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Selection When Traits Have Different Genetic and Phenotypic Variances in Different Environments

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ABSTRACT

Falconer's concept that performance in environment 2 is a different trait from performance in environment 1 allows calculation of expected response in environment 2 if selection is from environment 1. Response to selection in environment 1 and correlated response in environment 2 depend on heritability and phenotypic variance in environment 1, genetic covariance between performance of identical genotypes in the two environments, and selection intensity. If selection is from performance in environment 2, direct response in environment 2 and correlated response in environment 1 also can be calculated. If selection is from animals in both environments and if selected genotypes are expressed randomly in both environments, relative responses in environments 1 and 2 are weighted averages of direct and correlated responses with the weights being p_1 and p_2 , the fractions of animals selected from environments 1 and 2. Fraction selected from one environment determines the selection intensity factor for the direct and correlated responses in that and the other environment. Other terms determining relative responses are independent of fractions selected. A simple approach to finding the optimum fractions, p_1 and p_2 , is to calculate weighted average responses for environments one and two for all combinations of $p_1 + p_2 = p$, a fixed fraction.

INTRODUCTION

Hill (7) and Gianola (4) discussed selection from populations with different variances. For

milk records, heterogeneity of variance has been reported (1, 2, 8, 11, 12, 13, 14, 16, 17) with the difference associated with herd production. If heritability is equal in all herds, too many animals are likely to be selected from herds with greater variability. Heritability, however, is generally larger in herds with higher production than in herds with lower production (1, 9, 10, 11, 12, 20) with some exceptions (15, 19). Thus, if selection is for bull dams, the greater accuracy of evaluation due to larger heritability could compensate for the larger variance in higher production herds [e.g., Powell et al. (14)] and may result in selection of a near optimum fraction of cows from the various herd levels.

Evaluation of bulls in herds with different heritability and variance has been discussed by Hill (7) and Gianola (4). Mirande and Van Vleck (11) reported a reversal of the usual relationship between within sire variance and production when records are expressed as logarithms of yield.

Van Vleck et al. (20) reported larger heritability estimates in higher production than in lower production herds for both untransformed and log transformed records from daughter on dam regression. Hill et al. (8) reported smaller (20 to 30%) heritabilities in below average herds than in above average herds from among sire analyses. If smaller heritability and larger variance are associated with transformed records in low production herds as compared with higher production herds, then too many cows may be selected from low production herds than from high production herds when a common variance and heritability are assumed. Genetic evaluation under such conditions would be optimum under normality using Henderson's mixed model procedures if the correct genetic and phenotypic variances and covariances were used considering the expressions of a genotype in different environments to be different traits [see Henderson and Quaas (6) and Gianola (4)].

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The purpose of this paper is to describe a method for determining the fractions of cows to be selected as bull dams from two environments with different heritabilities and variances to maximize selection response in both environments (18). Although dairy environments cannot be separated into only two distinct environments, describing the method for two environments may illustrate the problems involved and their consequences on genetic improvement.

MATERIALS AND METHODS

The basic principle involved is due to Falconer (3), who proposed that the expressions of a genotype in different environments (e.g., production yields) be considered to be different traits. These traits may have genetic correlations of unity or less. Selection index theory can be used to calculate expected response in either environment when selection is based on records made in only one environment or on records of some cows made in one environment and on records of other cows made in another environment. The calculation of expected genetic superiority depends on multivariate normality of phenotypes and genetic expressions in all environments.

To illustrate the calculations, only two environments will be considered ($i = 1$ or 2). Let:

- σ_{w_i} = residual standard deviation from an among sires analysis,
- h_i^2 = heritability, and
- D_i = selection intensity factor in environment i .

Because:

$$\sigma_{w_i}^2 = \sigma_{y_i}^2 - h_i^2 \sigma_{y_i}^2 / 4$$

Then:

$$\sigma_{y_i}^2 = \sigma_{w_i}^2 / (1 - h_i^2 / 4) \text{ is the phenotypic variance, and}$$

$$\sigma_{G_i}^2 = h_i^2 \sigma_{y_i}^2 \text{ is the genetic variance for environment } i.$$

Sire Evaluation

In environment i , assume the evaluation

is $I_i = b_i \bar{X}_i$ where \bar{X}_i is the average of records of n daughters adjusted for fixed nongenetic effects and b_i is the weighting factor.

$$\sigma_{\bar{X}_i}^2 = \sigma_{y_i}^2 [1 + (n-1)h_i^2 / 4] / n$$

Cow Evaluation

In environment i , a simple evaluation is $I_i = h_i^2 y_i$ or $I_i = k y_i$ where y_i is a record of a cow in environment i adjusted for fixed nongenetic effects and k is a common heritability assumed for both environments.

Correlated Response

Let selection be based on the genetic evaluation, I_i , from records made in environment i .

The expected genetic superiority in environment i is:

$$\Delta G_i = [\text{covariance}(G_i, I_i) / \sigma_{I_i}] D_i$$

For sire evaluation based on daughter records covariance $(G_i, I_i) = b_i \sigma_{G_i}^2 / 2$ and $\sigma_{I_i} = b_i \sigma_{\bar{X}_i}$.

Thus:

$$\Delta G_i = (.5 \sigma_{G_i}^2 / \sigma_{\bar{X}_i}) D_i$$

The correlated genetic superiority in environment j is:

$$\Delta G_j = (.5 \sigma_{G_i G_j} / \sigma_{\bar{X}_i}) D_i$$

where $\sigma_{G_i G_j}$ is the genetic covariance between genotypes expressed in environments i and j .

If r_{gij} (genetic correlation) = 1, then $\sigma_{G_i G_j} = \sigma_{G_i} \sigma_{G_j}$.

For cow evaluation based on $I_i = b_i y_i$ with $b_i = h_i^2$ or k ,

$$\text{cov}(G_i, b_i y_i) = b_i \sigma_{G_i}^2 \text{ and}$$

$$\sigma_{I_i}^2 = b_i^2 \sigma_{y_i}^2 \text{ with } \sigma_{I_i} = b_i \sigma_{y_i} \text{ so that}$$

$$\Delta G_i = (\sigma_{G_i}^2 / \sigma_{y_i}) D_i \text{ and}$$

$$\Delta G_j = (\sigma_{G_i G_j} / \sigma_{y_i}) D_i$$

The terms for direct and indirect response can be broken into two parts so that the part other than D_i is a constant, which can be

multiplied by the appropriate selection intensity factor, depending on the fraction selected. This partition is convenient for the calculation of responses when cows are selected jointly from two environments.

Let:

$$\Delta g_1 = \sigma_{G_1}^2 / \sigma_{y_1}$$

$$\Delta g_2 = \sigma_{G_1 G_2} / \sigma_{y_1}$$

$$\Delta g_1 = \sigma_{G_1 G_2} / \sigma_{y_2}$$

$$\Delta g_2 = \sigma_{G_2}^2 / \sigma_{y_2}$$

Let p_1 be the fraction of cows selected from environment 1 with corresponding selection intensity factor D_1 and p_2 be the fraction from environment 2 with selection intensity factor D_2 .

If these cows are bull dams and their sons are used equally in both environments 1 and 2, the average relative responses due to the bull dam selection path in environments 1 and 2 are:

$$\Delta G_1 = \frac{(p_1 D_1 \Delta g_1 + p_2 D_2 \Delta g_1)}{(p_1 + p_2)} \quad [1]$$

$$\Delta G_2 = \frac{(p_1 D_1 \Delta g_2 + p_2 D_2 \Delta g_2)}{(p_1 + p_2)} \quad [2]$$

Selection of bull dams may be from a mixture of the two environments based on assumption of common heritability and variance with a common truncation point corresponding to a desired fraction, p , selected from the combined population. The net effect is a fraction selected from each environment with corresponding truncation points and selection intensity factors. Calculation of these fractions is somewhat complicated, but an approximation can be based on a common truncation point, which would be the average of the truncation points from selection from only environment 1 or from only environment 2 (Figure 1). From the common truncation point, T , the truncation point, t_i , for environment i can be determined as shown in Figure 1 from $T = t_i \sigma_{I_i}$. From t_i , p_i^* , the corresponding fraction selected, and D_i^* , the selection intensity factor, can be determined for $i = 1, 2$. Because $(p_1^* + p_2^*)/2$ may not equal p , the p_i^* can be approximated as:

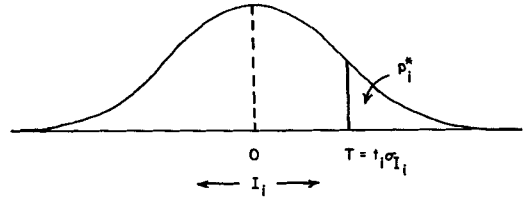


Figure 1. Selection of cows from index, I_i , with a common truncation point = T . Note t_i corresponds to a fraction selected, p_i^* , and selection intensity factor, D_i^* . For $I_i = h_{iy_i}^2$, $\sigma_{I_i} = h_i^2 \sigma_{y_i}$ and for $I_i = ky_i$, $\sigma_{I_i} = k \sigma_{y_i}$.

$$p_i = (2p)[p_i^* / (p_1^* + p_2^*)]$$

so that the corresponding selection intensity factor, D_i , can be determined. Then, p_1 , p_2 , D_1 , and D_2 can be used to calculate average expected superiorities (see Equations [1] and [2]).

EXAMPLES

The examples correspond somewhat to relative standard deviations and heritabilities estimated in low and high producing herds for untransformed and log transformed milk yield (11, 20). Heritabilities of .18 and .30 are assumed for lower and higher management, respectively. Within sire residual standard deviations for untransformed records are assumed to be in the ratio of 1.0 to 1.2 for lower and higher management and for log transformed records are assumed to be in the ratio of 1.1 to 1.0. Genetic correlations between genotypes expressed in the two environments were varied between .50 and 1.00, although evidence suggests that for milk yield the genetic correlation is near unity (10, 15, 16). Calculations were multiplied by 2,000 for ease of illustration.

Bull Evaluation

For selection of bulls from bull proofs based on a total of 50 daughters from a mixture of daughters from both environments, the weighting factor was assumed to be a constant when common heritability and variance are assumed:

$$I = b(n_1 \bar{X}_1 + n_2 \bar{X}_2) / (n_1 + n_2)$$

where \bar{X}_i is the average of n_i daughters with

records in environment *i*. Then the expected genetic superiority of selected bulls when used in environment *i* is:

$$\Delta G_i = (\text{cov}(G_i, I) / \sigma_I) D$$

where *D* is the selection intensity factor (assumed to be unity for the example) with:

$$\begin{aligned} \text{cov}(G_i, I) &= [.5b / (n_1 + n_2)] [n_i \sigma_{G_i}^2 + n_j \sigma_{G_j}^2] \\ \sigma_I^2 &= [b / (n_1 + n_2)]^2 [n_1^2 V(X_1) + n_2^2 V(X_2) + 2n_1 n_2 (\text{cov}(X_1, X_2))] \end{aligned}$$

where:

$$\text{cov}(X_i, X_j) = \sigma_{G_1 G_2} / 4$$

The number of records from each environment was varied from 0 to 50 by increments of 5 with a total of 50 records from both environments.

The calculations for bull evaluations are summarized in Figures 2 and 3.

Evaluation of bulls exclusively in herds with larger heritability gives greatest genetic gain in both environments if the genetic correlation is unity (7, 16). If the genetic correlation is less than 1, then gain in the environment with larger heritability is still maximum when all daughters are in that environment but gain in the environment with smaller heritability also may be greater when all daughters are in the environment with larger heritability. If the genetic correlation is substantially less than unity, inappropriate allocation of daughters to test environments can reduce genetic progress.

Figures 2 and 3 are for the two cases when the ratios of within sire standard deviations are 1.0:1.2 and 1.1:1.0. The figures also show the combined effects of numbers of daughters from each environment and genetic correlations of less than unity. Assume after testing that selected bulls are used equally in both environments. The proportion of the 50 daughters to be sampled in each environment to optimize average response in the two environments can be determined from averaging the expected responses in the two environments for each combination of daughters. For ex-

ample, as can be determined from Figure 2, by averaging responses in environments 1 and 2, the maximum average response when the genetic correlation is .50 is when 15 to 20 daughters are from environment 1 and 35 to 30 daughters are from environment 2. With a genetic correlation of .75, the maximum average response is for 10 to 15 daughters from environment 1 and 40 to 35 from environment 2. With a genetic correlation of 1.00, the maximum average response and in both environments is when all 50 daughters are from environment 2. The pattern is similar in Figure 3, which indicates for this example that differences in heritability are more important than differences in residual variances in determining optimum bull testing strategies. Higher heritability leads to more accurate evaluation than lower heritability with the same number of daughters or equal accuracy with fewer daughters. The increased genetic standard deviation also results in larger differences in evaluations. The combination leads to larger genetic superiorities from selection.

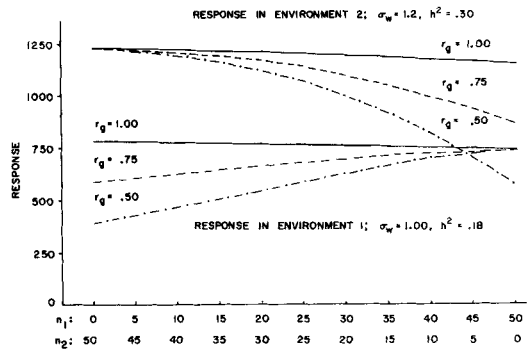


Figure 2. Relative genetic response to selection of bulls based on evaluation in two environments when selection is based on various numbers of daughters (*n*₁ and *n*₂) from the two environments having different heritabilities (.18 and .30) and different residual standard deviations (1.0 and 1.2) for genetic correlations of 1.00, .75, or .50 between expressions of genotypes in the two environments. Relative responses are proportional to the selection intensity factor associated with fraction selected except for a selection intensity factor of zero.

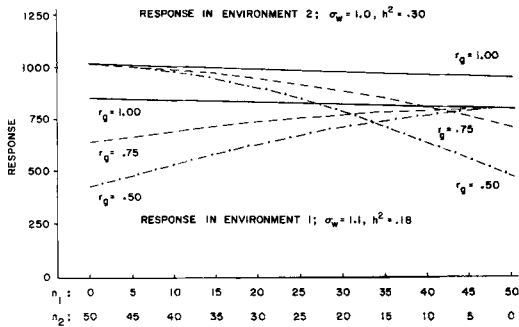


Figure 3. Relative genetic response to selection of bulls based on evaluation in two environments when selection is based on various numbers of daughters (n_1 and n_2) from the two environments having different heritabilities (.18 and .30) and different residual standard deviations (1.1 and 1.0) for genetic correlations of 1.00, .75, or .50 between expressions of genotypes in the two environments. Relative responses are proportional to the selection intensity factor associated with fraction selected except for a selection intensity factor of zero.

Optimum Fraction of Cows from Lower and Higher Production Herds

Again, two situations will be considered — with $\sigma_{w1} = 1.1$ and $\sigma_{w2} = 1.0$ and with $\sigma_{w1} = 1.0$ and $\sigma_{w2} = 1.2$. Different phenotypic standard deviations result in different fractions selected if a common truncation point is the basis of selection. The heritability used in the evaluation will also determine the fraction selected from each group. A smaller heritability results in fewer cows being selected than with higher heritability and the same standard deviation. For purposes of illustration, a common truncation point was chosen, which corresponds to 7% selected from a population with constant variance. Because the actual fractions selected from each environment depend on heritabilities and phenotypic standard deviations, the fractions selected from each environment were adjusted so that the equivalent of 7% from the combined environments would be selected. The fractions that would be selected from lower and higher environments are shown in Table 1 when using the correct heritability for each environment (.18 and .30) and when using a common heritability of either .25 or .30 for both environments. Table 1 shows that if correct heritabilities are used (rows 1 and 4),

more cows would be selected from higher environment (smaller heritability results in smaller evaluations even when the residual standard deviation is larger as with the log transformed records). The difference between rows 1 and 4 is due to larger relative variance in environment 1 for transformed and in environment 2 for untransformed records. However, using a common heritability would result in more cows being selected from the environment with larger residual standard deviations. None of these combinations is likely to be optimum, but are the selection responses much less than optimum?

Expected responses in both lower and higher environments from combinations of different fractions of cows selected from lower and higher environments are shown in Figures 4 and 5 when a fraction of .07 of cows in the combined populations are selected with genetic correlations of 1.00, .75, or .50.

The influence of true heritability on genetic response with a genetic correlation of 1.00 is apparent as the optimum combination for both log transformed and untransformed records is the top .045 of cows from lower environment and the top .095 of cows from higher environment. In other words, for each

TABLE 1. Example of selection of a total fraction of .07 from combined environments 1 and 2 with fractions selected by truncation from lower and higher management herds using appropriate heritabilities (.18 and .30) or a common heritability (.25 or .30) for prediction of genetic value.

Heritabilities ¹	Fraction selected from	
	Lower	Higher
When $\sigma_{w1} = 1.1$ $\sigma_{w2} = 1.0$		
.18 and .30	.0273	.1127
.25 and .25	.0778	.0622
.30 and .30	.0918	.0482
When $\sigma_{w1} = 1.0$ $\sigma_{w2} = 1.2$		
.18 and .30	.0132	.1268
.25 and .25	.0520	.0880
.30 and .30	.0537	.0863

¹ Used for genetic evaluation in lower and higher management herds, with true heritabilities of .18 and .30.

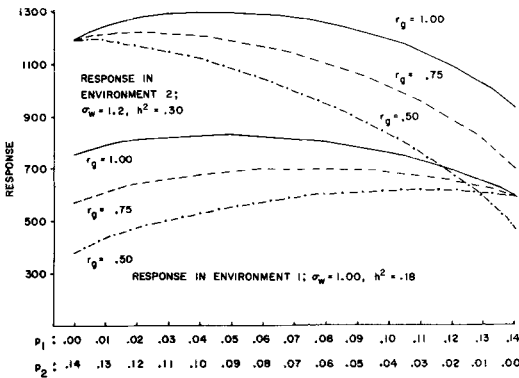


Figure 4. Relative genetic response to selection of bull dams from two environments having different heritabilities (.18 and .30) and different residual standard deviations (1.0 and 1.2) for genetic correlations of 1.00, .75, or .50 with different fractions (p_1 and p_2) of the cows selected from the two environments totaling 7% from the combined populations.

three cows selected, two should come from higher environment. Examination of Figures 4 and 5 shows, however, that there is little difference in response over a wide range of fractions selected from lower and higher environments. The expected responses using untransformed records and common heritabilities of either .25 or .30 are only slightly less than optimum even though the fractions selected when a common heritability of .25 is used are .052 and .088 rather than .045 and .095 (.054 and .086 for common heritability of .30).

The expected responses, however, for log transformed records when common heritability of .25 or .30 is used are considerably less than maximum because the fractions selected from the two environments are considerably different from optimum. If common heritability of .25 is used for evaluation, expected responses in environments 1 and 2 are 880 and 1049 with fractions selected of .0778 and .0622 as compared with optimum fractions of .045 and .095 with expected responses of 906 and 1081. For a common heritability of .30, expected responses are 851 and 1014 with fractions selected of .0918 and .0482, which are proportionally the reverse of the optimum fractions. With log transformed records, evaluations based on heritabilities

corresponding to the environments have expected selection responses similar to the optimum (897 and 1070 with fractions selected of .0273 and .1127 vs. 906 and 1081 for optimum fractions of .045 and .095). The calculations for this example suggest that erring in the direction of a larger fraction from the environment with higher heritability is more desirable than taking too many from the lower heritability environment. Selecting all cows out of the higher environment has an expected response about 10% less than optimum, whereas taking all cows out of the low environment has an expected response about 30% less than optimum.

If the genetic correlation is considerably less than unity, as illustrated in Figures 4 and 5, the optimum proportion of cows selected from environments 1 and 2 is different to maximize genetic response in the two environments than if the genetic correlation is 1.00, in which case the fractions that are optimum for environment 1 are also optimum for environment 2. For example, from Figure 4, with genetic correlation of .75, the optimum fractions are .07 and .07 from environments 1 and 2 to maximize response in environment 1 but the fractions to maximize response in environment 2 are .02 and .12. The disparity becomes larger with smaller genetic correla-

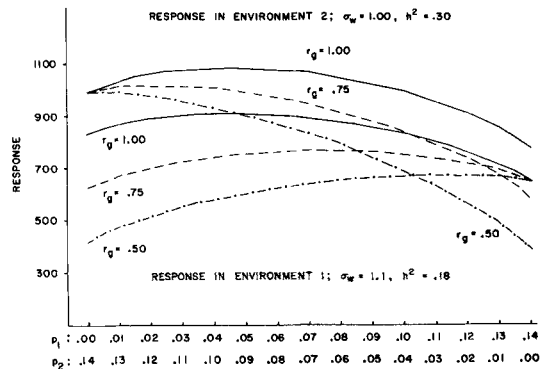


Figure 5. Relative genetic response to selection of bull dams from two environments having different heritabilities (.18 and .30) and different residual standard deviations (1.1 and 1.0) for genetic correlations of 1.00, .75, or .50 with different fractions (p_1 and p_2) of the cows selected from the two environments totaling 7% from the combined populations.

tions. The pattern is similar for the situation described by Figure 5 where the low heritability environment has the larger variation.

When selection is more intense (e.g., a fraction of .035 from combined environments 1 and 2), the patterns are similar. For both the log transformed and untransformed situations and genetic correlation of unity, the optimum fractions to select from environments 1 and 2 are .020 and .050 to maximize response in both environments. With genetic correlation of .75, the optimum fractions for response in environment 1 are .035 and .035 and for response in environment 2 are .005 and .065. With genetic correlation of .50, the optimum fractions are essentially all cows from the environment to be improved.

With a perfect genetic correlation and with more intense selection than for combined fractions of .07 or .035, an even greater fraction of cows should come from environment 2 to maximize response in both environments. For example, for a combined fraction of .020, the optimum fractions are about .005 and .015 for both transformed and untransformed cases.

The effects of different residual standard deviations when heritability is the same in both environments (.30, for example) also can be calculated. As expected, with a perfect genetic correlation the optimum is to select the same fraction from each environment. However, with genetic correlation less than unity, the optimum fraction includes more cows from the environment for which response is wanted.

CONCLUSIONS

The examples illustrate the importance of considering differences in heritabilities as well as differences in residual standard deviations in designing evaluation and selection strategies to maximize genetic response in different environments. The genetic correlation between expressions of a genotype in different environments also must be considered if the correlation is much different from unity. The examples imply that observed differences in heritability may be more important than observed differences in residual variation. If correct residual and genetic variances and covariances are known for each herd or environment, then multiple trait

mixed model procedures can be used to provide best evaluations on which selection can be based. These evaluations can then be used to select bulls or cows optimally for use in specified herds or environments. The problem, however, of obtaining good estimates of the needed variances and covariances is difficult. Gianola (4), Henderson (5), and Hill (7) have suggested a Bayesian approach where variance estimates from a sample within a herd or environment are averaged with prior estimates of some kind.

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