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# Expected Economic Responses to Selection for Direct and Fetal Genetic Effects

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## ABSTRACT

Expected responses in direct and fetal genetic values due to selection of heifers or bulls were computed for various combinations of heritabilities of direct and fetal effects, genetic correlations, economic weights, and kinds of relatives' records. If the economic weights are 1:3 for direct and fetal effects, then records of mates of the sire should be used for selection of both heifers and bulls for the heritabilities .16 to .32. If the economic weights are 1:1, use of records of the mates does not appear important for selection of bulls or heifers. Reliable estimates of genetic covariance and variances of direct and fetal genetic effects are required to decide whether fetal effects need to be considered in selection programs.

## INTRODUCTION

Skjervold and Fimland (2) and Adkinson et al. (1) presented evidence that fetal genetic effects may influence subsequent production of the dam. They also suggested that records of the mates of the sire might be useful in sire selection and may result in a reduction in error variance of prediction for a sire's transmitting ability. Taylor et al. (3) have shown results suggesting a large negative genetic correlation between direct and fetal genetic effects although the estimates of Skjervold and Fimland (2) and Adkinson et al. (1) are nearer zero. Therefore, the importance of considering averages of mates in sire selection was investigated. Goals of this investigation were 1) to determine how important the genetic correlation between the direct and fetal effects is in deciding which records to use for selection, 2) to determine whether the economic weights

assigned to fetal and direct genetic values are important in deciding which records to use for selection, and 3) to determine under what parameters the usual method of selection, which ignores fetal effects and the records of a sire's mates, should be changed to consider fetal effects and information. The case where the fetal effect also influences the lactation during the gestation of the fetus was not examined. Procedures similar to those of this study would be appropriate for that case.

Selection index theory can be used to calculate expected responses for selection for both direct and fetal genetic values. Expected responses were the criteria used to answer the objectives of this study. Selection is generally 1) for heifer replacements from information on dam and sire and 2) for bulls on progeny performance. Records on other relatives generally add little to accuracy of evaluation. If fetal effects are important, then the sire information likely to be available for heifer selection is the usual average production of other daughters of the sire and, in addition, the average production of the mates of the sire. For bull selection, the same information would be available, daughters' average and mates' average production.

## MATERIALS AND METHODS

Expected responses for direct and fetal genetic values were calculated for a number of the most likely combinations of variances of direct and fetal genetic values, genetic correlations between direct and fetal genetic values, economic weights for direct and fetal genetic values, and kinds of records used for selection. Only the most likely and potentially important combinations are reported here. The procedure described, however, can be used with any combination of parameters.

Two heritabilities (or standardized genetic variances) were used for each of the direct and fetal components, .32 and .16. Genetic correlations were .3, .0, and  $-.3$ , a range likely to encompass the real correlation for dairy records.

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The three sets of economic values were 1:1, equal emphasis on direct and fetal components, which corresponds to what was suggested as appropriate when the fetal effect influences only the subsequent lactation (6); 1:3, three times as much emphasis on the fetal as on the direct component, which corresponds to a permanent fetal effect on all subsequent lactations (6); and 1:0, which corresponds to ignoring the fetal effect as now.

Calculations used known properties of the selection index with normality for computing expected responses. Results in the tables are standardized and correspond to a standardized selection intensity factor ( $i = 1$ ). To convert the table values to absolute values, multiplication by the product of the appropriate selection intensity factor and phenotypic standard deviation is required.

The selection index procedure will be reviewed. The necessary variances and covariances also will be indicated for the various combinations of relatives. Let  $p$  be the vector of available information, e.g., average of sire's mates, sire's daughter average, and dam's record, all adjusted for fixed factors such as age, herd, and year effects. Then the index for selection is  $I = b'p$ , where  $b$  is the vector of weights defined by the selection index equations:

$$Vb = c$$

where  $V$  is the variance-covariance matrix of  $p$ , i.e.,  $V = E(pp')$ , and  $c$  is the vector of covariances between  $p$  and the defined aggregate economic genotype,  $T = v_g g_\alpha + v_f f_\alpha$ . The  $v$ 's are the economic weights for the direct ( $g$ ) and fetal ( $f$ ) genetic values of the animal,  $\alpha$ . Then  $c = E(Tp) = v_g E(g_\alpha p) + v_f E(f_\alpha p)$ .

Thus  $b = V^{-1}c$  and the standard deviation of the index,  $\sigma_I = (b'Vb)^{.5}$ . The expected superiority in  $T$  from truncation selection is as usual:

$$\Delta T = i\sigma_I$$

where  $i$  is the standardized selection intensity factor. The expected correlated responses also can be computed as usual:

$$\Delta g = [iCov(g_\alpha, I_\alpha)] / \sigma_I = [ib'E(g_\alpha p)] / \sigma_I$$

and

$$\Delta f = [iCov(f_\alpha, I_\alpha)] / \sigma_I = [ib'E(f_\alpha p)] / \sigma_I.$$

In this discussion,  $i = 1$  since relative responses will be proportional for any selection intensity.

All that is necessary to use the matrix equations is to describe the elements of the matrices and vectors. Use will be made of the model developed in (5) to write the covariances between relatives when both direct and fetal genetic effects influence the records. All records will be assumed to be from a distribution with mean, zero, and phenotypic variance,  $\sigma^2$ .

#### Phenotypic Variances and Covariances

Let  $p_1$  = the average of single records of  $n_1$  mates of a bull,  $n_1 = 200$  for the calculations in this report;  $p_2$  = the average of single records of  $n_2$  daughters of a bull;  $n_2 = 40$  for these calculations; and  $p_3$  = a single record of the dam of a heifer being evaluated.

Also let  $\sigma_f^2$  be the additive genetic variance of fetal effects;  $\sigma_g^2$  be the additive genetic variance of direct effects; and  $\sigma_{gf}$  be the covariance between additive direct and fetal effects.

For predicting the value of a heifer, any or all of the three  $p$ 's may be used. The heifer being evaluated will not have a record. For predicting the value of a bull, only the average of his progeny and of his mates will be used.

Then,

$$V_{11} = E[p_1^2] = [\sigma^2 + (n_1 - 1)(\sigma_f^2/4)] / n_1$$

$$V_{22} = E[p_2^2] = [\sigma^2 + (n_2 - 1)(\sigma_g^2/4 + \sigma_{gf}/4 + \sigma_f^2/16)] / n_2$$

(5), and

$$V_{33} = E[p_3^2] = \sigma^2.$$

The phenotypic covariances will depend on whether the record of the mate of the bull is started by the birth of a daughter of the sire.

$$V_{12} = \text{Cov}(\text{daughter, dam; daughter sired by mate of dam}) + (n_1 - 1)\text{Cov}(\text{cow sired by bull, cow having fetus of bull}) / n_1$$

$$= [(\sigma_g^2/2 + \sigma_f^2/2 + 5\sigma_{gf}/4) + (n_1 - 1)(\sigma_{gf}/4 + \sigma_f^2/8)] / n_1$$

$$= (\sigma_g^2/2 + 3\sigma_f^2/8 + \sigma_{gf})/n_1 + (\sigma_{gf}/4 + \sigma_f^2/8)$$

if the  $n_2 < n_1$  daughters of the sire which have records initiated the records of their mothers, as would usually be true.

$$V_{12} = (\text{Cov}(\text{cow sired by bull, cow having fetus of bull}) = \sigma_{gf}/4 + \sigma_f^2/8$$

if none of the daughters having records of the sire initiated the records of the mates of the sire.

If  $n_1$  is large, for practical purposes both expressions are numerically similar.

$$V_{13} = \sigma_f^2/4$$

if the sire of the fetus for the record of the dam is the same as the bull whose daughter is being evaluated.

$$V_{13} = [\sigma^2 + (n_1 - 1)(\sigma_f^2/4)]/n_1$$

if the record of the dam of the heifer is included as a record in the average of mates of the bull. (This case was not considered).

$$V_{13} = 0$$

if the fetus affecting record of dam is not from sire of heifer being evaluated.

$$V_{23} = \sigma_{gf}/4$$

if the sire of fetus for record of the dam is same as the sire of the heifer being evaluated (i.e., the fetus becomes the heifer).

$$V_{23} = 0$$

if the sire of the fetus for record of the dam is not the same as the sire of the heifer being evaluated.

Covariances contributing to the vector  $c$  for heifer selection are

$$E[g_\alpha, p_1] = \sigma_{gf}/4; E[f_\alpha, p_1] = \sigma_f^2/4$$

$$E[g_\alpha, p_2] = \sigma_g^2/4 + \sigma_{gf}/8; \\ E[f_\alpha, p_2] = \sigma_{gf}/4 + \sigma_f^2/8$$

$$E[g_\alpha, p_3] = \sigma_g^2/2 + \sigma_{gf}; \\ E[f_\alpha, p_3] = \sigma_{gf}/2 + \sigma_f^2$$

when the fetus starting the record of the dam is the heifer being evaluated. If the fetus starting the record of the dam is not the heifer being evaluated, then

$$E[g_\alpha, p_3] = \sigma_g^2/2 + \sigma_{gf}/4$$

and

$$E[f_\alpha, p_3] = \sigma_{gf}/2 + \sigma_f^2/4.$$

The covariances on the right sides for bull selection will depend on the definition of the aggregate genotype. The definition, most comparable to current sire selection, would include transmitting ability for both the direct and fetal components weighted by the economic values:

$$T = v_g(g_\alpha/2) + v_f(f_\alpha/2)$$

where  $\alpha$  is the bull being evaluated. Then the  $c$ 's corresponding to  $p_1$  and  $p_2$  are the same as for heifer evaluation.

Thus,

$$c_1 = \text{Cov}(p_1, T) = v_g(\sigma_{gf}/4) + v_f(\sigma_f^2/4)$$

$$c_2 = \text{Cov}(p_2, T) = v_g(\sigma_g^2/4 + \sigma_{gf}/8) + v_f(\sigma_{gf}/4 + \sigma_f^2/8)$$

In calculating correlated response on the basis of genetic value rather than transmitting ability, the covariance parts would be doubled. If  $T = v_g g_\alpha + v_f f_\alpha$ , then the right sides would be doubled. The doubled covariances would be used in calculating correlated response. The calculations will give the same answer in both cases since in the first instance  $\sigma_I$  will be one-half that in the second case.

Another reasonable definition is

$$T = v_s(g_\alpha/2 + f_\alpha/4) + v_t(f_\alpha/2)$$

$$= v_s s_\alpha + v_t t_\alpha$$

where  $s_\alpha$  is the usual prediction of a sire value coming out of most evaluation programs, and  $t_\alpha$  would be a corresponding value for the effect of sire of fetus if it were added to the sire evaluation model. The prediction of  $s_\alpha$  is really

a prediction of  $g_{\alpha}/2 + f_{\alpha}/4$ , since the sire of the heifer is also the grandsire of the fetus (5). The correspondence of economic weights (6) is that  $v_g = v_s$  and  $v_f = v_t + v_s/2$ . When this correspondence is satisfied, the correlated responses and indices for selection will be the same.

### RESULTS AND DISCUSSION

The relative expected responses from selection are in Tables 1 to 3 for heifer selection and in Table 4 for bull selection. Table 1 lists the relative expected responses for heifer selection for all three sources of information (dam's record, proof of sire of heifer, and records of mates of sire). The comparisons of interest are mainly those among the relative economic weights. The choice of 1:1 or 1:3 weights depends on whether there is a carry-over fetal effect. If the proper weight is 1:1, then 1:3 weighting does not do that much more poorly. For example, with variances .32 and .16 and with a zero correlation, the responses are (.27, .17) and (.20, .21), as on the left half of Table 1. If each component has equal value, then the total economic responses are .44 and .41. If the true economic weights are 1:3, then the total economic responses are .78 and .83. Such trends appear for most combinations of variances and correlations and whether the dam's record included the fetal effect of the heifer being selected. Assigning a zero economic weight to fetal effects, however, appears to be shortsighted if they exist. Continuing the same illustration, the responses are (.31, .08) for economic weights of 1:0. The total response if the true weights are 1:1 would be .39 vs. the optimum of .44, and if the true weights are 1:3, the response would be only .54 vs. the optimum of .83, an especially large difference. If the genetic correlation is positive (.3), then the difference in total economic response is still large, .82 vs. 1.00 for correct emphasis of 1:3 and especially large, .25 vs. .67, if the genetic correlation is negative (−.3).

Expected responses are generally smaller if the dam's record is not affected by the fetus being the heifer under evaluation, as would be the case when the heifer is a second calf and the record is the first lactation of the dam. More detailed analysis of use of multiple records will require knowledge of the extent of carry-over fetal effects and correlations among records when the fetus may affect the current lactation

as well as the subsequent lactations.

The expected responses (Table 2) for heifer selection involve selection using less than three kinds of records when the dam's record was made before the heifer being evaluated was born — this would be the usual situation when using a dam's record. Table 3 lists the less likely alternative. These tables should be compared with the right and left sides of Table 1 to indicate the expected loss in improvement by ignoring certain information.

Comparison of Table 2 with the right side of Table 1 reveals that ignoring the mates of the sire does not decrease expected aggregate improvement greatly if the true economic weights are 1:1. For the previous example, the expected responses ignoring the mates of the sire are (.29, .07) vs. (.25, .12) for all information. The total economic responses would be .36 and .37. The advantage of using the mates of the sire is greater if the genetic correlation is negative than if it is zero or positive.

If the true economic weights, however, are 1:3, then ignoring the mates of the sire results in a more serious decline in expected responses; i.e., for the previous parameters (.29, .07) vs. (.16, .18) and economic total response of .50 vs. .70. The expected responses using records of the dam and the sire's progeny when the dam's record is not initiated by birth of the heifer being evaluated are the same for any choice of economic weights. The result is caused by the proportionality of the right sides for records of the dam and the sire's progeny. The same peculiarity was reported for expected responses with a maternal effects model (4).

The right side of Table 2 considers use of only the dam's record and other mates of the sire. This combination of records is less effective than using records of dam and sire's progeny for true economic weights of 1:1 but is more effective for true economic weights of 1:3 since there are more mates and they supply more information on fetal values than do daughters of a sire.

The middle section of Table 2 illustrates the response expected from use of only one source of information for heifer selection. In such cases, economic weighting cannot be used. Of primary interest is the column using only mates of sires since this is information that could be obtained earlier than any other (2). The value of using the mates' records depends on

TABLE 1. Expected response in selecting heifers for direct ( $g$ ) and fetal ( $f$ ) genetic values from the dam's record, the records of 40 progeny of the sire, and the records of 200 mates of the sire.<sup>a</sup>

Genetic		Economic weights $v_g:v_f$											
		Birth of heifer initiated dam's record				Dam's record not initiated by heifer				1:0			
		1:1	1:3	g	f	1:0	1:1	g	f	1:3	g	f	1:0
Variance	Correlation	g	f	g	f	g	f	g	f	g	f	g	f
.32	.3	.34	.38	.31	.41	.37	.29	.27	.26	.22	.29	.31	.15
	.0	.26	.33	.20	.37	.32	.16	.23	.22	.14	.27	.30	.05
	-.3	.18	.27	.08	.33	.28	.01	.18	.17	.03	.26	.28	-.06
.32	.3	.32	.22	.28	.24	.34	.16	.28	.16	.23	.19	.31	.10
	.0	.27	.17	.20	.21	.31	.08	.25	.12	.16	.18	.30	.02
	-.3	.22	.12	.10	.19	.28	-.01	.23	.07	.07	.16	.29	-.05
.16	.3	.20	.39	.18	.40	.23	.29	.15	.28	.12	.29	.19	.15
	.0	.14	.35	.10	.37	.19	.15	.11	.25	.06	.28	.18	.04
	-.3	.06	.32	.02	.35	.17	-.02	.06	.23	-.01	.27	.17	-.07
.16	.3	.18	.22	.16	.24	.21	.16	.16	.18	.13	.20	.18	.10
	.0	.14	.19	.10	.22	.18	.07	.13	.15	.07	.19	.18	.02
	-.3	.09	.16	.02	.21	.17	-.03	.09	.12	.00	.18	.17	-.05

<sup>a</sup>To obtain absolute rather than relative expected response multiply by product of selection intensity factor and phenotypic standard deviation.

TABLE 2. Expected response in selecting heifers for direct (*g*) and fetal (*f*) genetic values from the dam's record and records of 40 progeny of the sire and from the dam's record and records of 200 mates of the sire when the dam's record was *not* initiated by the birth of the heifer.<sup>a</sup>

Economic weights $v_g/v_f$														
Using records of only														
Genetic			Using records of dam and sire's progeny				Dam				Sire's progeny			
Variance			1:1				1:0				1:0			
<i>g</i>	<i>f</i>	Correlation	<i>g</i>	<i>f</i>	<i>g</i>	<i>f</i>	<i>g</i>	<i>f</i>	<i>g</i>	<i>f</i>	<i>g</i>	<i>f</i>	<i>g</i>	<i>f</i>
.32	.32	.3	.30	.21	.30	.21	.18	.13	.17	.08	.28	.18	.29	.17
		.0	.28	.14	.28	.14	.18	.13	.24	.17	.00	.10	.26	.07
		-.3	.26	.06	.26	.06	.14	.03	.22	.05	+.08	.03	.23	-.04
.32	.16	.3	.30	.13	.30	.13	.18	.07	.25	.10	.08	.19	.18	.16
		.0	.29	.07	.29	.07	.16	.04	.24	.06	.00	.12	.16	.07
		-.3	.27	.01	.27	.01	.14	.06	.23	.01	+.08	.07	.12	-.03
.16	.32	.3	.18	.21	.18	.21	.10	.11	.15	.18	.06	.28	.10	.30
		.0	.16	.16	.16	.16	.08	.08	.14	.14	.00	.00	.28	.03
		-.3	.14	.10	.14	.10	.06	.05	.12	.09	+.06	-.28	.27	-.04
.16	.16	.3	.18	.13	.18	.13	.09	.06	.16	.11	.06	.19	.10	.09
		.0	.17	.08	.17	.08	.08	.04	.15	.07	.00	.00	.18	.03
		-.3	.15	.04	.15	.04	.07	.02	.14	.03	+.06	-.19	.17	-.04

<sup>a</sup>To obtain absolute rather than relative expected response multiply by product of selection intensity factor and phenotypic standard deviation.

TABLE 3. Expected response in selecting heifers for direct (*g*) and fetal (*f*) genetic values from the dam's record and records of 40 progeny of the sire and from the dam's record and records of 200 mates of the sire when the dam's record was initiated by the birth of the heifer.<sup>a</sup>

Economic weights $v_g/v_f$														
Using records of only														
Genetic			Using records of dam and sire's progeny				Dam				Sire's progeny			
Variance			1:1				1:0				1:0			
<i>g</i>	<i>f</i>	Correlation	<i>g</i>	<i>f</i>	<i>g</i>	<i>f</i>	<i>g</i>	<i>f</i>	<i>g</i>	<i>f</i>	<i>g</i>	<i>f</i>	<i>g</i>	<i>f</i>
.32	.32	.3	.34	.39	.33	.39	.26	.37	.24	.17	.08	.28	.25	.40
		.0	.26	.25	.25	.34	.16	.32	.23	.11	.00	.00	.14	.36
		-.3	.19	.17	.16	.28	.06	.27	.22	.05	+.08	-.28	.03	.32
.32	.16	.3	.32	.21	.32	.21	.23	.19	.25	.10	.08	.19	.22	.24
		.0	.28	.16	.26	.17	.16	.16	.24	.06	.00	.14	.21	.11
		-.3	.24	.10	.20	.12	.09	.13	.23	.01	.08	-.19	.06	.17
.16	.32	.3	.20	.39	.20	.39	.15	.35	.15	.18	.06	.28	.14	.40
		.0	.14	.34	.14	.35	.08	.32	.14	.14	.00	.00	.06	.37
		-.3	.08	.29	.07	.30	.12	.29	.11	.09	.06	-.28	.02	.35
.16	.16	.3	.20	.21	.19	.21	.13	.18	.16	.11	.06	.19	.13	.24
		.0	.16	.17	.15	.17	.08	.16	.15	.07	.00	.00	.06	.22
		-.3	.12	.12	.10	.14	.03	.14	.14	.03	.06	-.19	.01	.20

<sup>a</sup>To obtain absolute rather than relative expected response multiply by product of selection intensity factor and phenotypic standard deviation.

TABLE 4. Expected response in selecting sires for direct (*g*) and fetal (*f*) genetic values from records of 40 daughters and 200 mates of the sire.<sup>a</sup>

Genetic		Economic weights $v_g \cdot v_f$									
		Using daughter and mate averages						Using only			
		1:1		1:3		1:0		Progeny		Mates	
Variance	Correlation	<i>g</i>	<i>f</i>	<i>g</i>	<i>f</i>	<i>g</i>	<i>f</i>	<i>g</i>	<i>f</i>	<i>g</i>	<i>f</i>
<i>g</i>	<i>f</i>										
.32	.3	.40	.46	.29	.53	.50	.19	.48	.34	.16	.55
.0	.0	.34	.41	.15	.53	.50	.01	.46	.23	.00	.55
-.3	-.3	.26	.35	-.02	.52	.50	-.18	.43	.10	.16	-.55
.32	.3	.44	.29	.33	.36	.50	.14	.49	.21	.16	.38
.0	.0	.40	.23	.21	.35	.50	.01	.48	.12	.00	.38
-.3	-.3	.36	.16	.06	.34	.50	-.12	.46	.02	.16	-.38
.16	.3	.24	.50	.17	.54	.32	.22	.31	.36	.12	.55
.0	.0	.16	.48	.07	.54	.32	.01	.28	.28	.00	.55
-.3	-.3	.07	.46	-.06	.54	.32	-.20	.24	.18	.12	-.55
.16	.3	.26	.33	.19	.37	.32	.16	.32	.22	.11	.38
.0	.0	.21	.29	.09	.36	.32	.01	.30	.15	.00	.38
-.3	-.3	.15	.25	-.02	.36	.32	-.13	.27	.06	.11	-.38

<sup>a</sup>To obtain absolute rather than relative expected response multiply by product of selection intensity factor and phenotypic standard deviation.



the size and sign of the genetic correlation. A positive correlation of .3 would make the mates' records more valuable than the dam's records for 1:1 and especially for 1:3 true economic weights. With the same positive correlation, the mates' records are not as effective as progeny records for 1:1 but are more effective for 1:3 economic weights. In addition, the record would be available much sooner. When the correlation is negative, the mate information is difficult to use by itself because of the inherent antagonism in expected responses.

Table 3 gives the expected responses when the dam's record is influenced by the fetal effect of the heifer being evaluated.

Expected responses from bull selection are in Table 4. The important comparisons are between using both daughter and mate averages with using mate average alone and with using daughter average alone since that is the current basis of sire evaluation. If the correct economic weights are 1:1 (fetal effects on only the subsequent lactation), then the daughter average alone gives nearly the same total expected economic response as also using the mates' average if the genetic correlation is positive (.3). For example, if  $\sigma_g^2 = .32$  and  $\sigma_f^2 = .16$ , the expected total response using both daughters and mates is .73 and using daughters only is .70. The difference in response is greater if the genetic correlation is zero and even more if negative (-.3). Thus, the importance of using mate information will depend on what the genetic correlation is. The estimates of Skjervold and Fimland (2) and Adkinson et al. (1) suggest a value of near zero while the results of Taylor et al. (3) project a negative value of about -.5. Use of records of mates alone is generally not a good substitute to using both mates and daughters or even daughters for most combinations of parameters except if  $\sigma_g^2 = .16$  and  $\sigma_f^2 = .32$ .

With correct economic weights of 1:3, the usefulness of daughter and mate averages reverses. Progeny alone are not a good substitute for using both progeny and mate averages and become an even poorer substitute if the genetic correlation is zero or negative. If,

for example,  $\sigma_g^2 = .32$  and  $\sigma_f^2 = .16$ , the expected total economic responses if the correlation is .3 are 1.41 using both, 1.12 using progeny, and 1.30 using mates; if the correlation is .0, the corresponding responses are 1.26, .84, and 1.14; and if the correlation is -.3, the responses are 1.08, .52, and .98 (by reversing the direction of selection). If  $\sigma_g^2 = .16$  and  $\sigma_f^2 = .32$ , using mate information would be expected to give responses nearly equal to using both daughter and mate averages: 1.79 vs. 1.77, 1.69 vs. 1.65, and 1.56 vs. 1.53 for genetic correlations of .3, .0, and -.3.

### CONCLUSIONS

The importance of selecting jointly for direct and fetal genetic effects depends on the genetic correlation, economic weights, and ratio of direct and fetal genetic variances. If the correlation is positive, considering mate averages is less important than if the correlation is zero or negative. Use of mate of sire averages for both heifer and bull selection is suggested if economic weights are 1:3 rather than 1:1 for direct and fetal effects. These calculations point to the necessity of determining reliable estimates of the genetic covariance and variances in contrast to the situation with some traits where the correlation has relatively little effect on expected responses.

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