mathbf{a} \cdot \mathbf{a}^T \mathbf{P} \mathbf{a}}} \end{aligned} \quad (23.17)$$

Although the base index can be applied without estimates of  $\mathbf{G}$  and  $\mathbf{P}$ , it still requires the assignment of economic weights. If estimates of these covariance matrices are available, the method of desired-gains to be discussed shortly can be used to construct an index without having to specify  $\mathbf{a}$ . In the extreme case where  $\mathbf{P}$ ,  $\mathbf{G}$  and  $\mathbf{a}$  are all unknown, Elston (1963) suggests the nonlinear index

$$I_e = (z_1 - m_1)(z_2 - m_2) \cdots (z_n - m_n) = \prod_{j=1}^n (z_j - m_j)$$

where  $m_j$  is the minimal value of character  $j$  and each character is scaled to have unit variance (Figure 23.2 shows the form of this index for two characters). In effect, this index assumes all characters are equally weighted (Elston 1963, Baker 1974). Theoretical results (Cotterhill 1985) suggest that if the traits in the index are positively correlated (both genetically and phenotypically) the Smith-Hazel, base, and Elston indices give very similar responses. However, if there are negative correlations (genetically or phenotypically) the Smith-Hazel index is significantly superior. Experimental studies comparing base versus estimated indices reviewed later (Table 23.4) show that both often give similar responses.

**Example 1.** Brim et al. (1959) estimated the genetic and phenotypic covariances for several characters in soybeans. Consider three of these traits,  $z_1$  = oil content,  $z_2$  = protein content, and  $z_3$  = yield. For these characters, Brim et al. estimated

$$\hat{\mathbf{P}} = \begin{pmatrix} 287.5 & 477.4 & 1266 \\ 477.4 & 935 & 2303 \\ 1266 & 2303 & 5951 \end{pmatrix}, \quad \hat{\mathbf{G}} = \begin{pmatrix} 128.7 & 160.6 & 492.5 \\ 160.6 & 254.6 & 707.7 \\ 492.5 & 707.7 & 2103 \end{pmatrix}$$

Assume characters have equal economic weight so that  $a_i = 1$ . The resulting vector of weights  $\hat{\mathbf{b}}_s$  for the (estimated) Smith-Hazel index is

$$\hat{\mathbf{b}}_s = \hat{\mathbf{P}}^{-1} \hat{\mathbf{G}} \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix} = \begin{pmatrix} 2.4 \\ -2.9 \\ 1.2 \end{pmatrix}$$

giving the index as  $\hat{I}_s = 2.4z_1 - 2.9z_2 + 1.2z_3$ . In contrast, the base index is  $I_b = \mathbf{a}^T \mathbf{z} = z_1 + z_2 + z_3$ . Suppose two individuals are examined, one of which will be saved. The oil, protein, and yield scores of these individuals are (1, 2, 3) and (1, 1, 1) respectively. Under the estimated index, these individuals have scores of  $2.4 \cdot 1 - 2.9 \cdot 2 + 1.2 \cdot 3 = 0.2$  and  $2.4 - 2.9 + 1.2 = 0.7$ , while under the base index these individual have scores  $1 + 2 + 3 = 6$  and  $1 + 1 + 1 = 3$ . Hence, individual two is saved under the Smith-Hazel index, while individual one is saved under the base selection. To compare the responses under the base versus Smith-Hazel index, assume that the error from using the estimates of  $\mathbf{P}$  and  $\mathbf{G}$  is small. Since  $\sqrt{\mathbf{a}^T \hat{\mathbf{G}} \hat{\mathbf{P}}^{-1} \hat{\mathbf{G}} \mathbf{a}} \simeq 49.67$ , from Equation 23.12 the response in  $H$  to selection on  $\hat{I}_s$  is  $\bar{v} \cdot 49.67$ . For the base index where  $\mathbf{b} = \mathbf{a} = (1, 1, 1)^T$ ,  $\sigma_I = \sqrt{\mathbf{a}^T \hat{\mathbf{P}} \mathbf{a}} \simeq 123.6$  and  $\mathbf{a}^T \hat{\mathbf{G}} \mathbf{a} \simeq 5208$ . Substituting these into Equation 23.2 (assuming that the errors in the estimates of  $\mathbf{P}$  and  $\mathbf{G}$  are small) gives

$$\frac{R_I}{\bar{v}} = \frac{\mathbf{a}^T \hat{\mathbf{G}} \mathbf{a}}{\sqrt{\mathbf{a}^T \hat{\mathbf{P}} \mathbf{a}}} \simeq \frac{5208}{123.6} \simeq 23.1$$

which is only 85 percent of the expected response under the Smith-Hazel index. Applying Equation 23.17, the correlation between the two indices (assuming that the estimated index is the correct Smith-Hazel index) is

$$\frac{\mathbf{a}^T \hat{\mathbf{G}} \mathbf{a}}{\sqrt{\mathbf{a}^T \hat{\mathbf{G}} \hat{\mathbf{P}}^{-1} \hat{\mathbf{G}} \mathbf{a} \cdot \mathbf{a}^T \hat{\mathbf{P}} \mathbf{a}}} \simeq \frac{5208}{49.67 \cdot 123.6} \simeq 0.85$$

as expected from the response in the base index relative to the Smith-Hazel index.

While Equation 23.17 gives the relative efficiency of using the base index in place of the true Smith-Hazel index, just is how much error is introduced by using the estimated index  $\hat{\mathbf{b}}_s = \hat{\mathbf{P}}^{-1} \hat{\mathbf{G}} \mathbf{a}$  in place of the true index  $\mathbf{b} = \mathbf{P}^{-1} \mathbf{G}$ ? As Harris (1964) notes, we need to distinguish the optimal response (that obtained using the true Smith-Hazel index  $I_s$ ) from the predicted response (which assumes  $\hat{\mathbf{G}}$  and

$\hat{\mathbf{P}}$  are correct) and the achieved response (the expected response using  $\hat{I}_s$ ), where

$$\frac{R}{\bar{i}} = \begin{cases} \sqrt{\mathbf{b}_s^T \mathbf{P} \mathbf{b}_s} & \text{optimal response} \\ \sqrt{\hat{\mathbf{b}}_s^T \hat{\mathbf{P}} \hat{\mathbf{b}}_s} & \text{predicted response} \\ \frac{\mathbf{a}^T \mathbf{G} \hat{\mathbf{b}}_s}{\sqrt{\hat{\mathbf{b}}_s^T \hat{\mathbf{P}} \hat{\mathbf{b}}_s}} & \text{achieved response} \end{cases}$$

The expression for achieved response was obtained by substituting  $\mathbf{b} = \hat{\mathbf{b}}_s$  into Equation 23.5. Thus there are two classes of errors using the estimated index. Errors in estimates of  $\mathbf{P}$  and  $\mathbf{G}$  not only give incorrect index weighting they also yield incorrect predictions of the response to selection on this index. Several workers (Cochran 1951, Tallis 1960, Williams 1962a,b, Harris 1964, Sales and Hill 1976a,b, Hayes and Hill 1980, Tai 1986) have examined these errors, although the results are often extremely complicated even for two characters and are highly dependent on the particular experimental design used to estimate  $\mathbf{G}$  and  $\mathbf{P}$ .

One situation where standard errors for predicted response are easily obtained is when the index parameters are estimated from a parent-offspring regression (Tallis 1960). Assuming the joint distribution of the vector of additive genetic and phenotypic values is multivariate normal, the regression of the vector of additive genetic values  $\mathbf{g}$  on the vector of phenotypic values  $\mathbf{z}$  is given by Equation 31.39a and can be written as  $\mathbf{g} = \mathbf{c} + \mathbf{G}\mathbf{P}^{-1}\mathbf{z} + \mathbf{e}$  where  $\mathbf{c}$  is a vector of constants and  $\mathbf{e}$  the vector of errors associated with predicting  $\mathbf{g}$  from  $\mathbf{z}$ . Premultiplying by  $\mathbf{a}^T$  gives

$$H = \mathbf{a}^T \mathbf{g} = \mathbf{c}^* + \mathbf{a}^T \mathbf{G}\mathbf{P}^{-1} \mathbf{z} + \mathbf{e}^*$$

Thus the slope of the regression of offspring merit  $H$  on parental phenotypes  $\mathbf{z}$  is  $\mathbf{a}^T \mathbf{G}\mathbf{P}^{-1} = \mathbf{b}_s^T$  and hence the Smith-Hazel index weights can be directly estimated from such a regression. Standard regression theory can then be used to place error bounds on  $\mathbf{b}_s$  (using the standard errors of the slope estimates) and on the expected change in  $H$ .

A third class of errors, which occurs even if  $\mathbf{P}$  and  $\mathbf{G}$  are estimated exactly, is that selection changes the genetic covariance structure (Chapters 27, 33) and hence changes the optimal weighting each generation.

Given all these potential sources of error, how well is the use of the Smith-Hazel index supported by experimental data? Caballero (1989) reviews experiments from mice, *Drosophila melanogaster*, and *Tribolium castaneum* (Table 23.1) and finds that the predicted response overestimates, often dramatically, the achieved response.

**Table 23.1.** Summary of 19 experiments in *Drosophila*, mice, and *Tribolium* examining the relative efficiency of selection on the estimated index, measured as the ratio of achieved to predicted response. Original index estimates refers to the expected response using estimates of the genetic and phenotypic covariances used in constructing the initial index, while improved parameter estimates refers to the predicted response based on covariances estimated from either a larger base population or from estimates during selection. From Caballero (1989).

	Expected response computed using:	
	Original index estimates	Improved parameter estimates
Single-generation response	67% (range not available)	87% (range: 23% - 94%)
Multiple-generation response	37% (range: 16% - 95%)	50% (range: 25% - 69%)

This table highlights two sources of errors that reduce the efficiency of the estimated index: those due to poor estimates and those due to changes in the genetic parameters as selection proceeds. The data show, as expected, that poor estimates of population parameters results in a loss of efficiency. Achieved single-generation responses averaged 67% of that predicted based on an index constructed using the original parameter values. When improved parameter values were used, the achieved/predicted response ratio increased to an average value 87%. Table 23.1 also shows that changes in genetic parameters as selection proceeds are a significant source of error that incorrect estimates. Achieved response dropped from 67% to 37% and from 87% to 50% when the response is considered over multiple generations. Caballero (1989) presents evidence that this is due to changes in genetic variances and covariances during the course of selection. Another feature seen when replicated experiments are used is that while the index may show a reasonably consistent response over replicates, considerable variation is found in the response of component traits making up the index.

One especially interesting situation is when the relative economic weights on pairs of traits have opposite sign to the additive genetic correlations between those characters, e.g.,  $H = z_1 - z_2$  when the genetic correlations between characters is positive or  $H = z_1 + z_2$  when this correlation is negative. Such situations have been referred to by several authors as *antagonistic index selection*. The experimental results when antagonistic indices occur are mixed: no response was observed on an antagonistic index based on early weight gain and adult weight in mice which have an additive-genetic correlation  $\rho_g \simeq 0.55$  (von Bulter et al. 1980), while antagonistic indices based on litter size and body weight in mice ( $\rho_g \simeq 0.6$ ; Eisen 1977a, 1978), plant height and number of leaves in tobacco ( $\rho_g \simeq 0.7$ ; Matzinger

et al. 1977), and pupal and adult weight in *Tribolium* ( $\rho_g \simeq 0.9$ ; Campo et al. 1990) showed a reasonable response.

**The Hayes-Hill transformation: detecting flaws in the estimated index.** One obvious sign that the estimated index is flawed is if  $\hat{\mathbf{G}}$  is not positive-definite and hence not a proper covariance matrix. There is a significant probability of this when sample size is small and/or the number of traits large (Hill and Thompson 1978). Even if  $\hat{\mathbf{G}}$  is positive-definite, it may be inconsistent with estimates of  $\hat{\mathbf{P}}$  as estimated heritabilities can exceed one. While simple inspection of  $\hat{\mathbf{G}}$  and  $\hat{\mathbf{P}}$  may reveal obvious problems such as negative variances or correlations that exceed unity, others (such as partial correlations exceeding unity) can easily be overlooked. Hayes and Hill (1980) note that this problem can be avoided by considering the eigenvalues of  $\mathbf{H} = \mathbf{P}^{-1}\mathbf{G}$ . Their motivation is as follows. The *canonical transformation* introduced in Chapter 31 transforms a vector of correlated variables into a new vector whose elements are uncorrelated. Let  $\mathbf{U}$  be the matrix giving the canonical transformation of  $\mathbf{H} = \mathbf{P}^{-1}\mathbf{G}$ , e.g.,  $\mathbf{U} = (\mathbf{e}_1, \mathbf{e}_2, \dots, \mathbf{e}_n)$  where  $\mathbf{e}_i$  are the normalized eigenvectors of  $\mathbf{H}$ . Hayes and Hill show that the transformed phenotypic and additive genetic values

$$\tilde{\mathbf{g}} = \mathbf{U}\mathbf{g} \quad \text{and} \quad \tilde{\mathbf{z}} = \mathbf{U}\mathbf{z} \quad (23.18a)$$

have covariances matrices

$$\tilde{\mathbf{P}} = \sigma(\tilde{\mathbf{z}}, \tilde{\mathbf{z}}) = \sigma(\mathbf{U}\mathbf{z}, \mathbf{U}\mathbf{z}) = \mathbf{U}\mathbf{P}\mathbf{U}^T = \mathbf{I} \quad (23.18b)$$

$$\tilde{\mathbf{G}} = \sigma(\tilde{\mathbf{g}}, \tilde{\mathbf{g}}) = \sigma(\mathbf{U}\mathbf{g}, \mathbf{U}\mathbf{g}) = \mathbf{U}\mathbf{G}\mathbf{U}^T = \mathbf{\Lambda} \quad (23.18c)$$

where  $\mathbf{I}$  is the identity matrix and  $\mathbf{\Lambda}$  a diagonal matrix whose diagonal elements are given by the eigenvalues of  $\mathbf{H} = \mathbf{P}^{-1}\mathbf{G}$ . Hence the transformed characters are uncorrelated and the eigenvalues of  $H$  corresponds to the heritabilities of the transformed characters (as each character as unit phenotypic variance). Under this transformation the merit function can be written as  $\alpha^T \tilde{\mathbf{g}}$  where  $\alpha = \mathbf{U}^T \mathbf{a}$  is the vector of transformed economic weights. Substituting into Equation 23.12 the response to selection on the Smith-Hazel index can be expressed as

$$\frac{R}{i} = \sqrt{\alpha^T \tilde{\mathbf{G}} \mathbf{P}^{-1} \tilde{\mathbf{G}} \alpha} = \sqrt{\alpha^T \mathbf{\Lambda} \mathbf{I}^{-1} \mathbf{\Lambda} \alpha} = \sqrt{\alpha^T \mathbf{\Lambda}^2 \alpha} = \sqrt{\sum_{i=1}^n \alpha_i^2 \lambda_i^2} \quad (23.19)$$

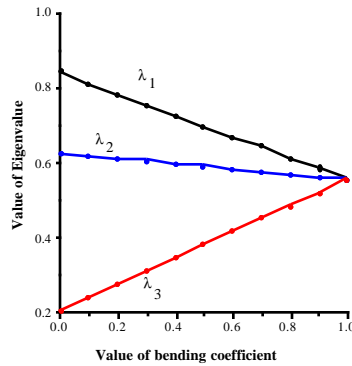
Hence for any vector of economic weights  $\mathbf{a}$  and (non-singular) covariance matrices  $\mathbf{P}$  and  $\mathbf{G}$ , the Hayes-Hill transformation considerably reduces these  $n(n+2)$  parameters ( $n(n+1)/2$  for both  $\mathbf{P}$  and  $\mathbf{G}$  and  $n$  for  $\mathbf{a}$ ) to just  $2n$  parameters ( $n$  transformed economic weights  $\alpha_i$  and  $n$  heritabilities of the transformed variables  $\lambda_i$ ).

In light of this, Hayes and Hill (1980) suggest that the eigenvalues of  $\hat{\mathbf{H}} = \hat{\mathbf{P}}^{-1}\hat{\mathbf{G}}$  be examined, since these correspond to the heritabilities of the transformed variables and hence should be between zero and one if the estimates of  $\hat{\mathbf{P}}$  and  $\hat{\mathbf{G}}$  are well-behaved. If this is not the case, the estimated covariance matrices can be modified until the estimates are consistent. While one approach is to set negative variances to zero and heritabilities and correlations that exceed unity to unity, the methods of bending and rounding discussed below are preferred.

\* **“Bending” and “rounding” corrections of the estimated index.** Hayes and Hill (1981), noting that estimates of eigenvalues tend to be biased with large eigenvalues overestimated and eigenvalues underestimated, suggest a *bending* procedure to improve the efficiency of the estimated index. Their idea is to increase small eigenvalues and decrease large ones while holding the average eigenvalue constant. This is done by computing the eigenvalues of the modified matrix

$$\hat{\mathbf{H}}^* = (1 - \gamma) \cdot \hat{\mathbf{H}} + \gamma \cdot \bar{\lambda}\mathbf{I} \quad \text{for } 0 \leq \gamma \leq 1 \quad (23.20)$$

where  $\gamma$  is the bending factor,  $\bar{\lambda} = n^{-1} \sum \lambda_i$  is the average eigenvalue of  $\hat{\mathbf{H}} = \hat{\mathbf{P}}^{-1}\hat{\mathbf{G}}$ , and  $\mathbf{I}$  the identity matrix.  $\gamma = 0$  corresponds to  $\hat{\mathbf{H}}^* = \hat{\mathbf{H}}$ , while  $\gamma = 1$  corresponds to  $\hat{\mathbf{P}}^{-1}\hat{\mathbf{G}} = \bar{\lambda} \cdot \mathbf{I}$  or  $\hat{\mathbf{P}} = \bar{\lambda} \cdot \hat{\mathbf{G}}$  in which case where the base index equals the Smith-Hazel index. Hence  $\gamma$  can be viewed as scaling the data from the Smith-Hazel ( $\gamma = 0$ ) to the base index ( $\gamma = 1$ ). Figure one shows how the eigenvalues based on the covariance matrices used in Example one change during bending.



**Figure 23.1.** The effects of bending. Using the estimates of  $\mathbf{P}$  and  $\mathbf{G}$  from Example one, the eigenvalues of  $\hat{\mathbf{H}} = \hat{\mathbf{P}}^{-1}\hat{\mathbf{G}}$  are found to be  $\lambda_1 = 0.84$ ,  $\lambda_2 = 0.622$ ,

and  $\lambda_3 = 0.205$ , for an average value of  $\bar{\lambda} = 0.555$ . The eigenvalues for the "bent" matrix  $\widehat{\mathbf{H}}^* = (1 - \gamma) \cdot \widehat{\mathbf{H}} + \gamma \cdot 0.555 \cdot \mathbf{I}$  are plotted as a function of the bending coefficient  $\gamma$ . As  $\gamma$  increases towards one, the eigenvalues smoothly converge towards  $\bar{\lambda}$ .

Simulation studies by Hayes and Hill show bending always improves the estimated index, but the optimal bending factor depends on the unknown parameters. While this is obviously a problem, one common situation where the choice of bending parameter is fairly clear is when eigenvalues of  $\widehat{\mathbf{H}}$  are either negative or exceed one. Suppose one eigenvalue is negative. In this case,  $\widehat{\mathbf{H}}$  is bent until this eigenvalue increases to zero. Likewise, if an eigenvalue exceeds one, the matrix is bent until this eigenvalue decreases to one. Even if the eigenvalues of  $\widehat{\mathbf{H}}$  are between one and zero, Hayes and Hill suggest the sample size alone can be used to obtain the optimal the bending parameter, but the theory is not fully developed.

Tai (1988) suggests a different procedure, *rounding*, again based on the canonical transformation of  $\widehat{\mathbf{H}}$ . Let  $\mathbf{U} = (\mathbf{e}_1, \mathbf{e}_2, \dots, \mathbf{e}_n)$  again denote the transformation matrix associated with  $\widehat{\mathbf{H}}$  where  $\mathbf{e}_i$  is the normalized eigenvector corresponding to eigenvalue  $\lambda_i$ . Under this transformation, we can write the index  $\widehat{I}_s = \widehat{\mathbf{b}}_s^T \mathbf{z} = \mathbf{d}^T \mathbf{y}$ , where  $\mathbf{d} = \mathbf{U} \widehat{\mathbf{b}}_s$  and  $\mathbf{y} = \mathbf{U}^T \mathbf{z}$ . Rounding assigns a vector of zeros for each eigenvector associated with a negative eigenvalue. For example, suppose eigenvalues one through  $n - k$  are between zero and one, while the last  $k$  eigenvalues are negative. Rounding consists of using the index

$$I = \mathbf{d}^T \mathbf{y}_k \quad \text{where} \quad \mathbf{y}_k = \widehat{\mathbf{U}}_k^T \mathbf{z} \quad \text{with} \quad \widehat{\mathbf{U}}_k = (\mathbf{e}_1, \mathbf{e}_2, \dots, \mathbf{e}_{n-k}, \mathbf{0}, \dots, \mathbf{0}) \quad (23.21)$$

While this procedure may seem somewhat less ad hoc than bending, it does not correct the bias caused by overestimation of large eigenvalues. Rather, it compounds this bias by retaining large eigenvalues while discarding small (and likely underestimated) ones.

#### \*Extensions: Restricted, Desired-gains, and Nonlinear Indices

While the Smith-Hazel index results in the largest response in a linear combination of characters, often we have slightly different objectives in mind and there are different indices that allow us to accomplish these goals. For example, we may wish the largest possible response in some linear combinations of characters while ensuring that another set of characters remains unchanged. This is done by constructing a *restricted index*. Likewise, instead of maximizing the response in  $H$ , we may wish to find a linear combination of characters that gives a prespecified

response in the vector of characters means. Using such a *desired-gains* index gives us more control over the individual responses in each character.

**Restricted indices.** Suppose  $n$  characters are of interest, but that characters one to  $k$  are at their optimum values and we desire these characters to remain unchanged. Subject to this constraint we wish to maximize the response of some linear combination  $\sum_{i=k+1}^n a_i z_i$  of the remaining characters. By defining the vector of weights as  $\mathbf{a}^T = (0, \dots, 0, a_{k+1}, \dots, a_n)$  the index to optimize under the constraint can be written as  $\mathbf{a}^T \mathbf{z}$ . This problem was first considered by Morely (1955) with a general solution developed by Kempthorne and Nordskog (1959). Since response to selection on an index is proportional to  $\mathbf{G}\mathbf{b}$  (Equation 23.4), our constraint of no response can be restated as the first  $k$  elements of the vector resulting from this matrix product are zero. In matrix form,  $\mathbf{C}\mathbf{G}\mathbf{b}_r = \mathbf{0}$  where  $\mathbf{C}$  is an  $k \times n$  matrix with ones on the diagonal and all other elements zero. The method of Lagrange multipliers (Chapter 31) can be used to find the index giving the maximal response in  $H$  for a fixed amount of selection subject to this constraint. Using this approach, Kempthorne and Nordskog obtained the vector of weights for the restricted index as

$$\mathbf{b}_r = \left[ \mathbf{I} - \mathbf{P}^{-1} \mathbf{G} \mathbf{C}^T \left( \mathbf{C} \mathbf{G} \mathbf{P}^{-1} \mathbf{G} \mathbf{C}^T \right)^{-1} \mathbf{C} \mathbf{G} \right] \mathbf{P}^{-1} \mathbf{G} \mathbf{a} \quad (23.22a)$$

where  $\mathbf{I}$  is the identity matrix. We refer to this restriction of no change in  $k$  specified characters as the *Kempthorne-Nordskog restriction*. Akbar et al. (1984) extend these results to allow for different number of traits in the index  $I$  and merit  $H$ , while Lin (1985) presents a derivation that does not use Lagrange multipliers. For two characters where the goal is to maximize response in character one with no response in character two, the resulting index (after rescaling) becomes

$$I_r = z_1 + \left( \frac{\sigma_{g_1, g_2}}{\sigma_{g_2}^2} \right) \cdot z_2 \quad (23.22b)$$

as obtained by Morely (1955).

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**Example 2.** Consider the soybean data from Example one. Suppose that character  $z_1$  (oil content) is at its optimal value, but we wish to optimize the sum of protein content and yield,  $H = z_2 + z_3$ . Here,

$$\mathbf{C} = (1 \ 0 \ 0) \quad \text{and} \quad \mathbf{a} = \begin{pmatrix} 0 \\ 1 \\ 1 \end{pmatrix}$$

Substituting  $\widehat{\mathbf{P}}$  and  $\widehat{\mathbf{G}}$  for  $\mathbf{P}$  and  $\mathbf{G}$  and applying Equation 23.22 gives

$$\mathbf{b}_r = \begin{pmatrix} -3.3 \\ -0.8 \\ 1.1 \end{pmatrix}$$

Hence  $\sigma_{I_r} = \sqrt{\mathbf{b}_r^T \mathbf{P} \mathbf{b}_r} \simeq 23.2$  and from Equation 23.4 the resulting change in the vector of character means is

$$\Delta \boldsymbol{\mu} = \frac{\bar{v}}{\sigma_{I_r}} \cdot \mathbf{G} \mathbf{b}_r = \bar{v} \cdot \begin{pmatrix} 0 \\ 4.0 \\ 11.2 \end{pmatrix}$$

If instead of restricting the change in character one, the Smith-Hazel index is applied with  $\mathbf{a}$  as above so that no weight is placed on changes in  $z_1$ , then

$$\mathbf{b}_s = \mathbf{G} \mathbf{P}^{-1} \mathbf{a} = \begin{pmatrix} 0.38 \\ 0.16 \\ 1.17 \end{pmatrix} \quad \text{giving} \quad \Delta \boldsymbol{\mu} = \frac{\bar{v}}{\sigma_{I_s}} \cdot \mathbf{G} \mathbf{b}_s = \bar{v} \cdot \begin{pmatrix} 6.4 \\ 9.2 \\ 27.3 \end{pmatrix}$$

where now  $\sigma_{I_s} = \sqrt{\mathbf{b}_s^T \mathbf{P} \mathbf{b}_s} \simeq 101.4$ . Hence, the response to  $H$  is  $36.5 \cdot \bar{v}$  under the Smith-Hazel index, but only  $23.2 \cdot \bar{v}$  under the restricted index. The price paid for no change in character one is that response in  $H$  is only 42 percent of that under no restrictions.

A variety of restricted indices handling different classes of constraints have been proposed (e.g., Tallis 1962, 1985, 1986, James 1968, Cunningham et al. 1970, Harville 1975, Niebel and Van Vleck 1982). For example, Tallis (1962) considers the case where a specified response is desired in  $k$  linear combinations of characters,

$$L_1 = \sum_{j=1}^n c_{j1} \Delta \mu_j = d_1, \quad L_2 = \sum_{j=1}^n c_{j2} \Delta \mu_j = d_2, \quad \dots, \quad L_k = \sum_{j=1}^n c_{jk} \Delta \mu_j = d_k \quad (23.23)$$

Here the constraint is  $\mathbf{C} \Delta \boldsymbol{\mu} = \mathbf{C} \mathbf{G} \mathbf{b}_r = \mathbf{d}$ , where the  $k \times n$  matrix  $\mathbf{C}$  has its  $ij$ -th element given by  $c_{ij}$  and  $\mathbf{d}$  is the vector  $(d_1, \dots, d_k)^T$ . This *Tallis restriction* is a more general form of the Kempthorne-Nordskog restriction. Again using the method of Lagrange multipliers, response is maximized subject to these constraints by selecting on the index with weights

$$\mathbf{b}_r = \left[ \mathbf{I} - \mathbf{P}^{-1} \mathbf{G} \mathbf{C}^T \left( \mathbf{C} \mathbf{G} \mathbf{P}^{-1} \mathbf{G} \mathbf{C}^T \right)^{-1} \mathbf{C} \mathbf{G} \right] \mathbf{P}^{-1} \mathbf{G} \mathbf{a} + \mathbf{P}^{-1} \mathbf{G} \mathbf{C} \left( \mathbf{C}^T \mathbf{G} \mathbf{P}^{-1} \mathbf{G} \mathbf{C} \right)^{-1} \mathbf{d} \quad (23.24)$$

Additional features of restricted indices are reviewed by Brascamp (1984), while sampling properties have been considered by Hill and Meyer (1984). Other reviews can be found in Mallard (1972), who gives a geometric interpretation of restricted indices and Harville (1974). Famula (1992) suggests an alternative approach for constraining response in correlated characters based on linear programming. The advantage with this approach is that it gives a smaller mean-squared deviation of the constrained trait from zero relative to restricted index selection, but at a cost of a smaller response in the unconstrained characters. Thus if reducing response is deemed more important than maximal response in the unconstrained characters, linear programming methods should be considered.

**Desired-gains indices.** Here the objective is to find the linear index  $I_d = \mathbf{b}_d^T \mathbf{z}$  giving a prespecified vector of proportional responses in each character. Besides providing control over how each individual character changes, the desired-gains index does not require specification of economic weights  $\mathbf{a}$ . It does, however, still require estimates of  $\mathbf{P}$  and  $\mathbf{G}$  (if these are not available and one is still reluctant to assign values for  $\mathbf{a}$ , then the Elston index might be considered). Let  $\Delta_d$  denote the vector of desired changes, so that the ratio of any two elements,  $\Delta_i/\Delta_j$  is the desired ratio of response in characters  $i$  and  $j$ . From Equation 23.4, selection  $I = \mathbf{b}^T \mathbf{z}$  gives a vector of response proportional to  $\mathbf{G}\mathbf{b}$ . Hence  $\mathbf{G}\mathbf{b}_d = \Delta_d$ , giving the vector of weights for the desired-gains index as

$$\mathbf{b}_d = \mathbf{G}^{-1} \Delta_d \quad (23.25)$$

as obtained by Pešek and Baker (1969) and Yamada et al. (1975). If  $\mathbf{C}$  in Equation 23.24 is of full rank ( $n$  linearly independent restrictions are imposed) then the responses of all characters are completely specified and the Tallis-restricted index reduces to the desired-gain index.

Equation 23.25 assumes that desired response is specified for all  $n$  measured traits. More generally, suppose there are  $n$  traits in the phenotypic index and  $m < n$  traits whose responses are of interest. Denote by  $\mathbf{G}_r$  the  $m \times n$  matrix whose  $ij$ -th element denotes the additive genetic covariance between measured trait  $i$  and response trait  $j$ . Solutions are still of the form  $\mathbf{G}_r \mathbf{b}_d = \Delta_d$ , but this does not yield a unique solution for  $\mathbf{b}_d$  as  $\mathbf{G}_r$  is not a square matrix and hence  $\mathbf{G}_r^{-1}$  is not defined. A unique solution can be obtained by imposing the standard constraint of maximizing response for a fixed amount of selection. For a fixed selection intensity  $\bar{i}$ , response increases as  $\sigma_I^2 = \mathbf{b}^T \mathbf{P} \mathbf{b}$  decreases (see Equation 23.4). A unique solution can thus be obtained by solving  $\mathbf{G}_r \mathbf{b} = \Delta_d$  subject to the additional constraint that  $\mathbf{b}^T \mathbf{P} \mathbf{b}$  is minimized (Itoh and Yamada 1985), giving

$$\mathbf{b}_d = \mathbf{P}^{-1} \mathbf{G}_r^T (\mathbf{G}_r \mathbf{P}^{-1} \mathbf{G}_r^T)^{-1} \Delta_d \quad (23.26)$$

This was first obtained by Tai (1977), although in a much more cryptic form. As expected, this reduces to Equation 23.25 when  $\mathbf{G}_r = \mathbf{G}$ . Itoh and Yamada

(1988) have further modified the desired-gains index to allow for restrictions in the response of specified characters.

**Example 3.** Once again using the soybean data from Example one, suppose we wish to increase  $(z_1, z_2, z_3) = (\text{oil content, protein content, yield})$  by relative amounts  $(1 : 1 : 1)$  giving the vector of desired gains as

$$\Delta_d = \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix}$$

Using  $\tilde{\mathbf{G}}$  for  $\mathbf{G}$  and rescaling  $\mathbf{b}_d$  so that its first element is one gives

$$\mathbf{b}_d = \begin{pmatrix} 1.0 \\ 0.8 \\ -0.5 \end{pmatrix}$$

Selection on the index  $I_d = z_1 + 0.8 \cdot z_2 - 0.5 \cdot z_3$  thus gives the same response in each character. To verify this, first note that  $\sigma_{I_d} = \sqrt{\mathbf{b}_d^T \mathbf{P} \mathbf{b}_d} \simeq 5.45$ , giving

$$\Delta\boldsymbol{\mu} = \begin{pmatrix} \bar{z} \\ \sigma_{I_d} \end{pmatrix} \cdot \mathbf{G} \mathbf{b}_d = 2.22 \bar{z} \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix}$$

To distinguish between a desired-gains and Smith-Hazel index, compare this response with that expected from the Smith-Hazel index on the merit function  $z_1 + z_2 + z_3$ . Under the desired-gains index, the response in merit is  $\Delta\mu_1 + \Delta\mu_2 + \Delta\mu_3 = 6.66 \cdot \bar{z}$ , only 13 percent of the expected response of  $49.67 \cdot \bar{z}$  under the Smith-Hazel index (Example one), illustrating the cost of specifying response in each character as opposed to being concerned with the maximal response in merit. Now suppose that while all three characters are measured, we are only interested in having equal response in oil and protein content and are unconcerned with yield. Here  $n = 3$  and  $m = 2$ , with

$$\Delta_d = \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix} \quad \text{and} \quad \mathbf{G}_r = \begin{pmatrix} 128.7 & 160.6 & 492.5 \\ 160.6 & 254.6 & 707.7 \end{pmatrix}$$

Applying Equation 23.26,

$$\mathbf{b}_d = \mathbf{P}^{-1} \mathbf{G}_r^T (\mathbf{G}_r \mathbf{P}^{-1} \mathbf{G}_r^T)^{-1} \Delta_d = \begin{pmatrix} 0.0131 \\ -0.0049 \\ 0.0002 \end{pmatrix}$$

This gives  $\sigma_{I_d}^2 = \mathbf{b}_d^T \mathbf{P} \mathbf{b}_d = 0.01286$  so that the vector of responses is

$$\Delta \boldsymbol{\mu} = \begin{pmatrix} \bar{i} \\ \sigma_{I_d} \end{pmatrix} \cdot \mathbf{G} \mathbf{b}_d = 8.82 \bar{i} \begin{pmatrix} 1.0 \\ 1.0 \\ 3.4 \end{pmatrix}$$

giving the change in the merit (defined by Example one) as  $\bar{i} \cdot 8.82 \cdot (1 + 1 + 3.4) = 47.63 \cdot \bar{i}$ , 96 percent of the response under the Smith-Hazel index.

While it is usually assumed that errors from incorrect estimates have more serious consequences for restricted indices than for unrestricted (Smith-Hazel) indices, the evidence is mixed. Hill and Meyer (1984) extended the Hayes-Hill transformation to restricted indices but as with unrestricted indices general statements of the effects of incorrect estimates are difficult to obtain. A second source of error, changes in genetic parameters as selection proceeds, has been examined by Mortimer and James (1987), who found for a four-locus model that the restricted index is particularly sensitive to changes in genetic parameters. If the assumptions of the infinitesimal model holds, changes in the covariance matrices under restricted index selection can be computed using Equations 23.7b-d, but this has not been explored. Certainly any error in parameter estimates or changes in genetic parameters results in some change in the restricted character, but the efficiencies of restricted indices (measured by actual response in the index versus predicted response) appear similar to those for unrestricted indices (Caballero 1989). Table 23.2 summarizes the results of several experiments on restricted indices. The general conclusions are that the observed response is almost always less (and often considerably so) than the predicted response, and the response under a restricted index is usually less than the response from direct selection on the character of interest, as expected. While significant responses in constrained characters are common, they are usually less (and often considerably so) than the correlated response that occurs when using an unconstrained index. Hence estimated restricted indices are effective at reducing, but not necessarily eliminating, undesirable correlated responses. Likewise, significant change in genetic parameters can occur. For example, Matzinger et al. (1989) performed a restricted selection experiment in tobacco to increase response in total alkaloids (TA) while constraining the response in yield (expected to be negative under unconstrained selection as the additive genetic correlation between these two characters is  $-0.7$ ). After three cycles of selection, genetic variance in yield was unchanged and additive genetic variance in TA decreased by 60% from its initial value while the genetic correlation was reduced to  $-0.3$ .

**Table 23.2.** Results of experiments examining restricted indices.

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Garwood et al. 1978 3 egg production traits in poultry.	Excellent fit. Nonsignificant response in constrained character while the response of the index of unconstrained characters was as predicted.
Abplanalp et al. 1963 8- and 24-week weight in turkeys.	Poor fit. Response in unconstrained character three times that expected. Negative response in the constrained character.
Scheinberg et al. 1967 Five traits in <i>Tribolium castaneum</i> .	Poor fit. Response in unconstrained character far less than expected and constrained characters displayed a significant negative response.
Okada and Hardin 1967, 1970 Larval and adult weight in <i>Tribolium castaneum</i> .	Modest fit. Response in unconstrained character far less than expected. Constrained character displayed a negative response, however this response under the restricted index was much smaller than the correlated response from direct selection on the unconstrained character. Index response asymmetrical.
Campo and Villanueva 1987 Adult and pupal weight in <i>Tribolium castaneum</i> .	Modest fit. Nonsignificant response in constrained characters in two separate sets of experiments, response in unconstrained characters less than half expected value.
Campo and Velasco 1989 Adult and pupal weight in <i>Tribolium castaneum</i> .	Good fit for using both the Tallis restriction and desired-gain index in spite of very high genetic and phenotypic correlations (both $\rho > 0.9$ ).
McCarthy and Doolittle 1977 5- and 10-week body weight in mice.	Modest fit. Four different restriction indices applied to two highly correlated characters ( $\rho_g \simeq 0.9$ ) Only two of the four indices gave no response in the constrained character. Responses in the unconstrained characters below expectations.
Eisen 1977a,b Weight gain and feed intake in mice.	Modest-Good fit. Response in unconstrained character close to expected value. No response in the constrained character over first four generations of selection followed by positive correlated response.
Eisen 1992 Body fat and body weight in mice.	Poor fit. Significant and asymmetric response in the constrained character.
Matzinger et al. 1989 Total alkaloids (TA) and yield (Y) in tobacco.	Excellent fit. Significance response in TA while nonsignificant response in the constrained character Y despite strong negative genetic correlation ( $\rho_g \simeq -0.7$ ). Response in unconstrained character matched predicted response.

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**Linear indices for nonlinear functions.** While we have dealt exclusively with linear merit functions, nonlinear functions naturally arise in many settings (ratios

$H(z_1, z_2) = z_1/z_2$  and products  $H(\mathbf{z}) = \prod z_j$  being two examples). Unfortunately the theory of constructing optimal indices for nonlinear merit functions is only partly developed. Care is required in considering the goals of any nonlinear merit function as apparently subtle differences in the desired outcomes can become critical (Moav and Hill 1966, Goddard 1983, Itoh and Yamada 1988, Burdon 1990). For example, is the goal to improve the average merit of all individuals in the population  $E[H]$  or to improve the merit of the population average  $H(E[z]) = H(\mu)$ ? These goals are equivalent under a linear merit function (as  $E[H] = E[\mathbf{a}^T \mathbf{g}] = \mathbf{a}^T \mu = H[\mu]$ ) but are generally different when nonlinear merit functions are used. For example, suppose  $H = z^2$  so that  $E[z^2] = \sigma_z^2 + \mu^2 \geq \mu^2 = (E[z])^2$ . A related concern is whether we wish to maximize the additive genetic value in merit in the parents or in their offspring. To see this problem, again consider the simple merit function  $H = z^2$ . To further simplify matters, assume that the population mean is initially zero and that phenotypic and additive-genetic values are symmetrically distributed around the mean. Choosing adults with the largest  $g^2$  values generates a group of parents with a mean  $g$  value of zero. Mating these parents at random gives offspring with a mean breeding value of zero. While there will be a transient increase in merit due to the transient increase in variance caused by the generation of positive gametic-phase disequilibrium (this merit function is akin to disruptive selection, Chapter 27), this increase decays away after selection stops. A much larger (and permanent) change in the merit occurs by just selecting the largest individuals (select to increase  $z$  rather than  $z^2$ ), which increases the mean and hence increases  $z^2$ . Nonrandom mating among selected individuals can also increase response when the merit function is nonlinear (Allaire 1980). In this example, positive assortative mating among selected individuals will further increase response by generating positive disequilibrium.

While nonlinear indices for specific situations have been proposed (e.g., Wilton et al. 1968, Rønningen 1970, Magnussen 1991), Goddard (1983) suggested when genetic variation is completely additive that the largest response occurs by selecting on a linear, rather than nonlinear, index. As first sight, this assertion does not seem well-supported by the experimental evidence. Campo and Rodriguez (1990) found selection on a nonlinear index gave a larger response than selection using a linear index when selecting for an increase in the ratio of egg mass to adult body weight in *Tribolium castaneum*. Fairfull et al. (1977) and Campo and de la Blanca (1988) also observed this with another nonlinear trait (total biomass = number of offspring  $\times$  offspring weight) in *Tribolium castaneum*. These observations, however, do not necessarily invalidate Goddard's assertion, as there is still some uncertainty as how to construct the linear index giving the largest response in a nonlinear  $H$ . Many of the linear indices considered in these experiments were somewhat arbitrary and perhaps not surprisingly were outperformed by a specialized non-linear index. Finally, the contribution of nonadditive genetic variation to response in nonlinear indices is an open issue.

How might the best linear index be obtained? The simplest situation is when

the nonlinear index can be transformed into a linear index, which can then be maximized using the standard linear theory. For example, if the merit function is a simple polynomial, say  $H(z) = z_1 + z_2^2 + z_3$ , by defining  $\tilde{z}_2 = z_2^2$  the index becomes linear, viz.  $H(z) = z_1 + \tilde{z}_2 + z_3$ . This approach was first hinted at by Smith (1936) and formally suggested by Kempthorne and Nordskog (1959), but requires the phenotypic and additive genetic covariances of the transformed variables. Two more general approaches have been proposed. The first approximates  $H$  by a first-order Taylor series about the population mean (Chapter 31),

$$H(z_1, z_2, \dots, z_n) \simeq H(\boldsymbol{\mu}) + \sum_{i=1}^n a_i(z_i - \mu_i) \quad \text{where} \quad a_i = \left. \frac{\partial H}{\partial z_i} \right|_{\mathbf{z}=\boldsymbol{\mu}} \quad (23.27a)$$

and then constructs the Smith-Hazel index for this linear function. Thus the vector of economic weights  $\mathbf{a}$  for the Smith-Hazel are given by the gradient of  $H$  evaluated at the present population mean (Moav and Hill 1966, Harris 1970),

$$\mathbf{a} = \nabla_{\mathbf{z}}[H] \Big|_{\mathbf{z}=\boldsymbol{\mu}} \quad (23.27b)$$

Since  $\mathbf{a}$  depends on the population mean, these weights change each generation. Goddard (1983) notes that this approximation may be satisfactory when selection intensity is low, but is poor for highly non-linear functions when selection intensity is high (and hence the extremes of the nonlinear function are selected). Burton (1990) shows when the heritability of the characters underlying the index is low that a linear approximation is usually reasonable. Hence, if the heritability of the index obtained by using Equation 23.27b is low and the selection intensity weak then the Taylor approximation is likely to be reasonable.

The second approach is based on a graphical method suggested by Moav and Hill (1966) for two characters and holds even when selection intensity is strong and heritability high. Starting with  $\Delta\boldsymbol{\mu} = (\bar{i}/\sigma_I)\mathbf{G}\mathbf{b}$ , substituting  $\mathbf{b}^T\mathbf{P}\mathbf{b}$  for  $\sigma_I^2$  and then solving the response for  $\mathbf{b}$  shows that the range of response for a fixed selection intensity forms an ellipsoid satisfying  $\Delta\boldsymbol{\mu}^T\mathbf{G}^{-1}\mathbf{P}\mathbf{G}^{-1}\Delta\boldsymbol{\mu} = \bar{i}^2$ . These response ellipses are then plotted onto contour plots of the merit function and by inspection the weighting  $\mathbf{b}$  for the linear selection index that produces the largest response for fixed selection intensity can be located. Unlike the Taylor approximation method, the index is a function of the selection intensity. Goddard (1983) shows this method gives the optimal single-generation response when concerned with merit as a function of the population mean  $H[\boldsymbol{\mu}]$ . Itoh and Yamada (1988) and Pasternak and Weller (1993) analytically extend this method to  $n$  characters.

**Summary.** A variety of linear indices, which often have very different goals, have been introduced in the last few sections. Table 23.3 reviews the salient features of these.

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**Table 23.3.** Summary of the linear selection indices introduced in this chapter.

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**Smith-Hazel index,**  $I_s = \mathbf{b}_s^T \mathbf{z}$ , where  $\mathbf{b}_s = \mathbf{P}^{-1} \mathbf{G} \mathbf{a}$ .

Selection on  $I_s$  maximizes the expected response in  $\mathbf{a}^T \mathbf{z}$ .

**Estimated index,**  $\hat{I}_s = \hat{\mathbf{b}}_s^T \mathbf{z}$ , where  $\hat{\mathbf{b}}_s = \hat{\mathbf{P}}^{-1} \hat{\mathbf{G}} \mathbf{a}$ .

The estimate of the Smith-Hazel index using the sample phenotypic and additive genetic covariance matrices.

**Base index,**  $I_b = \mathbf{a}^T \mathbf{z}$ .

Suggested as an alternative to the Smith-Hazel index when confidence in the precision of estimates of  $\mathbf{P}$  and (especially)  $\mathbf{G}$  is low.

**Restricted indices:**

**The Kempthorne-Nordskog restriction,**  $I_r = \mathbf{b}_r^T \mathbf{z}$  where

$$\mathbf{b}_r = \left[ \mathbf{I} - \mathbf{P}^{-1} \mathbf{G} \mathbf{C}^T \left( \mathbf{C} \mathbf{G} \mathbf{P}^{-1} \mathbf{G} \mathbf{C}^T \right)^{-1} \mathbf{C} \mathbf{G} \right] \mathbf{P}^{-1} \mathbf{G} \mathbf{a}$$

Selection on  $I_r$  maximizes the response in  $\mathbf{a}^T \mathbf{z}$  for  $k + 1 \leq z_i \leq n$  while allowing no response in characters  $z_1, \dots, z_k$ .  $\mathbf{C}$  is an  $k \times n$  matrix with ones on the diagonal and all other elements zero.

**The Tallis restriction,**  $I_r = \mathbf{b}_r^T \mathbf{z}$  where

$$\mathbf{b}_r = \left[ \mathbf{I} - \mathbf{P}^{-1} \mathbf{G} \mathbf{C}^T \left( \mathbf{C} \mathbf{G} \mathbf{P}^{-1} \mathbf{G} \mathbf{C}^T \right)^{-1} \mathbf{C} \mathbf{G} \right] \mathbf{P}^{-1} \mathbf{G} \mathbf{a} + \mathbf{P}^{-1} \mathbf{G} \mathbf{C} \left( \mathbf{C}^T \mathbf{G} \mathbf{P}^{-1} \mathbf{G} \mathbf{C} \right)^{-1} \mathbf{d}$$

Selection on  $I_r$  maximizes the response in  $\mathbf{a}^T \mathbf{z}$  for  $k + 1 \leq z_i \leq n$  while specifying the response of  $k$  linear constraints of  $\mathbf{z}$ , such that  $\mathbf{C} \Delta \boldsymbol{\mu} = \mathbf{d}$ , where  $\Delta \boldsymbol{\mu}$  is the vector of responses and the elements of  $\mathbf{C}$  specify the linear combinations. The Kempthorne-Nordskog restriction follows as a special case ( $\mathbf{d} = 0$ ).

**Desired-gains indices:**

**Pešek-Baker index,**  $I_d = \mathbf{b}_d^T \mathbf{z}$ , where  $\mathbf{b}_d = \mathbf{G}^{-1} \Delta_d$ .

Selection on  $I_d$  gives a vector of proportional responses  $\Delta_d$ , where the ratio of the  $i$ -th and  $j$ -th elements of this vector gives the ratio of desired responses in these characters. The assumption is that response in all characters in  $\mathbf{z}$  is of interest.

**Tai-Itoh-Yamada index,**  $I_d = \mathbf{b}_d^T \mathbf{z}$ , where  $\mathbf{b}_d = \mathbf{P}^{-1} \mathbf{G}_r^T (\mathbf{G}_r \mathbf{P}^{-1} \mathbf{G}_r^T)^{-1} \Delta_d$ .

Selection on  $I_d$  gives the maximal vector of desired proportional responses  $\Delta_d$  when we are only interested in the response of a subset of  $\mathbf{z}$ .  $\mathbf{G}_r$  denotes the additive-genetic covariance matrix for this subset of variables.

**Retrospective index,**  $I_{rt} = \mathbf{b}_{rt}^T \mathbf{z}$ , where  $\mathbf{b}_{rt} = \mathbf{G}^{-1} \Delta \boldsymbol{\mu}$

The difference from the Pešek-Baker index is one of interpretation. Here, the vector of responses  $\Delta \boldsymbol{\mu}$  is *observed* rather than desired and we construct an index that would have accounted for this response. A retrospective index can also be constructed for the observed change within a generation by using  $\mathbf{b}_{ret} = \mathbf{P}^{-1} \mathbf{s}$ .

### Independent Culling, Tandem, and Multistage Index Selection

Several strategies other than index selection have been proposed for artificial selection on multiple characters and we briefly examine the most common of these (*independent culling* and *tandem selection*) and their efficiencies relative to index selection. Throughout, the goal is to maximize  $H = \sum a_i g_i$  (or equivalently, the response in  $J = \mathbf{a}^T \mathbf{z}$ ) for a fixed amount of selection  $\bar{i}$  applied each generation. Under the assumptions of the multivariate breeders' equation,  $\Delta H = \mathbf{a}^T \Delta \boldsymbol{\mu} = \mathbf{a}^T \mathbf{G} \mathbf{P}^{-1} \mathbf{s}$ , so that the goal for each method is to obtain the vector of directional selection differentials  $\mathbf{s}$  that maximizes  $\Delta H$  for a fixed amount of selection.

**Tandem selection.** Under tandem selection, only a single character is selected each generation but selection intensity is assumed to remain constant (as would occur when the same fraction of individuals are selected each generation). Thus if character  $j$  is the character on which individuals are chosen in a particular generation, then  $s_j = \bar{i} \sigma_{z_j}$  is the selection differential on that character. If other characters are phenotypically correlated, they also experience a selection differential. If the vector of phenotypes is multivariate normal, then the regression of any particular character (say the  $i$ th) on character  $j$  is  $z_i = (\sigma_{z_i, z_j} / \sigma_{z_j}^2) z_j$ . Thus the expected selection differential on character  $i$  when selection occurs on  $j$  is  $s_i = (\sigma_{z_i, z_j} / \sigma_{z_j}^2) s_j = \bar{i} \sigma_{z_i, z_j} / \sigma_{z_j}$ . Summing over generations, the expected response to  $m$  generations of tandem selection is  $\Delta H = \bar{i} \cdot \mathbf{a}^T \mathbf{G} \mathbf{P}^{-1} \mathbf{s}$  where

$$s_i = \sum_{j=1}^n m_j \frac{\sigma_{z_i, z_j}}{\sigma_{z_j}}$$

where  $m_j$  is the number of generations individuals are chosen solely on character  $j$ . The optimal response is obtained by solving for the weights  $m_j$  given  $\mathbf{P}$ ,  $\mathbf{G}$ , and  $\mathbf{a}$ . For the special case of no phenotypic or genetic correlations,

$$\Delta H = \bar{i} \sum_{j=1}^m a_j h_j^2 s_j = \bar{i} \sum_{j=1}^m m_j \theta_j \quad \text{with} \quad \theta_j = a_j h_j \sigma_{g_j}$$

Optimal response occurs by selecting the character with the initially largest value of  $\theta_j$  in the first generation and the character with the value of  $\theta_j$  in each subsequent generation. If the  $\theta_j$ 's remain unchanged as selection proceeds, the optimal strategy is to continue to select only on the character that gave the largest response in the first generation. This is also the optimum strategy for arbitrary  $\mathbf{P}$  and  $\mathbf{G}$ , provided these remain unchanged (Turner and Young 1969). This is the optimal strategy is rarely used. Rather the breeder usually changes the character being selected after some desired level of performance is reached (in effect, changing the economic weights  $a$  as additional response in the initial character loses some of its desirability relative to response in other characters).

**Independent culling.** Under independent culling (Figure 23.2), threshold values are preset for each character, with any individual not exceeding the threshold value in all characters being culled. Operationally, if selection occurs on  $n$  characters, then for an individual to be saved, it must have  $z_i \geq T_i$  for all characters, where  $T_i$  is the threshold value for character  $i$ . If any character fails to exceed its threshold, the individual is automatically culled without measuring any remaining characters. By contrast, under index selection all characters must first be measured as culling takes place on the index score. Thus if characters are expensive to measure there can be considerable economic savings using independent culling. An important application of this is when characters occur in different life cycle stages, for example, germination time and adult plant height. With independent culling, selection can occur in stages (*multistage selection*), resulting in few individuals to rear through all stages. For example, selection at the stage where germination time can be first scored requires rearing fewer individuals to adulthood to score for height. Under index selection, culling could only occur after both characters are measured in all individuals, requiring all individuals to be raised to adults before selection occurs.

Since one potential advantage of independent culling is reduced cost due to having to measure fewer individuals, instead of maximizing genetic gain, an alternative approach is to specify a function for the cost of measuring characters and then maximize the gain/cost ratio. Namkoong (1970) provides tabular solutions to maximize this ratio for two characters, while Xu (1993, based on Xu and Muir 1991, 1992) provides a program for multiple characters.

**Figure 23.2.** Graphical representation of truncation selection on two characters using different multivariate selection methods. The shaded area represents the fraction saved. **Upper left:** under index selection, all individuals above the line  $b_1 z_1 + b_2 z_2$  are saved so that the values of the two characters are weighted. **Upper right:** under the Elston index, individuals whose values are above a quadratic curve are saved. **Lower left:** under independent culling an individual must be

exceptional in both characters (both must exceed their thresholds) to be saved.

**Lower right:** under selection of extremes the individual needs only be exceptional in a single character (either exceeding its threshold value is sufficient) to be saved.

A major problem with applying independent culling has been computing the optimal threshold values when more than a few characters are considered. For a fixed total fraction  $p$  of individuals to be saved, the problem is to find the optimum threshold values  $(T_1, \dots, T_n)$  giving the value of  $\mathbf{s}$  such that  $\mathbf{a}^T \mathbf{G} \mathbf{P}^{-1} \mathbf{s}$  is maximized. This requires optimization over the set of all values  $(T_1, \dots, T_n)$  subject to the constraints that  $\int_{T_1}^{\infty} \dots \int_{T_n}^{\infty} \phi(\mathbf{z}) d\mathbf{z} = p$  where  $\phi(\mathbf{z})$ , the multivariate phenotypic distribution of  $\mathbf{z}$ , is assumed to be Gaussian. Computing the multidimensional integrals to check each point in this set is computationally impractical for more than a few characters. For two characters, Young and Weiler (1960) and Williams and Weiler (1964) give graphs of optimal truncation points while Smith and Quaas (1982) have developed an iterative solution. Saxton (1989) and Ducrocq and Colleau (1989) developed programs for more than two characters, but these are extremely slow for more than five characters. Approximate solutions assuming either weak selection or low phenotypic correlations between characters have been developed by Cunningham (1975), Cotterill and James (1981), and Muir and Xu (1991). Recently, Xu and Muir (1992) suggested a method for finding the optimal truncation points by solving a set of nonlinear equations and a program has been developed for this by Xu (1993). Because their approach does not require numerical integration, it is very significantly faster than standard methods — a five character problem required 11 seconds of CPU time using this method while the same problem solved by numerical integration required around 11 hours of CPU time (Xu 1993). Further, their approach can be applied to either maximizing the gain or maximizing the gain/cost ratio.

Young (1964) suggested an extension of independent culling when selection occurs at different stages, *multistage index selection*. The first culling takes place as usual, with only individuals with  $z_1 \geq T_1$  being saved. However, in subsequent culling, linear combinations of characters are used, so that if  $z_2$  and  $z_3$  are the characters being selected in in the next two stages, then individuals are saved at these stages provided  $b_{11}z_1 + b_{12}z_2 \geq T_2$  and  $b_{21}z_1 + b_{22}z_2 + b_{23}z_3 \geq T_3$  (contrasted with independent culling where individuals are saved if  $z_2 \geq T_2, z_3 \geq T_3$ ). Computational aspects of multistage index selection have been examined by Cunningham (1975), Cotterill and James (1981), and Saxton (1983). The method of Xu and Muir (1991, 1992) discussed above was first developed for multistage index selection (with independent culling as a special case), see Xu (1993) for a program that implements this procedure.

**Selection of extremes.** Abplanalp (1972) has proposed a method related to independent culling, *selection of extremes*. As Figure 23.2 shows this method selects a

fixed proportion of the highest ranking individuals for *each character*. Selection of extremes and independent culling are complementary in that selection of extremes for the upper  $p$  individuals is equal to independent culling of the lowest  $1 - p$  individuals.

Under independent culling, an individual must be superior in *all* characters to be selected so that an individual superior in all but one character would still be culled. Index selection considers a weighted average of all characters, so that an individual extremely superior in a few characters and average or inferior in all others can still be selected. Selection of extremes is somewhere in between — it allows for the retention of individuals superior in at least some traits along the advantage of independent culling in that not all characters need to be measured before selection. Abplanalp shows that selection of extremes is superior to independent culling with the proportions of individuals culled in less than half, so that this is method should be considered when selection is weak and there are costs associated with measuring all characters.

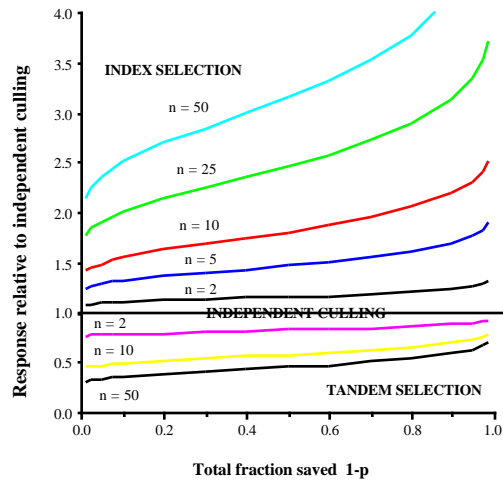
**Relative efficiencies of index selection, independent culling, and tandem selection.** While tandem selection is perhaps the most conceptually straightforward approach of artificial selection on multivariate characters and independent culling can have significant cost savings, index selection is theoretically the most efficient method. This was first demonstrated by Hazel and Lush (1942) who examined the simple case of no genetic or phenotypic correlations between characters. When all  $n$  characters have equal value (all have the same economic weight  $a$ , heritability  $h^2$ , and phenotypic variance  $\sigma_z^2$ ), the expected response from a single cycle of selection (assuming, as usual, an infinite population) is

$$\frac{\Delta H}{\bar{\tau} \cdot \sigma_z \cdot a \cdot h^2} = \begin{cases} \sqrt{n}, & \text{Index selection;} \\ 1, & \text{Tandem selection;} \\ n \bar{\tau}_{p,n} / \bar{\tau} & \text{Independent culling} \end{cases} \quad (23.28)$$

where  $\bar{\tau}$  is the selection intensity for a fraction  $p$  culled and  $\bar{\tau}_{p,n}$  the selection intensity for a fraction  $p^{-n}$  culled. Under the conditions leading to Equation 23.28, the response under index selection is  $\sqrt{n}$  larger than tandem selection, while independent culling is intermediate in efficiency between the other two methods. For example, suppose 5 characters are under selection and the upper ten percent of the population is culled. Here  $p_{0.1,5} = 0.1^{1/5} \simeq 0.63$  so that the upper 63 percent of individuals in each character are saved, giving a selection intensity on each character of  $\bar{\tau}_{0.1,5} = 0.60$ . For  $p = 0.10$ , the intensity of selection on all individuals is  $\bar{\tau} = 1.75$  giving the response under index selection relative to independent culling as  $(\sqrt{n} \cdot \bar{\tau}) / (n \cdot \bar{\tau}_{p,n}) = (\bar{\tau} / \bar{\tau}_{p,n}) / \sqrt{n} = (1.75 \cdot 0.6) / \sqrt{5} \simeq 1.3$ , while the ratio of response of index selection to tandem culling is  $\sqrt{n} = \sqrt{5} \simeq 2.2$ .

Figure 23.3 plots the expected responses of index and tandem selection relative to the response under independent culling for different  $p$  and  $n$  values. For

weak selection ( $p$  close to one), tandem selection and independent culling give essentially the same response with index selection being far superior, while with strong selection ( $p$  near zero) independent culling and index selection have essentially the same efficiency, both being far superior to tandem selection. Figure 23.3 also shows that the superiority of index selection to independent culling and of independent culling to tandem selection increases with  $n$  the number of characters under selection.



**Figure 23.3.** Relative efficiencies (the expected response in an infinite population for the same selection intensity) of index selection and tandem selection relative to independent culling for the special case of no genetic or phenotypic correlations when all characters have the same economic weight, heritability and additive genetic variance.

Young (1961) and Finney (1962) relaxed the assumptions of Hazel and Lush and generalized their result that index selection is at least as good as independent culling which in turn is at least as good as tandem selection. However, these authors found that in many cases these differences are sufficiently small that these methods are essentially equivalent. When economic weights, heritabilities and phenotypic variances differ, Young (1961) showed that the maximal difference in response between methods occurs when the quantity  $\gamma_i = a_i h_i^2 / \sigma_{z_i}$  is the same for each character. As these  $\gamma_i$  differ between characters, differences between methods decrease. The conditions examined by Hazel and Lush are those that

maximize differences between the three methods and present the best case for index selection. When the characters being selected are phenotypically negatively correlated, Young found index selection is far more efficient than independent culling. When characters are strongly positively correlated, index selection and independent culling are essentially equivalent. This makes sense in that when characters are strong correlated, an extreme value in one character implies extreme values in most/all other characters of interest. Since the methods differ in how the extreme values of character are weighted, as these values become correlated, differences in the methods decrease. Abplanalp (1972) numerically examined selection of extremes and found that while it was always superior to tandem selection and always inferior to index selection, it is inferior to independent culling under strong selection (fraction culled  $p > 0.5$ ) and superior under weak selection ( $p < 0.5$ ).

The above theoretical examinations are restricted to a single generation of change in an infinite population when all parameters are assumed to be exactly known. Even if the last two conditions hold, as selection proceeds it generates gametic-phase disequilibrium and can change allele frequencies, changing  $\mathbf{G}$  and  $\mathbf{P}$ . This not only changes the weighting of the Smith-Hazel index, but different selection schemes can generate different amounts of disequilibrium and allele frequency change. Thus the asymptotic value of  $\mathbf{G}$  under the same selection intensity can be different under independent culling, index, and tandem selection. A small two-trait simulation study (60 loci, 20 affecting each trait independently, 20 jointly affecting both traits) by Bennet and Swiger (1980) found that while index selection gave the largest asymptotic response, the difference in ultimate response were much less than the initial single-generation differences. This was confirmed by Villanueva and Kennedy (1993), who compared the long-term response of index and tandem selection under the assumption of the infinitesimal model (all changes in  $\mathbf{G}$  and  $\mathbf{P}$  are due to gametic-phase disequilibrium and are given by Equation 23.7). They found that while the largest response occurs when the index is updated (Smith-Hazel weights recomputed each generation using the current values of  $\mathbf{G}$  and  $\mathbf{P}$ ), the benefit from updating is small (a maximum of 1.5% for the cases studied).

A variety of experiments have examined the relative efficiencies of index selection, independent culling (including multistage selection), and tandem selection (Table 23.4). While all used very small effective population sizes and hence have a high variance in response, the consensus is that response under index selection  $>$  response under independent culling  $>$  response under tandem culling. It should be noted that in most cases the economic weights were equal, the situation giving the largest differences between methods. In those experiments where both were compared, the base and estimated indices gave essentially identical results. Elgin et al. (1970) found that while base index had essentially the same performance as Smith-Hazel index, selection on the base index gave a much smoother response to selection. Perhaps the most notable exception to the general trend of

index selection being superior was Rasmuson (1964) who examined bristle selection in *Drosophila*. She found independent culling was superior in all up-selected lines, while index selection was superior in all down-selected lines. Rasmuson suggested one reason for this difference is that while index selection allows individuals that are extreme in only one character to be saved, these individuals are lost under independent culling which requires both characters to be extreme. Hence, loci giving an extreme value in one character but not others are favored under index selection, but can be selected against under independent culling.

As mentioned above, selection in multiple stages is equivalent to a type of independent culling, even when partial selection indices form the basis of selection in each stage, and hence is expected to be less efficient than index selection. Wing et al. (1983) estimated that two-stage index selection is slightly less efficient than a single-stage index for a set of Whitehorn chickens, and this general trend is seen in Table 23.4 for experiments comparing single- and multi-stage selection.

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**Table 23.4.** Results of experiments examining the relative efficiencies of different methods for simultaneous selection of multiple characters.  $\hat{I}_s$  = selection using the estimated Smith-Hazel index,  $I_b$  = selection using the base index,  $IC$  = independent culling,  $TS$  = tandem selection.

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Elgin et al. 1970 Cutting recovery time and four fungal resistance traits in Alfalfa	$\hat{I}_s$ and $I_b$ were equally effectively, both superior to $IC$ , which in turn was superior to $TS$ .
Sen and Robertson 1964 Abdominal and sternopleural bristles <i>Drosophila melanogaster</i>	Considerable heterogeneity between replicate lines, but general trend was $\hat{I}_s > IC > TS$ .
Rasmuson 1964 Abdominal and sternopleural bristles <i>Drosophila melanogaster</i>	$TS$ gave poorest response. In all four up-selected lines, $IC$ gave a larger response than $\hat{I}_s$ , while in all four down-selected lines $\hat{I}_s$ was superior to $IC$ .
Doolittle et al. 1972 Weight gain and litter size in mice	Averaged over replicates, $\hat{I}_s > IC > TS$ , but these differences were not significant.
Eagles and Frey 1974 Grain and straw yield in Oats	$\hat{I}_s$ , $I_b$ , and $IC$ gave similar responses when averaged across different environments and selection intensities.
Orozco et al. 1980 Pupal weight and egg number in <i>Tribolium castaneum</i>	$\hat{I}_s$ gave a larger response than $F_1$ crosses between lines each selected for a single trait (equivalent to $TS$ ).

Campo and Rodriguez 1985 Adult weight and egg number in <i>Tribolium castaneum</i>	A modified base-index (adjusted empirically each generation to improve response) gave a larger (but not significant) response than $\hat{I}_s$ .
Campo and Rodriguez 1986 Adult weight and egg number in <i>Tribolium castaneum</i>	Replicated single-generation responses were significantly higher under $\hat{I}_s$ than IC.
Ayvagari et al. 1985 Egg number, egg weight and body weight in White Leghorn chickens	Six different two-stage index selection schemes between 60 and 80 percent as efficient as single-stage index selection.
Campo and de la Fuente 1991 Pupal weight and egg number in <i>Tribolium castaneum</i>	Single- versus two-stage index selection were compared, with different amounts of selection intensity during the second stage. Two-stage selection was equally effective as standard $\hat{I}_s$ when second-stage culling was moderate, but much poorer when 2nd-stage culling was stronger.

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Finally, like index selection, modifications have been proposed for independent culling to allow for restriction in the response of a character (Evans 1980) and for desired gains (Xu and Muir 1991, 1992). Campo and Villanueva (1987) experimentally compared restriction via independent culling with restriction by index selection for two sets of traits in *Tribolium castaneum*, finding that while both methods restrict response in the constrained character, index selection gave a larger response in the unconstrained characters.