

Considerations for the Genetic Evaluation of Straightbred and Crossbred Bulls in Large Multibreed Populations¹

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Introduction

The purpose of this discussion is to help identify aspects that need to be considered for the design and implementation of a national program for multibreed genetic evaluations. Although no specific citations are made, many of the ideas discussed here are based on those contained in the references listed in the bibliography section. The discussion follows the following outline.

Multibreed population.

Multibreed genetic evaluation.

Objective.

Assumptions.

Multibreed genetic model.

Factors affecting the form of multibreed genetic evaluation strategies.

Definitions of multibreed populations.

Genetic predictions.

Genetic base.

Genetic grouping strategies.

Connectedness.

Estimation of covariance components.

Complex multibreed population.

Simple multibreed population.

Simplifying Assumptions for the Estimation of Multibreed Covariances.

Ranking of bulls by additive, nonadditive, and total EPD.

Implications.

Bibliography.

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Multibreed Population

Population composed of straightbred and crossbred animals of various fractions of the parental breed that interbreed. For example, a two-breed Angus (A)-Brahman (B) multibreed population would be composed of A, B, Brangus, and other $A \times B$ crossbred animals.

Multibreed Genetic Evaluation

Objective

Evaluation of straightbred and crossbred animals for additive and nonadditive direct and maternal genetic effects for traits of economic importance in a multibreed population.

Assumptions

- a. Traits are determined by a large number of alleles that are inherited in mendelian fashion, no linkage, and no selection, except for selection that can be accounted for by the records included in the evaluation.
- b. Multibreed sire additive (direct and maternal) genetic effects are defined within a sire subclass. A sire subclass comprises all progeny of the matings of a bull to dams of various breed compositions. Additive covariances are assumed to differ across breed groups (straightbred and crossbred). Thus, a very large number of multibreed additive covariance matrices is needed. However, these covariances are computed as linear combinations of intrabreed and interbreed covariances. Thus, the number of additive covariances that need to be known is much smaller than the number of multibreed additive covariances required. For example, 3 covariance matrices are needed for a two-breed multibreed population. In general, the number of intrabreed and interbreed covariance matrices for a multibreed population composed of nb breeds is $nb(nb+1)/2$.
- c. Sire nonadditive (direct and maternal) genetic effects are also defined within a sire subclass. For simplicity, they are explained only in terms of interactions between sire and dam alleles of different breeds at 1 locus (intraconfiguration and interconfiguration intralocus interbreed

interactions), within a sire subclass. Because of this assumption only one block-diagonal nonadditive covariance matrix is needed, where the diagonal blocks are matrices of intraconfiguration and interconfiguration covariances for direct and maternal effects.

Examples of intralocus configurations are A/B and S/B, where A = Angus, B = Brahman, and S = Simmental. Intraconfiguration intralocus interbreed interactions refer to differences in intralocus interactions that occur within a specific interbreed configuration, summed over all loci (e.g., differences in A/B interactions at one locus, summed over all loci). Interconfiguration intralocus interbreed interactions alludes to differences in the expected values of intralocus interactions of different interbreed configurations, summed over all loci (e.g., differences between the expected values of A/B and S/B interactions at one locus, summed over all loci).

d. Multibreed environmental covariances can also be assumed to differ across breed groups (straightbred and crossbred). Assuming that multibreed environmental covariances depend only on the breed composition of the individual and its parents, they can be computed as linear combinations of intrabreed and interbreed environmental covariances.

Multibreed Genetic Model (MGM)

The MGM will be illustrated using a multiple trait bull (i.e., sire-maternal grandsire) model.

$$y = Xb + Z_a u_a + Z_n u_n + e \quad [1]$$

$$E[y] = Xb$$

$$\text{var}(y) = Z_a G_a Z_a' + Z_n G_n Z_n' + R$$

where

y = vector of records from straightbred and crossbred calves,

u_a = vector of sire additive direct and maternal genetic effects,

u_n = vector of sire nonadditive direct and maternal genetic effects, where nonadditive refers to intraconfiguration and interconfiguration intralocus interbreed interactions; intraconfiguration and interconfiguration sets of direct and maternal effects are independent of one another, and treated as separate sets of different traits,

e = vector of residual effects,

Z_a = matrix of 1's and 0's that relates calf records to elements of u_a ,

Z_n = matrix of square roots of t 's (for intraconfiguration effects), square roots of products of t 's (for interconfiguration effects) and 0's, $0 \leq t \leq 1$, $t = [p_b^s p_{b'}^d + p_{b'}^s p_b^d]$, where the p 's are expected fractions of breeds (b, b') in the sire (s) and the dam (d) of a calf,

G_a = $\text{var}(u_a)$, cannot be written as the product of the relationship matrix among bulls (A) times a common additive covariance matrix (G_0) because the multibreed additive covariance between two animals depends on the multibreed additive covariances of their common ancestors which may be different,

G_n = $\text{var}(u_n)$ = direct product of the relationship matrix among bulls (A) times the block-diagonal covariance matrix among intraconfiguration and interconfiguration intralocus interbreed interaction effects (G_{0n}), and

R = $\text{var}(e)$, a block-diagonal matrix.

Because multibreed additive covariances are computed as linear combinations of additive intrabreed and interbreed covariances, these are the only additive covariance matrices that need to be stored; specific multibreed additive covariances can be recomputed when needed. The multibreed additive covariance between traits Y and Z is computed as follows:

$$\text{cov}_a(Y,Z) = \sum_{b=1}^{nb} p_b^i (\sigma_{aYZ})_b + \sum_{b=1}^{nb-1} \sum_{b'>b}^{nb} (p_b^s p_{b'}^s + p_b^d p_{b'}^d) (\sigma_{aYZ})_{bb'} \quad , \quad [2]$$

where the superscripts i, s and d correspond to individual animal, sire and dam, the subscripts b and b' represent two breeds and

nb = number of breeds,

p_b^x = expected fraction of breed b in animal x , $x = i, s, d$,

$(\sigma_{aYZ})_b$ = additive intrabreed covariance for breed b , and

$(\sigma_{aYZ})_{bb'}$ = additive interbreed covariance for the pair of breeds b and b' .

Multibreed environmental covariances are computed using a formula similar to that used for multibreed additive covariances. Only intrabreed and interbreed covariance matrices need to be stored. The multibreed environmental covariance between traits Y and Z, is computed as follows:

$$cov_e(Y,Z) = \sum_{b=1}^{nb} p_b^i (\sigma_{eYZ})_b + \sum_{b=1}^{nb-1} \sum_{b'>b}^{nb} (p_b^s p_{b'}^s + p_b^d p_{b'}^d) (\sigma_{eYZ})_{bb'} , \quad [3]$$

where the superscript i represents an individual animal, the subscripts b and b' represent two breeds and

$(\sigma_{eYZ})_b$ = environmental intrabreed covariance for breed b, and

$(\sigma_{eYZ})_{bb'}$ = environmental interbreed covariance for the pair of breeds b and b'.

Nonzero elements of the multibreed residual covariance matrix R are computed as a linear combination of multibreed additive (and nonadditive maternal if the maternal grandsire is unknown), and environmental covariances. The multibreed residual covariance between traits Y and Z for a bull model is computed as follows:

$$\begin{aligned} cov_v(Y,Z) &= cov_a(Y,Z)^i - \delta^s .25 cov_a(Y,Z)^s - \delta^{mgs} .0625 cov_a(Y,Z)^{mgs} \\ &\quad + (1 - \delta^{mgs}) cov_n(Y,Z)^{mgs} \\ &\quad + cov_e(Y,Z)^i \end{aligned} \quad [4]$$

where the superscripts i, s, and mgs refer to an animal, its sire, and its maternal grandsire, the subscripts v, a, n, and e represent residual, additive genetic, nonadditive genetic and environmental, and

δ^x = indicator equal to 1 if animal x is not identified and to 0 if animal x is identified, x = s, mgs,

$cov_a(Y,Z)^i = cov_a(Y_D, Z_D)^i + cov_a(Y_M, Z_M)^d + .5 cov_a(Y_D, Z_M)^d + .5 cov_a(Y_M, Z_D)^d$, where

the subscripts D = direct genetic effects, and M = maternal effects,

$$\begin{aligned} \text{cov}_a(Y,Z)^s &= \text{cov}_a(Y_D,Z_D)^s, \\ \text{cov}_a(Y,Z)^{\text{mgs}} &= \text{cov}_a(Y_D,Z_D)^{\text{mgs}} + 4 \text{cov}_a(Y_M,Z_M)^{\text{mgs}} + 2 \text{cov}_a(Y_D,Z_M)^{\text{mgs}} + \\ &\quad 2 \text{cov}_a(Y_M,Z_D)^{\text{mgs}}, \text{ and} \\ \text{cov}_n(Y,Z)^{\text{mgs}} &= \text{cov}_n(Y_M,Z_M)^{\text{mgs}}. \end{aligned}$$

Additive genetic covariances in Equation [4] are computed using Equation [2], and environmental covariances using Equation [3]. The intralocus interbreed maternal covariance due to the maternal grandsire, $\text{cov}_n(Y_M,Z_M)^{\text{mgs}}$, is computed as

$$\text{cov}_n(Y_M,Z_M)^{\text{mgs}} = \sum_{i=1}^I t_i (\sigma_{nmXZ})_i + \sum_{i=1}^I \sum_{i'>i}^I t_i t_{i'} (\sigma_{nmXZ})_{ii'} \quad [5]$$

where $t = [p_b^s p_b^d + p_b^s p_b^d]$, $(\sigma_{nmXZ})_i = i^{\text{th}}$ intraconfiguration intralocus interbreed covariance between traits X and Z, $(\sigma_{nmXZ})_{ii'} = ii'^{\text{th}}$ interconfiguration intralocus interbreed covariance, and the subscripts n = nonadditive, m = maternal, i = i^{th} interbreed configuration (e.g., A/B, S/B), and I is the number of different intralocus interbreed configurations in a given multibreed population. The terms intraconfiguration and interconfiguration when referring to nonadditive covariances are equivalent to intrabreed and interbreed when referring to additive covariances.

Factors Affecting the Form of Multibreed Genetic Evaluation Strategies

Definitions of National Multibreed Populations

Probably the most important aspect of multibreed evaluations is the definition of the multibreed populations of interest. Three possibilities are:

- a. **a single multibreed population** comprising all beef breeds and crossbred groups, which implies the existence of a single genetic evaluation for all beef cattle (straightbred and crossbred),
- b. **several overlapping multibreed subpopulations** formed by several breeds and their crossbred groups. Each subpopulation would be evaluated separately. The overlapping could be

constructed with breed groups whose (complete) data would be included in the genetic evaluation of at least two multibreed subpopulations, and

c. **several extended breeds** formed by straightbred bulls and dams of various breed compositions including straightbred; these extended breeds would allow bulls to be evaluated for straight-breeding and crossbreeding purposes.

Genetic Predictions

Three types of Expected Progeny Differences (EPD) can be obtained from the bull genetic predictions of the MGM: additive, nonadditive, and total EPD.

Additive Expected Progeny Differences (AEPD). Expected genetic value of all progeny of a bull mated to dams of various breed groups. There would be one AEPD value for each multibreed population in which a bull is represented.

Nonadditive Expected Progeny Differences (NEPD_{III}). Maximum expected value of intralocus interbreed interactions (III) of a bull mated to dams of several breed groups. There would be one NEPD for each interbreed combination expected to be present in a given crossbred mating. For example, a Simmental (S) bull mated to F1 Angus (A) × Brahman (B) dams would have (i) two intraconfiguration NEPD's: one for S/A intralocus interactions (NEPD_{SA}) and another one for S/B intralocus interactions (NEPD_{SB}), and (ii) one interconfiguration NEPD: one due to differences in the expected values of S/A and S/B intralocus interbreed interactions (NEPD_{SASB}). To predict the NEPD value of a bull mated to dams of a specific breed group (SNEPD), the bull's NEPD values for specific breed combinations need to be weighted by the square root of (i) the probabilities of intralocus interbreed interactions (square root of t values), and (ii) the products of the probabilities of two intralocus interbreed interactions (square root of $t_1 t_2$ values), corresponding to that specific crossbred mating (i.e., $SNEPD = (t_1)^{.5} NEPD_1 + \dots + (t_{(i-1)} t_i)^{.5} NEPD_{NIII}$, where the subscript NIII = number of (intraconfiguration and interconfiguration) intralocus interbreed interactions present in a specific bull × breed-group-of-dam mating). For example, the SNEPD value of the Simmental bull above when mated to .5A .5B dams is equal to $[(1.0)(.5) +$

$(.0)(.5)]^{.5} * NEPD_{SA} + [(1.0)(.5) + (.0)(.5)]^{.5} * NEPD_{SB} + [[(1.0)(.5) + (.0)(.5)] * [(1.0)(.5) + (.0)(.5)]]^{.5} * NEPD_{SASB}$. On the other hand, if this Simmental bull were mated to .5S .5B dams, its SNEPD would be equal to $[(1.0)(.5) + (.0)(.5)]^{.5} * NEPD_{SB}$. The SNEPD could be interpreted as bull "specific combining abilities".

Total Expected Progeny Differences (TEPD). Equal to the sum of AEPD + SNEPD. There would be one TEPD per bull × breed-group-of-dam mating combination. For example, consider the TEPD values of an Angus bull mated to Angus and F1 A × B dams in an Angus-Brahman multibreed population. Assume that the Angus bull has the following EPD values for weaning weight direct: AEPD = 40 lb and $NEPD_{AB} = 30$ lb. Thus, its TEPD values are equal to: i) $40 + [(1.0)(.5) + (.0)(.5)]^{.5}(30) = 40 + 21 = 61$ lb, when mated to F1 A×B dams, and ii) $40 + [(1.0)(1.0) + (.0)(.0)]^{.5}(30) = 40 + 30 = 70$ lb, when mated to Brahman dams.

The potentially large number of NEPD's, SNEPD's, and TEPD's per bull arising from the MGM makes the publication of these predictions impractical. Thus, alternative ways of publishing these genetic evaluations would be needed. Two options for Sire Summaries (within a given multibreed population) could be: 1) to publish only AEPD, and provide (electronically or by hard-copy) NEPD, SNEPD, and TEPD for specific bulls, on request, and 2) to publish AEPD and NEPD for the most frequent mating combinations, and other NEPD, SNEPD, and TEPD for specific bulls, on request.

Genetic Base

The structure of a genetic base will depend on the defined national multibreed populations.

Single multibreed population. In a single multibreed population additive and nonadditive genetic predictions are computed relative to a floating genetic base composed of animals of all breed compositions (i.e., a **multibreed genetic base**). Thus, if a fixed genetic base were to be defined, then it could be composed of bulls of all breed compositions that were born or that entered the stud in a given year.

Several overlapping multibreed subpopulations. Two alternatives could be: (i) to define one or

more breed groups in common to all defined multibreed subpopulations as the **common genetic base**, and (ii) to choose one or several breed groups not entirely in common across multibreed subpopulations as the **reference genetic base**. The first alternative would allow predictions to be computed independently within each multibreed subpopulation. The second alternative would require genetic predictions from some multibreed subpopulations to be readjusted to the reference genetic base.

Several extended breeds. Defining a genetic base for all bulls across extended breeds will probably be difficult. Connections across extended breed would be based on dams and maternal grandsires, rather than sires. Some multibreed herds may be required to be used to connect these extended breeds in order to compare bulls to a reference genetic base. However, these links may not be representative enough of the bulls in each extended breed. Thus, bulls' predictions relative to a reference genetic base may not be very accurate.

Genetic Grouping Strategies

The factors considered for genetic grouping strategies would depend on how multibreed populations were defined.

Single multibreed population. Multibreed procedures for a single multibreed population could use genetic grouping strategies similar to those used in intrabreed procedures. For example, animals could be grouped according to unidentified ancestors using an accumulated grouping strategy for both additive and nonadditive genetic effects.

Several overlapping multibreed subpopulations. If few relationships among animals of different breed groups (especially straightbred groups) exist, particularly with animals in the common or reference base groups, then there may be a need to incorporate **breed group combination** to the grouping strategy for additive genetic effects. Breed group combination would be needed instead of breed group because of the interbreed additive genetic effects that are present in breed groups other than straightbreds and F1 crossbreds. For example, a straightbred Brahman (B) bull belongs to the $B \times B$ breed group combination, and a backcross .75 Angus (A) .25 Brahman (B)

bull, produced by crossbreeding an A bull to a F1 $A \times B$, belongs to the $A \times (A \times B)$ breed group combination. Similarly, **breed group** may need to be incorporated to the grouping strategy for nonadditive genetic effects.

Several extended breeds. Relationships among sires within extended breeds would be similar to those in intrabreed genetic evaluations. Because dams are allowed to be of different breed groups, the degree of relationship among dams and maternal grandsires would probably be less than those existing in intrabreed genetic analyses. Thus, genetic evaluation models would need an accumulated grouping strategy that, in addition to ancestors unidentified, would include breed group composition of the unidentified animals.

Connectedness

Multibreed contemporary groups. Multibreed genetic evaluation procedures require that calves of various breed group combinations are kept under the same environmental conditions. Thus, except for the exclusion of breed group of calf, the definition of contemporary groups for multibreed genetic evaluation procedures is the same as the one for intrabreed genetic evaluation procedures.

Because of the three multibreed scenarios described in A.1. above, two types of connectedness need to be considered: within multibreed populations and across multibreed populations.

Connectedness within multibreed populations. The existence of appropriately connected multibreed contemporary groups will ensure connectedness only if there is a single multibreed population. Straightbred and crossbred bulls could be used to connect multibreed contemporary groups.

Connectedness across multibreed populations. If several multibreed subpopulations are defined, then the problem of connectedness across multibreed subpopulations will have to be solved if bulls are to be compared across all breed groups. One possibility would be to include bulls from one or more breed groups for the purpose of connecting these multibreed subpopulations. For

the case of extended breeds the problem of connectedness is more serious, given that their assumed main interest is the evaluation of straightbred bulls. Here, multibreed contemporary groups which include progeny of bulls of other breeds will need to be constructed if bull comparisons across breeds are to be made.

Estimation of Covariance Components

Complex Multibreed Population

A complex multibreed population is defined as a multibreed population composed of straightbreds, first generation crossbreds, second generation crossbreds and other crossbreds. In a complex multibreed population multibreed additive and environmental covariances are a linear function of both intrabreed and interbreed additive covariances. Thus, intrabreed and interbreed additive and environmental covariances, as well as nonadditive covariances due to intralocus interbreed interactions, would need to be estimated. REML estimates of these covariances in small experimental and simulated complex multibreed data sets have been obtained using a multibreed version of a generalized expectation-maximization (MREMLEM) algorithm. To ensure that estimates of covariance matrices were positive definite, maximization was done with respect to the elements of the Cholesky Decomposition of the covariance matrices. Multicollinearity existed in the set of equations solved in the M-step (MREMLEM equations). To prevent problems of multicollinearity, the diagonal elements of the MREMLEM equations were augmented by a small amount if the condition number (ratio of the smallest to the largest eigenvalues) was smaller than a pre-defined small number (e.g., 10^{-4}). Partial steps were used to ensure that the log-likelihood was increased at each EM iteration. Tables 1 and 2 present examples of these analyses. Table 1 shows estimates of direct and maternal covariances for birth weight from an Angus-Brahman experimental multibreed herd. Table 2 contains means and ranges of covariance estimates, from five small simulated data sets and three sets of covariance priors, for two hypothetical weight traits.

Simple Multibreed Population

A simple multibreed population is one composed of straightbreds and first crosses only. Here, multibreed additive and environmental covariances are linear functions of intrabreed covariances only (the interbreed component of multibreed covariances is zero). Thus, intrabreed additive genetic and environmental covariances, and nonadditive intraconfiguration and interconfiguration intralocus interbreed covariances would only need to be estimated.

Simplifying Assumptions for the Estimation of Multibreed Covariances

Additive and Environmental Covariances. If bulls used for straightbred matings are also used for crossbred matings, then intrabreed additive and environmental covariance estimates could be used in the computation of multibreed additive and environmental covariances.

In complex multibreed populations intrabreed covariance estimates: i) could be used as prior values for multibreed covariance estimation procedures, and ii) could be assumed to be accurate estimates of intrabreed covariances in the multibreed population, and used as part of a reduced multibreed covariance estimation procedure used to estimate only additive and environmental interbreed covariance components, and nonadditive covariance components.

In simple multibreed populations intrabreed covariance estimates could be used to compute all multibreed additive and environmental covariances. Only nonadditive intralocus interbreed covariances would need to be estimated.

Nonadditive Covariances. If the number of breed combinations were too large, beef breeds could be placed into various groups, and covariances due to intralocus interactions within each group could be assumed to be equal. For example, if breeds were grouped according to their population of origin, there could be four major groups: 1) British (B) breeds, 2) Continental (C) breeds, 3) African (A) breeds (predominantly *Bos taurus*), and 4) Zebu (Z) breeds. The number of nonadditive covariance matrices needed would be 10, i.e., BB, BC, BA, BZ, CC, CA, CZ, AA, AZ, and ZZ.

Ranking of bulls by additive, nonadditive, and total EPD

The ranking of bulls by AEPD, SNEPD, and TEPD will **not** necessarily be the same. Table 3 illustrates this point with the rankings of predictions for birth weight direct of Brahman bulls from the Angus-Brahman experimental herd of the University of Florida. The ranking of some Brahman bulls (e.g., 16, 42) changed little or nothing for additive, nonadditive (assume matings to Angus dams), and total EPD. Other Brahman bulls (e.g., 29, 73) showed substantially larger changes in ranking between AEPD and SNEPD, which resulted in moderate changes in their ranking by TEPD. From the point of view of the commercial producers the ranking of bull by TEPD will probably be the most important. The ranking of a bull by TEPD (i) may be higher than its ranking by AEPD because of a high SNEPD value (e.g., bull 43, which went from 3 (AEPD) to 1 (TEPD), Table 3), (ii) may be the same as its AEPD ranking (e.g., bull 42, whose ranking was 2 for AEPD, SNEPD, and TEPD, Table 3), or, (iii) may be lower than its AEPD ranking because of a low SNEPD value (e.g., bull 73, whose ranking fell from 1 (AEPD) to 8 (TEPD), Table 3).

Differences in the ranking of bulls for additive, nonadditive, and total EPD would need to be studied in the defined national multibreed populations. However, the decision to include or ignore nonadditive genetic effects in a national multibreed sire evaluation should depend more on the value of nonadditive predictions than on the reranking of bulls that may occur between AEPD and TEPD.

Implications

Although linear methodology for multibreed genetic evaluation currently exist, it has not been applied to large unbalanced data sets. Additional research is needed 1) to define suitable definitions of (overlapping) multibreed populations, 2) workable models and assumptions, particularly concerning covariance components and random nonadditive effects, 3) efficient computational algorithms for genetic predictions and estimation of large numbers of covariance

components, and 4) develop nonlinear multibreed methodology.

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Table 1. REML covariance estimates for birth weight in an experimental Angus-Brahman multibreed herd

Covariance	Trait pair ^a	Covariance estimate ^b
Additive		
Intrabreed A	(d,d)	15.2
	(d,m)	-2.7
	(m,m)	11.6
Intrabreed B	(d,d)	12.1
	(d,m)	-1.4
	(m,m)	10.5
Interbreed AB	(d,d)	2.8
	(d,m)	-1.7
	(m,m)	17.1
Nonadditive		
Intralocus Interbreed AB	(d,d)	19.0
	(d,m)	.2
	(m,m)	12.5
Environmental		
Intrabreed A	(e,e)	20.4
Intrabreed B	(e,e)	21.1
Interbreed AB	(e,e)	6.6

^ad = direct, m = maternal, and e = environmental.

^bCovariance estimates expressed in kg²

Table 2. Relative means and ranges of REML covariance estimates for direct genetic effects of two traits from five simulated data sets and three sets of preliminary covariance estimates

Covariance	Trait pair	Simulated covariance	Covariance estimate	Covariance range
Additive				
Intrabreed A	(1,1)	4.0	.9 ^a	(.2, 1.8) ^b
	(1,2)	5.0	.9	(.5, 1.6)
	(2,2)	40.0	1.0	(.7, 1.5)
Intrabreed B	(1,1)	8.0	1.0	(.7, 1.5)
	(1,2)	17.0	.9	(.7, 1.1)
	(2,2)	60.0	.8	(.5, 1.2)
Interbreed AB	(1,1)	2.0	1.8	(.1, 4.6)
	(1,2)	4.0	2.2	(-.1, 6.2)
	(2,2)	20.0	2.8	(.0, 5.5)
Nonadditive				
Intralocus				
Interbreed AB	(1,1)	6.0	1.0	(.8, 1.5)
	(1,2)	20.0	1.0	(.8, 1.5)
	(2,2)	80.0	1.0	(.8, 1.3)
Environmental				
Intrabreed A	(1,1)	6.0	1.1	(.7, 1.4)
	(1,2)	4.0	1.2	(.6, 1.8)
	(2,2)	90.0	1.0	(.9, 1.1)
Intrabreed B	(1,1)	22.0	1.0	(.8, 1.1)
	(1,2)	45.0	1.0	(.9, 1.1)
	(2,2)	240.0	1.0	(.9, 1.1)
Interbreed AB	(1,1)	14.0	1.0	(.4, 1.6)
	(1,2)	10.0	1.0	(-.6, 2.1)
	(2,2)	70.0	.9	(.2, 1.8)

^aMean of 15 (covariance estimate/covariance value) ratios.

^b(Smallest, largest) value among 15 (covariance estimate/covariance value) ratios.

Table 3. Ranking of Brahman bulls by predicted total genetic value for birth weight in ascending order

Bull	Number of progeny	BWT ADD ^a	BWT NAD ^b	BWT TOD ^c
43	7	3	1	1
42	10	2	2	2
19	7	5	3	3
61	16	7	2	3
46	14	3	5	4
16	11	4	5	5
70	14	5	5	6
44	10	6	6	7
73	26	1	10	8
54	35	9	4	9
45	8	8	8	10
29	14	12	6	11
17	36	10	7	12
71	29	10	7	12
18	48	11	9	13

^aBWT ADD = birth weigh additive direct.

^bBWT NAD = birth weight nonadditive intralocus interbreed direct.

^cBWT TOD = birth weight total (additive plus nonadditive) direct.