

# COVARIANCES AMONG SIRE BY BREED GROUP OF DAM INTERACTION EFFECTS IN MULTIBREED SIRE EVALUATION PROCEDURES<sup>1</sup>

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## ABSTRACT

In multibreed populations, bulls need to be evaluated for additive and nonadditive genetic effects. When the nonadditive genetic effects associated with a bull are defined as sire  $\times$  breed-group-of-dam interactions, they can be expressed as linear combinations of interactions between alleles of one or more breeds at one or more loci. If these specific allelic interactions are assumed to be independent, then variances and covariances between sire  $\times$  breed-group-of-dam interaction subclasses can be shown to be linear combinations of variances and covariances of specific intra- and interlocus intra- and interbreed allelic interactions. Furthermore, covariances between sire  $\times$  breed-group-of-dam interactions due to specific interactions at one, two, or more loci are zero. If dams are assumed to be unrelated to bulls and among themselves, except through their sires and maternal grandsires, efficient procedures to compute the inverse of the covariance matrices of nonadditive genetic effects can be devised, both in subclass and in regression models. Recursive procedures developed make possible the evaluation of large numbers of bulls for nonadditive genetic effects using mixed-model methodology. For completeness, recursive procedures to compute nonadditive covariance matrices in subclass and in regression models also were developed. The prediction of nonadditive genetic values for bulls, in addition to their additive genetic values, will help plan matings, make selection decisions more accurate and, possibly, make economic projections better.

(Key Words: Mixed-Models, Sire Evaluation, Nonadditive Genetic Variation, Interactions, Crossbreeding, Beef Cattle.)

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## Introduction

The genetic value of a sire in a multibreed population can be defined as the sum of two parts: one affected by additive genetic effects and another affected by nonadditive genetic effects (Elzo and Famula, 1985). The additive genetic component corresponds to the expected progeny difference (EPD) in within-breed sire evaluation procedures. The nonadditive component refers to the interaction between a sire and dams of several breed compositions.

Studies dealing with the evaluation of sire  $\times$  breed-group-of-dam (BGD) interaction effects in cattle have considered them to be either fixed (Koger et al., 1975) or random with a common variance and uncorrelated (Benyshek, 1979; Massey and Benyshek, 1981). The genetic evaluation procedures to evaluate bulls for additive and nonadditive genetic effects in multibreed populations proposed by Elzo and Famula (1985) accounted for covariances among bull additive genetic effects only. Covariances among bull nonadditive genetic effects (i.e., covariances among sire  $\times$  BGD interaction effects) were assumed to be zero in all procedures. This assumption restricted the prediction of nonadditive genetic effects to only those sires that had progeny with records. Accounting for covariances among bull nonadditive genetic effects in these genetic evalua-

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tion procedures will both increase the accuracy of prediction of nonadditive genetic effects for bulls with little information and allow the prediction of these effects for bulls without progeny. For instance, young bulls without progeny will be able to be preselected for progeny testing or for use in specific crosses. Thus, the objectives of this paper are 1) to find a genetic expression for the covariances among sire  $\times$  BGD interaction effects in procedures used to evaluate bulls for nonadditive genetic

effects in multibreed populations, 2) to develop a recursive procedure to compute the covariance matrix of sire  $\times$  BGD interaction effects ignoring inbreeding, and 3) to develop a recursive procedure to compute the inverse of the covariance matrix of sire  $\times$  BGD interaction effects ignoring breeding. This inverse is needed to construct the left-hand side of the mixed-model equations that compute the predictions of additive and nonadditive bull genetic effects in multibreed populations.

#### FINDING GENETIC EXPRESSIONS FOR THE SIRE $\times$ BREED-GROUP-OF-DAM INTERACTION COVARIANCES IN MULTIBREED SIRE EVALUATION PROCEDURES

A multibreed population is defined as one composed of breeding animals of various breeds and crossbred groups or one formed by animals from various distinct subpopulations within a breed. For instance, a population composed of Simmental (S), Brahman (B) and S  $\times$  B crossbreds of various expected S and B fractions is a multibreed population.

Throughout this development, the following assumptions are being made: 1) traits are determined by alleles from a large number of loci, 2) random segregation and assortment of alleles during meiosis, 3) given a sire and dams of breed group, male and female gametes unite at random, 4) there is one progeny per dam in a breed group; if a dam has two or more progeny, they are assumed to come from different dams, 5) dams are unrelated among themselves and to sires (except for relationships among male ancestors of the dams included in the analysis), and 6) constant additive and nonadditive genetic variances and covariances over time.

The formulas to be developed for the covariance matrices of sire  $\times$  BGD interactions in the models considered here account for inbreeding. For the sake of brevity, the recursive procedures that compute these covariance matrices and their inverses ignore inbreeding. However, inbreeding can be accounted for in these procedures in a manner similar to that described by Elzo (1990) for the recursive procedures used to compute the covariance matrix of additive genetic effects and its inverse in multibreed populations.

Multibreed bull evaluation procedures (Elzo and Bradford, 1985; Elzo and Famula, 1985) explicitly account for additive and nonadditive genetic effects. Nonadditive genetic effects are defined as sire  $\times$  BGD interactions. Sire  $\times$  BGD interactions can 1) be considered individually as entire effects (subclass models) or 2) be explained in terms of other parameters (regression models). One alternative is to reparameterize sire  $\times$  BGD interactions in terms of intra- and interlocus interactions among alleles of the same and of different breed origin. The incidence matrix that relates calf records to sire  $\times$  BGD interaction effects in subclass models has a single 1 in the row of a calf pointing at the sire  $\times$  BGD interaction subclass the calf belongs to and zeroes elsewhere. On the other hand, calf records also can be related to intra- and interlocus interactions through probabilities of occurrence of these interactions. Consequently, each row of the incidence matrix relating calf records to intra- and interlocus interactions has at least one (usually several) nonzero value. Elzo and Famula (1985) assumed that the covariance matrix among sire  $\times$  BGD interaction effects in subclass models and in regression models was diagonal. Also, no attempt was made to define the structure of the covariance matrix of sire  $\times$  BGD interaction effects in subclass models. Here, the assumption of diagonality of the sire  $\times$  BGD interaction effects in both subclass and regression models is dropped. Variances of and covariances among sire  $\times$  BGD interaction effects in subclass models are defined in terms of variances of intra- and interlocus interaction effects. Intra- and interlocus interaction effects are assumed to be random and independent of one another and of additive genetic as well as environmental random effects. Thus, the  $n^{\text{th}}$  type of interaction among alleles at  $m$  loci has a mean of zero and a covariance of  $\sigma_{mn}^2$ . Because of the assumption of independence, the matrices of covariances among individual

sire  $\times$  BGD interactions in subclass models and among intra- and interlocus interactions due to individual sires mated to dams of several breed groups in regression models are block diagonal. Each block is a submatrix of variances and covariances due to interaction effects at  $m$  loci,  $m = 1, 2, \dots, M$  loci. In subclass models, a covariance between two sire  $\times$  BGD interaction effects exists when the sires involved received the same alleles at  $m$  loci from a common ancestor and the same interaction among alleles at  $m$  loci occurs in the two sire  $\times$  BGD interaction subclasses. In regression models, a covariance between interactions among alleles at  $m$  loci of two sires mated to several BGD exists when these sires share the same alleles from a common ancestor at  $m$  loci.

Let the expression sire interaction effects equal the sire  $\times$  BGD interaction effects for subclass models and intra- and interlocus interactions among a sire and several BGD for regression models.

In subclass models, the diagonal blocks of covariances among sire interaction effects due to interactions among alleles at  $m$  loci are as follows:

$$V_{mS} = \{ \text{cov} (s_{ik} \times \text{BGD}_j, s_{i'k'} \times \text{BGD}_{j'})_m \}$$

$$V_{mS} = \left\{ \sum_{c=1}^C (a_{ik,i'k',ck''})^m \sum_{n=1}^{N_m} \min (t_{ck''jmn}, t_{ck''j'mn}) \sigma_{mn}^2 \right\} \quad [1]$$

where

- $s_{ik}, s_{i'k'}$  = sire  $k$  from breed group of sires  $i$ , sire  $k'$  from breed group of sires  $i'$ , respectively,
- $\text{BGD}_j, \text{BGD}_{j'}$  = breed groups of dams  $j$  and  $j'$ , respectively,
- $C$  = number of common ancestors between  $s_{ik}$  and  $s_{i'k'}$ ,
- $(a_{ik,i'k',ck''})^m$  = probability that  $s_{ik}$  and  $s_{i'k'}$  received the same alleles at  $m$  loci from common ancestor  $c$  of the  $k''$  breed group ( $s_{ck''}$ ),
- $N_m$  = number of assumed types of interactions among alleles at  $m$  loci,
- $t_{ck''jmn}, t_{ck''j'mn}$  = probabilities of interaction of type  $n$  among alleles of  $m$  loci when alleles from common ancestor  $s_{ck''}$  interact with alleles from  $\text{BGD}_j$  and  $\text{BGD}_{j'}$ , respectively,
- $\min (t_{ck''jmn}, t_{ck''j'mn})$  = smallest value of the two probabilities in brackets, and
- $\sigma_{mn}^2$  = variance of interaction  $n$  among alleles at  $m$  loci.

The expression for  $V_{mS}$  was found by conditioning the covariance between two sire  $\times$  BGD effects on the interaction effects that exist among alleles at  $m$  loci, and applying a theorem that states that given two random variables  $Y$  and  $X$ , the  $\text{var} (Y)$  is equal to the expected value of the variance of  $Y$  given  $X$  plus the variance of the expected value of  $Y$  given  $X$  (Theorem 7, page 159, Mood et al., 1974). Because interaction effects are assumed to be random with a mean of zero, the second term of the covariance between any two sire  $\times$  BGD effects is zero. Thus, covariances between any two sire  $\times$  BGD effects are weighted averages of interaction variances at 1, 2,  $\dots$ ,  $M$  loci. Details of this derivation are given in the appendix.

The term  $(a_{ik,i'k',ck''})^m \min (t_{ck''jmn}, t_{ck''j'mn})$  indicates the expected fraction of interaction of type  $n$  at  $m$  loci among alleles identical by descent received by  $s_{ik}$  and  $s_{i'k'}$  from common ancestor  $s_{ck''}$  and alleles of dams from  $\text{BGD}_j$  and  $\text{BGD}_{j'}$  that is expected to exist in the respective progenies of  $s_{ik} \times \text{BGD}_j$  and  $s_{i'k'} \times \text{BGD}_{j'}$ .

The complete covariance matrix of sire interaction effects due to interactions at 1, 2,  $\dots$ ,  $M$  loci, for subclass models is  $V_S = \text{block diagonal} \{V_{mS}\}$ ,  $m = 1, 2, \dots, M$ .

In regression models, the diagonal blocks of covariances among sire interaction effects among alleles at  $m$  loci are:

$$\begin{aligned}
 V_{mR} &= \{ \text{cov} (v_{ikmn}, v_{i'k'mn}) \} \\
 &= \left\{ \sum_{c=1}^C (a_{ik,i'k',ck'})^m \right\} * V_{m0} \\
 &= A_m * V_{m0}
 \end{aligned}
 \tag{2}$$

where

$v_{ikmn}, v_{i'k'mn}$  = interactions of type  $n$  among alleles at  $m$  loci due to the interaction of alleles of sires  $ik$  and  $i'k'$ , respectively, and dams of several BGD,  
 $V_{m0}$  = diagonal ( $\sigma_{mn}^2$ ), and  
 $*$  = direct product (Searle, 1966).

The complete matrix of covariances among sire interaction effects at 1, 2, . . . ,  $M$  loci, for regression models, is  $V_R$  = block diagonal  $\{V_{mR}\}$ ,  $m = 1, 2, . . . , M$ .

Notwithstanding the relationships that exist between subclass and regression models, they are not equivalent models (Henderson, 1984) because their respective covariance matrices of sire interaction effects are different. Let  $Z_S u_S$  and  $Z_R u_R$  be the parts of the subclass and regression models related to sire interaction effects, where  $Z_S$  is a known incidence matrix relating calf records to sire  $\times$  BGD interaction effects in vector  $u_S$  and  $Z_R$  is a known incidence matrix relating calf records to intra- and interlocus interaction effects in vector  $u_R$ , through probabilities of occurrence of these interactions (Elzo and Famula, 1985). Thus,  $\text{var} (Z_S u_S) = Z_S V_S Z_S'$ , where  $V_S$  = block diagonal  $\{V_{mS}\}$ , and  $\text{var} (Z_R u_R) = Z_R V_R Z_R'$ , where  $V_R$  = block diagonal  $\{V_{mR}\}$ . Each covariance term in  $Z_S V_S Z_S'$  is a linear function of the  $t_{ikjmn}$  and each term of  $Z_R V_R Z_R'$  is a linear function of the square of the  $t_{ikjmn}$ . Thus, the subclass and the regression models are not equivalent. Consequently, the error variances of prediction of sire  $\times$  BGD interaction effects predicted by these two models are likely to be different in most cases. Assuming that the nonadditive effects in a regression model account for all nonadditive effects in a sire  $\times$  BGD interaction, if the number of nonadditive effects in a regression model is less than the number of sire  $\times$  BGD interaction effects in a subclass model, then the error variances of prediction of the sire  $\times$  BGD interaction effects predicted using a regression model probably will be at least as accurate as those from a subclass model. More research is needed on this subject.

The description of subclass and regression approaches above suggests that many definitions of interactions might be devised to suit these models. For example, alleles could be categorized by function (e.g., structural and regulatory), by breed of origin (e.g., Simmental and Brahman), by a combination of the two, and so on. Here, alleles are categorized by breed of origin to explain the covariance matrices among sire interaction effects of subclass ( $V_S$ ) and regression ( $V_R$ ) models in more applied terms. For simplicity, this description considers the case of two breeds (e.g., S and B) and interactions among alleles of the same and of different breeds at one and at two loci only. Extension to more than two breeds and more than two loci is straightforward.

Let  $v_{ikmn}$  be interaction of type  $n$  among alleles of  $m$  loci of the  $k^{\text{th}}$  sire of the  $i^{\text{th}}$  breed group of sires ( $s_{ik}$ ) and alleles of  $m$  loci of dams from breed groups of various expected fractions of S and B (e.g., 1S 0B, .75S .25B, .5S .5B, .25S .75B, 0S 1B) at  $m$  loci.

Let  $t_{ikjmn}$  be the probability that interaction of type  $n$  among alleles of  $m$  loci occurs when  $s_{ik}$  is mated to dams of the  $j^{\text{th}}$  breed group (BGD $_j$ ).

Thus,

1) the  $v_{ikmn}$  and the  $t_{ikjmn}$  for one-locus ( $m = 1$ ) interactions could be defined, for example, as follows:

$v_{ik11}$  = interaction effect between S alleles from  $s_{ik}$  and S alleles from dams of all breed groups mated to  $s_{ik}$  at one locus,  
 $v_{ik12}$  = interaction effect between S alleles from  $s_{ik}$  and B alleles from dams of all breed groups mated to  $s_{ik}$ , or vice versa, at one locus,

$v_{ik13}$  = interaction effect between B alleles from  $s_{ik}$  and B alleles from dams of all breed groups mated to  $s_{ik}$  at one locus.

Associated with every  $v_{ikmn}$  there is a set of  $t_{ikjmn}$ , one for each group of dams that was mated to or potentially mated to  $s_{ik}$ . The  $t_{ikjmn}$  for one locus are:

$$\begin{aligned} t_{ikj11} &= \text{probability of } v_{ik11} \text{ when } s_{ik} \text{ is mated to } BGD_j, \\ &= p_{ik}(S) p_j(S), \end{aligned} \quad [3]$$

$$\begin{aligned} t_{ikj12} &= \text{probability of } v_{ik12} \text{ when } s_{ik} \text{ is mated to } BGD_j, \\ &= p_{ik}(S) p_j(B) + p_{ik}(B) p_j(S), \end{aligned} \quad [4]$$

$$\begin{aligned} t_{ikj13} &= \text{probability of } v_{ik13} \text{ when } s_{ik} \text{ is mated to } BGD_j, \\ &= p_{ik}(B) p_j(B), \end{aligned} \quad [5]$$

where

$p_{ik}(S)$  = probability of alleles of breed S in  $s_{ik}$ ,  
 $p_{ik}(B)$  = probability of alleles of breed B in  $s_{ik}$ ,  
 $p_j(S)$  = probability of alleles of breed S in  $BGD_j$ ,  
 $p_j(B)$  = probability of alleles of breed B in  $BGD_j$ ,

2) the  $v_{ikmn}$  and the  $t_{ikjmn}$  for the possible allelic interactions occurring simultaneously among the alleles at two loci ( $m = 2$ ) could be defined, for example, as follows:

$v_{ik21}$  = interaction effect among two S alleles at two loci from  $s_{ik}$  and two S alleles at two loci from dams of all breed groups mated to  $s_{ik}$  at two loci,

$v_{ik22}$  = interaction effect among two S alleles at two loci from  $s_{ik}$  and two B alleles at two loci from dams of all breed groups mated to  $s_{ik}$ , or vice versa,

$v_{ik23}$  = interactions effect among two S alleles at two loci from  $s_{ik}$  and a S allele at one locus and a B allele at another locus from dams of all breed groups mated to  $s_{ik}$ , or vice versa,

$v_{ik24}$  = interactions effect among two B alleles at two loci from  $s_{ik}$  and a S allele at one locus and a B allele at another locus from dams of all breed groups mated to  $s_{ik}$ , or vice versa,

$v_{ik25}$  = interactions effect among a S allele at one locus and a B allele at another locus from  $s_{ik}$  and a S allele at one locus and a B allele at another locus from dams of all breed groups mated to  $s_{ik}$ ,

$v_{ik26}$  = interactions effect among B alleles from  $s_{ik}$  and B alleles from dams of all breed groups mated to  $s_{ik}$  at two loci.

The probabilities of occurrence of the  $v_{ik2n}$  when  $s_{ik}$  is mated to  $BGD_j$ , i.e., the  $t_{ikj2n}$ ,  $n = 1, \dots, 6$ , are:

$$\begin{aligned} t_{ikj21} &= \text{probability of } v_{ik21} \text{ when } s_{ik} \text{ is mated to } BGD_j, \\ &= [p_{ik}(S)]^2 [p_j(S)]^2, \end{aligned} \quad [6]$$

$$\begin{aligned} t_{ikj22} &= \text{probability of } v_{ik22} \text{ when } s_{ik} \text{ is mated to } BGD_j, \\ &= [p_{ik}(S)]^2 [p_j(B)]^2 + [p_{ik}(B)]^2 [p_j(S)]^2, \end{aligned} \quad [7]$$

$$\begin{aligned} t_{ikj23} &= \text{probability of } v_{ik23} \text{ when } s_{ik} \text{ is mated to } BGD_j, \\ &= [p_{ik}(S)]^2 [2p_j(S)p_j(B)] + [p_j(S)]^2 [2p_{ik}(S)p_{ik}(B)], \end{aligned} \quad [8]$$

$$\begin{aligned} t_{ij24} &= \text{probability of } v_{ik24} \text{ where } s_{ik} \text{ is mated to } BGD_j, \\ &= [p_{ik}(B)]^2 [2p_j(S)p_j(B)] + [p_j(B)]^2 [2p_{ik}(S)p_{ik}(B)], \end{aligned} \quad [9]$$

$$\begin{aligned} t_{ikj25} &= \text{probability of } v_{ik25} \text{ when } s_{ik} \text{ is mated to } BGD_j, \\ &= 4[p_{ik}(S)p_{ik}(B)][p_j(S)p_j(B)], \end{aligned} \quad [10]$$

$$\begin{aligned} t_{ikj26} &= \text{probability of } v_{ik26} \text{ when } s_{ik} \text{ is mated to } BGD_j, \\ &= [p_{ik}(B)]^2 [p_j(B)]^2. \end{aligned} \quad [11]$$

The definitions of interaction effects for one locus and for two loci lumped reciprocal interbreed interactions effects together. Had reciprocal interbreed interaction effects been considered separately, the number of one locus and two loci interaction effects would have increased to 4 and 10, respectively.

Although it may be desirable to define six interaction effects from a research standpoint to study and try to understand sire  $\times$  BGD interactions better, from a sire evaluation point of view this may be unnecessary. The objective of evaluating bulls for nonadditive effects is to predict the total interactive value of a bull when mated to groups of dams of various breed compositions. To accomplish this goal a number of interaction effects among alleles at two loci smaller than six could be used. This involves redefining the interaction effects at two loci. Given a set of data, a smaller number of interaction effects will be less descriptive, but they will be predicted more accurately. A set of three interaction effects at two loci could be defined. Two of them,  $v_{ik21}$  and  $v_{ik26}$ , would be defined as before, except that  $v_{ik26}$  would now be named  $v_{ik23}$ . The second interaction effect at two loci,  $v_{ik22}$ , would now be defined to be due to interactions among S and(or) B alleles from  $s_{ik}$  and S and(or) B alleles from dams of all breed groups mated to  $s_{ik}$ , with the condition that there is at least one S allele from  $s_{ik}$  and at least one B allele from the dams mated to  $s_{ik}$ , or vice versa. The probabilities for occurrence of these redefined interactions at two loci,  $v_{ik2n}$ ,  $n = 1, 2, 3$ , are as follows: 1)  $t_{ikj21} = \text{formula [6]}$ , 2)  $t_{ikj23} = \text{formula [11]}$ , and 3)  $t_{ikj22} = 1 - t_{ikj21} - t_{ikj23}$ . Considering the three intralocus interaction effects and the three interlocus interaction effects at two loci, the  $V_{m0}$  matrices are as follows:  $V_{10} = \text{diagonal } \{\sigma_{11}^2, \sigma_{12}^2, \sigma_{13}^2\}$  and  $V_{20} = \text{diagonal } \{\sigma_{21}^2, \sigma_{22}^2, \sigma_{23}^2\}$ .

The  $\{\sigma_{mn}^2\}$ ,  $m = 1, 2$ ,  $n = 1, 2, 3$ , would be used to construct  $V_{mR}$  in regression models and  $V_{mS}$  in subclass models. Again, extension to more than two breeds is simple, although computations become more involved, especially in large, unbalanced data sets; hence, there is a need for efficient computational procedures to build  $V_R$  and  $V_S$ . More important, however, is the need for fast procedures to compute the inverses of  $V_R$  and  $V_S$ , which are needed to construct the mixed-model equations (MME) for regression and for subclass models, respectively. These inverses will be difficult (or impossible) to obtain in large data sets, given current computer capabilities. Thus, recursive procedures to compute directly the matrices of intralocus and interlocus variances and covariances as well as their inverses were developed. These recursive procedures have a pattern of computations similar to those procedures developed for additive genetic effects in populations of one breed (Emik and Terrill, 1949; Van Vleck, 1974; Henderson, 1975, 1976) and for multibreed populations (Elzo, 1990).

#### RECURSIVE PROCEDURES TO COMPUTE THE MATRIX OF SIRE $\times$ BREED-GROUP-OF-DAM INTERACTION VARIANCES AND COVARIANCES IN SUBCLASS AND IN REGRESSION MODELS

The recursive procedures described below permit the computation of submatrices  $V_{mS}$  and  $V_{mR}$  directly when inbreeding is ignored. If inbreeding were accounted for, only the computation of the diagonal blocks of  $V_{mS}$  and  $V_{mR}$  would need to be modified. The computation of the offdiagonal blocks of  $V_{mS}$  and  $V_{mR}$  would not change.

Each of the  $V_{mS}$  and  $V_{mR}$ ,  $m = 1, \dots, M$ , submatrices is computed separately. The procedure used to compute the submatrices  $V_{mS}$  for subclass models is described first, followed by the one developed to compute the  $V_{mR}$  for regression models.

#### *Recursive Procedure to Compute the $V_{mS}$ for Subclass Models*

This procedure requires knowledge of the expected breed composition of the bulls and the breed groups of dams. If male ancestors of these bulls (i.e. sires and maternal grandsires) are known, their expected breed composition also is needed. In addition, the nonadditive variances due to the interaction among alleles at  $m$  loci, that is, the  $\{\sigma_{mn}^2\}$ ,  $n = 1, \dots, N_m$ ,  $m = 1, \dots, M$ ,

must be known.

All bulls are evaluated for their interaction with dams of all breed groups considered, whether or not actual matings did or will occur. Base animals (Henderson, 1976) are assumed to be unrelated, noninbred and of known breed composition.

The recursive procedure to compute  $V_{mS}$  has the following steps:

1. Identify:

- a) bulls to be evaluated in chronological order, from oldest (1) to youngest ( $n_b$ ),
- b) the sire and the maternal grandsire of each bull (store a zero when any of them is unknown),
- c) the breed group of bulls and their sires and maternal grandsires as well as the expected breed composition of each breed group.

2. Compute:

- a)  $(V_{mS})_{ik,ik}$ ,  $i = 1, \dots, I$ ,  $k = 1, \dots, K_i$ ,  $I =$  number of bull breed groups,  $K_i =$  number of bulls in the  $i^{\text{th}}$  breed group. Because inbreeding is being ignored, all bulls belonging to breed group  $i$ ,  $i = 1, \dots, I$ , have the same nonadditive covariance matrix. Thus, only  $I$  matrices of order  $J \times J$  need to be computed, where  $J$  is the number of dam breed groups. These matrices contain the nonadditive variances ( $\sigma_{ij}^2$ ) and covariances ( $\sigma_{ij,j'}$ ) due to the mating of bulls of breed group  $i$ ,  $i = 1 \dots, I$ , to dams of all breed groups, i.e.,  $j, j' = 1, \dots, J$ . The  $\sigma_{ij}^2$  and the  $\sigma_{ij,j'}$  are computed using formula [1]. To find the  $(V_{mS})_{ik,ik}$  simply make the  $ik^{\text{th}}$  diagonal block of  $V_{mS}$  equal to the nonadditive covariance matrix for bulls of the  $i^{\text{th}}$  breed group. To simplify notation, let  $u$  be the  $k^{\text{th}}$  bull from the  $i^{\text{th}}$  breed group. So, for instance,  $(V_{mS})_{uu} =$

$$(V_{mS})_{ik,ik}. \text{ Also, let } U = \sum_{i=1}^I K_i.$$

- b)  $(V_{mS})_{uu'}$ ,  $u = 1, \dots, U$ ,  $u \neq u'$ . The computation of these  $J \times J$  offdiagonal blocks of  $V_{mS}$  will depend on whether the sire and(or) the maternal grandsire of bull  $u'$  are identified. Thus,

- i) when the sire ( $s'$ ) and the maternal grandsire ( $g'$ ) of bull  $u'$  are identified, the offdiagonal blocks of  $V_{mS}$  are computed as:

$$(V_{mS})_{uu'} = (.5)^m (V_{mS})_{us'} + (.25)^m (V_{mS})_{ug'} \quad [12]$$

- ii) when only  $s'$  is identified, the offdiagonal blocks of  $V_{mS}$  are computed as:

$$(V_{mS})_{uu'} = (.5)^m (V_{mS})_{us'} \quad [13]$$

- iii) when only  $g'$  is identified, the offdiagonal blocks of  $V_{mS}$  are computed as:

$$(V_{mS})_{uu'} = (.25)^m (V_{mS})_{ug'} \quad [14]$$

and

- iv) when neither  $s'$  nor  $g'$  is identified, the elements of the offdiagonal blocks of  $V_{mS}$  are equal to zero.

The order of the resulting symmetric matrix  $V_{mS}$  is  $JU$ .

### *Recursive Procedure to Compute the $V_{mR}$ for Regression Models*

The same prior information required to compute the  $V_{mS}$  for subclass models must be known to compute the  $V_{mR}$  for regression models. Thus, there should be information on i) the expected breed composition of bulls and their known male ancestors as well as the dam breed groups mated to them, and ii) the values of the nonadditive variances due to the interaction among alleles at  $m$  loci.

In nonadditive regression models, however, bulls are evaluated for specific nonadditive effects rather than for linear combinations of them as in nonadditive subclass models. This fact facilitates the computation of the  $V_{mR}$  tremendously because specific nonadditive genetic effects are defined to be uncorrelated. Thus,  $V_{mR}$  is equal to the direct product of  $A_m$  and  $V_{m0}$ , where  $A_m$  is as defined in formula [2] and  $V_{m0}$  is a diagonal matrix of specific nonadditive effects

among alleles at  $m$  loci. Because  $V_{m0}$  is the same for all bulls,  $V_{mR}$  could be formed by first computing  $A_m$ , and then computing the direct product of  $A_m * V_{m0}$ . A second alternative would be to follow the rules given for the subclass model with the provision that all  $(V_{mS})_{uu}$  are equal to  $V_{m0}$ . For completeness, the first alternative will be outlined. The steps are:

1. Identify animals (bulls, sires, maternal grandsires), their breed groups and their expected breed composition as indicated in step 1 of the procedure for subclass models.
2. Compute  $A_m$ .
  - a. Store a 1 in the diagonal elements of  $A_m$ , i.e., place a 1 in  $(a_m)_{uu}$ ,  $u = 1, \dots, U$ .
  - b. Calculate the offdiagonal elements of  $A_m$ , i.e., the  $(a_m)_{uu'}$ ,  $u = 1, \dots, U$ ,  $u' \neq u$ , as follows:
    - i) if the sire of bull  $u'$  ( $s'$ ) and the maternal grandsire of bull  $u'$  ( $g'$ ) are known, then compute the offdiagonal elements of  $A_m$  as follows:
 
$$(a_m)_{uu'} = (.5)^m (a_m)_{us'} + (.25)^m (a_m)_{ug'} \quad [15]$$
    - ii) if only  $s'$  is identified, then the offdiagonal elements of  $A_m$  are computed as follows:
 
$$(a_m)_{uu'} = (.5)^m (a_m)_{us'} \quad [16]$$
    - iii) if only  $g'$  is known, then the offdiagonal elements of  $A_m$  are computed as follows:
 
$$(a_m)_{uu'} = (.25)^m (a_m)_{ug'} \quad [17]$$
 and
    - iv) if neither  $s'$  nor  $g'$  are known, then  $(a_m)_{uu'} = 0$ .

The rules to compute  $A_m$  reduce to the well-known rules to compute  $A$  (Emik and Terrill, 1949; Van Vleck, 1974; Henderson, 1976) when the number of loci considered for regression models is one.

3. Compute  $V_{mR}$  by multiplying each element of  $A_m$  by  $V_{m0}$ . The order of  $V_{mR}$  is equal to  $PU$ , where  $P =$  order of matrix  $V_{m0} =$  number of specific nonadditive genetic effects among alleles at  $m$  loci.

**RECURSIVE PROCEDURES TO COMPUTE THE INVERSE OF THE MATRIX  
OF SIRE  $\times$  BREED-GROUP-OF-DAM INTERACTION VARIANCES AND COVARIANCES  
IN SUBCLASS AND IN REGRESSION MODELS**

Because the matrices  $V_S$  and  $V_R$  are block diagonal, with diagonal blocks equal to  $V_{mS}$  and  $V_{mR}$ , computation of their inverses amounts to obtaining the inverse of each of the  $V_{mS}$  and the  $V_{mR}$ ,  $m = 1, \dots, M$ , respectively. Let  $C_{mS}$  be the inverse of  $V_{mS}$  and  $C_{mR}$  be the inverse of  $V_{mR}$ , for  $m = 1, \dots, M$ . The procedure to compute the  $C_{mS}$  is described first, followed by the one to compute  $C_{mR}$ . Inbreeding is ignored in these procedures. If inbreeding were accounted for, it would affect only the coefficients used by the rules to compute  $C_{mS}$  and  $C_{mR}$ . The rules would remain the same. Only the formulas and the procedures used to compute these coefficients would change.

*Recursive Procedure to Compute the  $C_{mS}$  for Subclass Models*

The procedure to compute the  $C_{mS}$  requires the same type of information to be known as that for the procedure to calculate  $V_{mS}$ . In addition, the diagonal blocks of  $V_{mS}$  corresponding to each breed group of bulls must be obtained in advance. These matrices are computed as explained in step 2.a) of the procedure to construct  $V_{mS}$ .

- The rules used to compute  $C_{mS}$  depend on the male ancestors identified for each bull. Thus,
- i) when the sire ( $s$ ) and the maternal grandsire ( $g$ ) of bull  $u$  are known, add:



$$\begin{aligned}
 & D_{\text{mu}}^{-1} \text{ to } (C_{\text{mS}})_{\text{uu}} \\
 & (.25)^{\text{m}} D_{\text{mu}}^{-1} \text{ to } (C_{\text{mS}})_{\text{ss}} \\
 & (.0625)^{\text{m}} D_{\text{mu}}^{-1} \text{ to } (C_{\text{mS}})_{\text{gg}} \\
 & (.125)^{\text{m}} D_{\text{mu}}^{-1} \text{ to } (C_{\text{mS}})_{\text{sg}}, (C_{\text{mS}})_{\text{gs}} \\
 & - (.5)^{\text{m}} D_{\text{mu}}^{-1} \text{ to } (C_{\text{mS}})_{\text{us}}, (C_{\text{mS}})_{\text{su}} \\
 & - (.25)^{\text{m}} D_{\text{mu}}^{-1} \text{ to } (C_{\text{mS}})_{\text{ug}}, (C_{\text{mS}})_{\text{gu}}
 \end{aligned}$$

where  $D_{\text{mu}}^{-1}$  is computed as:

$$D_{\text{mu}}^{-1} = [(V_{\text{mS}})_{\text{uu}} - (.25)^{\text{m}}(V_{\text{mS}})_{\text{ss}} - (.0625)^{\text{m}}(V_{\text{mS}})_{\text{gg}}]^{-1}, \quad [18]$$

ii) when only s is known, add:

$$\begin{aligned}
 & D_{\text{mu}}^{-1} \text{ to } (C_{\text{mS}})_{\text{uu}} \\
 & (.25)^{\text{m}} D_{\text{mu}}^{-1} \text{ to } (C_{\text{mS}})_{\text{ss}} \\
 & - (.5)^{\text{m}} D_{\text{mu}}^{-1} \text{ to } (C_{\text{mS}})_{\text{us}}, (C_{\text{mS}})_{\text{su}}
 \end{aligned}$$

where  $D_{\text{mu}}^{-1}$  is computed as:

$$D_{\text{mu}}^{-1} = [(V_{\text{mS}})_{\text{uu}} - (.25)^{\text{m}}(V_{\text{mS}})_{\text{ss}}]^{-1}, \quad [19]$$

iii) when only g is known, add:

$$\begin{aligned}
 & D_{\text{mu}}^{-1} \text{ to } (C_{\text{mS}})_{\text{uu}} \\
 & (.0625)^{\text{m}} D_{\text{mu}}^{-1} \text{ to } (C_{\text{mS}})_{\text{gg}} \\
 & - (.25)^{\text{m}} D_{\text{mu}}^{-1} \text{ to } (C_{\text{mS}})_{\text{ug}}, (C_{\text{mS}})_{\text{gu}}
 \end{aligned}$$

where  $D_{\text{mu}}^{-1}$  is computed as:

$$D_{\text{mu}}^{-1} = [(V_{\text{mS}})_{\text{uu}} - (.0625)^{\text{m}}(V_{\text{mS}})_{\text{gg}}]^{-1}, \quad [20]$$

and

iv) when neither s nor g are known, add:

$$D_{\text{mu}}^{-1} \text{ to } (C_{\text{mS}})_{\text{uu}}$$

where  $D_{\text{mu}}^{-1}$  is computed as:

$$D_{\text{mu}}^{-1} = [(V_{\text{mS}})_{\text{uu}}]^{-1}. \quad [21]$$

The matrices  $D_{\text{mu}}^{-1}$  and the  $(V_{\text{mS}})_{\text{xx}}$ ,  $x = u, s, g$ , are of order  $J \times J$ ,  $J =$  number of dam breed groups.

### *Recursive Procedure to Compute the $C_{\text{mR}}$ for Regression Models*

The same assumptions and prior data needed to compute  $V_{\text{mR}}$  apply to the computation of  $C_{\text{mR}}$ . Because  $V_{\text{mR}}$  can be written as a direct product of two matrices (i.e.,  $A_{\text{m}} * V_{\text{m0}}$ ), its inverse (Searle, 1966) is equal to  $(A_{\text{m}})^{-1} * (V_{\text{m0}})^{-1}$ . The matrix  $(V_{\text{m0}})^{-1}$  is computed by direct inversion of  $V_{\text{m0}}$ . Let  $B_{\text{m}}$  be  $(A_{\text{m}})^{-1}$ . The rules used to compute  $B_{\text{m}}$  are as follows:

i) if the sire (s) and the maternal grandsire (g) of bull u are known, add:

$$\begin{aligned}
 & d_{mu}^{-1} \text{ to } (b_m)_{uu} \\
 (.25)^m d_{mu}^{-1} & \text{ to } (b_m)_{ss} \\
 (.0625)^m d_{mu}^{-1} & \text{ to } (b_m)_{gg} \\
 (.125)^m d_{mu}^{-1} & \text{ to } (b_m)_{sg}, (b_m)_{gs} \\
 -(.5)^m d_{mu}^{-1} & \text{ to } (b_m)_{us}, (b_m)_{su} \\
 -(.25)^m d_{mu}^{-1} & \text{ to } (b_m)_{ug}, (b_m)_{gu}
 \end{aligned}$$

where

$$d_{mu}^{-1} = [1 - (.25)^m - (.0625)^m]^{-1},$$

ii) if only  $s$  is known add:

$$\begin{aligned}
 & d_{mu}^{-1} \text{ to } (b_m)_{uu} \\
 (.25)^m d_{mu}^{-1} & \text{ to } (b_m)_{ss} \\
 -(.5)^m d_{mu}^{-1} & \text{ to } (b_m)_{us}, (b_m)_{su}
 \end{aligned}$$

where

$$d_{mu}^{-1} = [1 - (.25)^m]^{-1},$$

iii) if only  $g$  is known, add:

$$\begin{aligned}
 & d_{mu}^{-1} \text{ to } (b_m)_{uu} \\
 (.0625)^m d_{mu}^{-1} & \text{ to } (b_m)_{gg} \\
 -(.25)^m d_{mu}^{-1} & \text{ to } (b_m)_{ug}, (b_m)_{gu}
 \end{aligned}$$

where

$$d_{mu}^{-1} = [1 - (.0625)^m]^{-1},$$

and

iv) if neither  $s$  nor  $g$  is known, add:

$$1 \text{ to } (b_m)_{uu}.$$

After the contribution of all bulls are added,  $B_m$  is complete. Next, each nonzero element of  $B_m$  is multiplied by the matrix  $(V_{m0})^{-1}$ . The matrix resulting from this direct product is  $C_{mR}$ .

The rules to compute  $(A_m)^{-1}$  directly are a generalization of those given by Henderson (1975) to compute  $A^{-1}$  for sires and maternal grandsires in a noninbred population. Thus, when  $m = 1$ ,  $(A_m)^{-1}$  becomes  $A^{-1}$ , the computational rules given above become those of Henderson (1975).

## DISCUSSION

Traditionally, within-breed sire evaluation procedures have emphasized additive genetic effects. Random nonadditive genetic effects usually are assumed to be negligible. This assumption may not be true in multibreed populations or when bulls of some breed or crossbred group are mated to dams of several breeds or crossbred groups. Benyshek (1979) and Massey and Benyshek (1981) found significant sire  $\times$  BGD interactions for various growth traits (e.g., birth weight, adjusted 205-d weaning weight, adjusted 365-d weight) when Limousin sires were mated to Hereford or Angus dams. Estimates of sire  $\times$  BGD interaction variances (.24% to 4% of the total variance) generally were smaller than estimates of sire additive genetic variances (1.5% to 6.5% of the total variance). The correlation between breeding values of sires for the same trait

across breeds ranged from .46 to .85, indicating the possibility of changes in sire ranking across breed group of dam and of selection errors. In cases like this, and depending on the objectives of the evaluation and the structure and number of data, a subclass or a regression model containing nonadditive as well as additive genetic effects should be used in the best linear unbiased prediction (BLUP) procedure to evaluate bulls. The recursive procedures of this paper facilitate the computation of the inverses of the matrices of nonadditive effects at one or more loci needed for the MME in subclass and in regression multibreed bull evaluation procedures. However, solving the MME still remains a formidable task, especially in subclass models. The evaluations of a bull for its nonadditive genetic values when mated to dams of several breed groups are treated as different traits in the subclass model. Also, these "traits" are correlated within  $m$  loci (i.e., the same type of nonadditive effects at  $m$  loci may exist in subclasses  $s_{ik} \times BGD_j$  and  $s_{ik} \times BGD_j$ ). In regression models, on the other hand, the "traits" are specific nonadditive effects at  $m$  loci. These specific nonadditive effects are uncorrelated within and across  $m$  loci. Thus, the number of nonzero elements to be added to the MME is smaller than in subclass models, but still it is large.

These computational considerations strongly suggest the need to use simplifying assumptions. In subclass models, broader ranges might be used to define breed groups. For instance, only three breed groups might be defined in a multibreed population of Simmental and Brahman: group 1 = (0 to .3)S (1 to .7)B, group 2 = (.31 to .70)S (.69 to .30)B and group 3 = (.71 to 1)S (.29 to 0)B. In regression models, interbreed nonadditive effects at  $m$  loci,  $m \leq 2$ , might be considered only. Estimates of group intralocus nonadditive genetic effects have been found to produce reasonably accurate estimates of breed-group-of-sire  $\times$  BGD interactions for several growth traits (Dillard et al., 1980; Kress et al., 1986; Elzo et al., 1990) and milk traits (Robison et al., 1981). Perhaps the inclusion of nonadditive effects at one locus might be sufficient to account for random sire  $\times$  BGD interaction effects as well. These assumptions reduce the number of nonadditive genetic matrices to be inverted to three in the subclass model and to two in the regression model if intralocus intrabreed interactions are assumed to have the same variance. The three predictions of bull nonadditive effects in subclass models will reflect the combined effect of all intralocus interactions present in each sire  $\times$  BGD subclass. In regression models, on the other hand, bulls will have predictions of their total nonadditive intralocus intrabreed and interbreed genetic effects. Linear combinations of these predicted values using the  $t_{ikjmn}$  yield predictions of specific sire  $\times$  BGD nonadditive effects.

These recursive procedures can be used in multibreed populations with any number of base breeds. The  $t_{ikjmn}$  will need to be redefined according to the assumptions made with respect to intra- and interlocus interactions among alleles of one or more breeds at one or more loci. The number of nonadditive genetic variances and covariances needed will also depend on the assumptions made.

If sires of a particular breed (e.g., Simmental) are used on dams of various breeds to produce market animals only, a subclass model could be appropriate. But, if animals of several breeds are mated to create a multibreed population (e.g., Simbrah), then a regression model seems reasonable. The recursive procedures of this paper allow the consideration of all covariances among sire  $\times$  BGD interaction effects both in regression and in subclass models. Accounting for these covariances not only increases the accuracy of prediction of nonadditive genetic effects but also allows one to obtain preliminary evaluations for bulls without progeny (e.g., young bulls) or for bulls mated within a breed and related to bulls also used in crossbred matings.

The definition of sire  $\times$  BGD interaction covariances and the recursive procedures to compute the matrices of sire  $\times$  BGD interaction effects, developed in this research, make the evaluation of large numbers of bulls for nonadditive genetic effects feasible. These procedures complement those developed for additive genetic effects in multibreed populations (Elzo, 1990) and help make possible the construction of MME for multibreed sire evaluation procedures. Because multibreed sire evaluation procedures yield predictions of direct and maternal additive and nonadditive bull genetic effects, they are useful in cases of semen importation, crossbreeding mating schemes, formation of new breeds and evaluation of bulls for crossbred matings. Within-breed or across-breeds sire summaries containing predictions of sire additive genetic values and sire nonadditive genetic values when sires are mated to dams of various breed groups could be

published. These summaries would be of help in making selection decisions and mating plans within and between breeds as well as economic projections.

#### NUMERICAL EXAMPLE

The recursive procedures to compute  $V_S$  and  $V_R$  will be illustrated with a small hypothetical example. Only two breeds (S and B) and a single trait are considered. It is assumed that bulls are mated to dams of two breed groups: 1S 0B and .5S .5B. Only interactions between alleles at one locus and at two loci are assumed to be important. Furthermore, intralocus and two-locus interactions among alleles of the same breed are assumed to have equal variance and are treated as a single effect. Thus, there are four nonadditive effects: 1) intralocus intrabreed interactions with variance  $\sigma_{11}^2 = 12$ , 2) intralocus interbreed interactions with variance  $\sigma_{12}^2 = 16$ , 3) two-locus intrabreed interactions with variance  $\sigma_{21}^2 = 10$ , and 4) two-locus interbreed interactions with variance  $\sigma_{22}^2 = 14$ .

#### *Computation of $V_S$ and $V_S^{-1}$ for Subclass Models*

There are four nonadditive effects per bull. The first two correspond to single-locus interactions resulting from the mating of bulls to 1S 0B dams and .5S .5B dams, and the second two refer to the two-locus interactions produced by these same two types of matings.

Table 1 shows the structure of the data for the example. Also, Table 1 displays the intralocus and two-locus interaction variances and covariances of bulls 1 to 5 when mated to dams from breed group 1 (1S 0B) and from breed group 2 (.5S .5B). Variances and covariances shown in Table 1 are used to build  $V_S$  and  $V_S^{-1}$ . These variances and covariances were computed using formula [1]. Because each bull belongs to a different breed group, the subscript for breed group of bull was dropped from the  $t$ 's. As an example, the computation of the interaction variances and covariances for bull 1 when mated to dams from breed group 1 (1S 0B) and 2 (.5S .5B) is described next.

The intralocus interaction variances and covariances for bull 1 were calculated as follows:

$$\begin{aligned} \text{cov}(11,11)_1 &= \text{var}(11)_1, \\ &= (1)[(t_{1111} + t_{1113}) \sigma_{11}^2 + t_{1112} \sigma_{12}^2] \text{ by formula [1]}, \\ &= (1 + 0) 12 + (0) 16, \\ &= 12, \end{aligned}$$

where  $t_{1111}$  was computed using formula [3],  $t_{1112}$  by formula [4] and  $t_{1113}$  by formula [5], and the first 1 in  $\text{cov}(11,11)_1$  indicates bull 1, the second 1 breed group of dams 1 and the subscript 1 outside the closing parenthesis means 1 locus,

$$\begin{aligned} \text{cov}(12,12)_1 &= \text{var}(12)_1, \\ &= (1) [(t_{1211} + t_{1213}) \sigma_{11}^2 + t_{1212} \sigma_{12}^2] \text{ by formula [1]}, \\ &= (.5 + 0) 12 + (.5) 16, \\ &= 14, \end{aligned}$$

where  $t_{1211}$ ,  $t_{1212}$  and  $t_{1213}$  were computed by formulas [3], [4] and [5], respectively,

$$\begin{aligned} \text{cov}(11,12)_1 &= (1) [\min(t_{1111}, t_{1211}) + \min(t_{1113}, t_{1213})] \sigma_{11}^2 + \min(t_{1112}, t_{1212}) \sigma_{12}^2 \text{ by} \\ &\quad \text{formula [1]}, \\ &= (.5 + 0) 12 + (0) 16, \\ &= 6. \end{aligned}$$

TABLE 1. PEDIGREE, BREED COMPOSITION AND NONADDITIVE GENETIC COVARIANCES FOR ALL MATINGS CONSIDERED PER BULL

Bull	Sire	Maternal grandsire	Expected breed composition of bulls	Expected breed composition of breed groups of dams						Bull nonadditive covariances	
				1S OB	1S 5B	1S 113	1S 112	1S 111	1S 122	1S 123	(i1,i1)
<b>One locus<sup>a</sup></b>											
1			1S OB	$\frac{1}{2}k_{111}$	$\frac{1}{2}k_{112}$	$\frac{1}{2}k_{113}$	$\frac{1}{2}k_{211}$	$\frac{1}{2}k_{212}$	$\frac{1}{2}k_{213}$		
2			OS 1B	0	1	0	.5	.5	0	12	6
3	2		.5S .5B	.5	.5	0	0	.5	.5	16	8
4		2	.25S .75B	.25	.75	0	.25	.5	.25	14	11
5	3	1	.75S .25B	.75	.25	0	.375	.5	.125	15	9.5
<b>Two loci<sup>b</sup></b>											
1			1S OB	$\frac{1}{2}k_{121}$	$\frac{1}{2}k_{122}$	$\frac{1}{2}k_{123}$	$\frac{1}{2}k_{221}$	$\frac{1}{2}k_{222}$	$\frac{1}{2}k_{223}$		
2			OS 1B	1	0	0	.25	.75	0	10	2.5
3			.5S .5B	0	1	0	0	.875	.25	14	10.5
4	2		.25S .75B	.25	.75	0	.0625	.84375	.0625	13	11.125
5	3	1	.75S .25B	.0625	.9375	0	.015625	.140625	.140625	13.75	11.96875
				.5625	.4375	0	.140625	.015625	.015625	11.75	7.53125

<sup>a</sup> $\frac{1}{2}k_{111}$  = probability of interaction type 1 among alleles at 1 locus when bull k is mated to dams of breed group 1; etc.

<sup>b</sup> $\frac{1}{2}k_{121}$  = probability of interaction type 1 among alleles at 2 loci when bull k is mated to dams of breed group 1; etc.

TABLE 2. MATRIX OF COVARIANCES AMONG SIRE  $\times$  BREED-GROUP-OF-DAM INTERACTION EFFECTS ( $V_S$ )

$V_S = \text{block diagonal } \{V_{1S} \ V_{2S}\}$

$$V_{1S} = \begin{bmatrix} 12 & 6 & 0 & 0 & 0 & 0 & 0 & 0 & 3 & 1.5 \\ & 14 & 0 & 0 & 0 & 0 & 0 & 0 & 1.5 & 3.5 \\ & & 16 & 8 & 8 & 4 & 4 & 2 & 4 & 2 \\ & & & 14 & 4 & 7 & 2 & 3.5 & 2 & 3.5 \\ & \text{Symmetric} & & & 14 & 11 & 2 & 1 & 7 & 5.5 \\ & & & & & 14 & 1 & 1.75 & 5.5 & 7 \\ & & & & & & 15 & 9.5 & 1 & .5 \\ & & & & & & & 14 & .5 & .875 \\ & & & & & & & & 13 & 8.5 \\ & & & & & & & & & 14 \end{bmatrix}$$

$$V_{2S} = \begin{bmatrix} 10 & 2.5 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & .625 & .15625 \\ & 13 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & .15625 & .8125 \\ & & 14 & 10.5 & 3.5 & 2.625 & .875 & .65625 & .65625 & .875 & .65625 \\ & & & 13 & 2.625 & 3.25 & .65625 & .8125 & .65625 & .8125 & .8125 \\ & & & & 13 & 11.125 & .21875 & .1640625 & 3.25 & 2.78125 & 2.78125 \\ & & & & & 13.5 & .1640625 & .203125 & 2.78125 & 3.375 & 3.375 \\ & & & & & & 13.75 & 11.96875 & .0546875 & .04101563 & .04101563 \\ & \text{Symmetric} & & & & & & 13.375 & .04101563 & .05078125 & .05078125 \\ & & & & & & & & 11.75 & 7.53125 & 7.53125 \\ & & & & & & & & & & 13.375 \end{bmatrix}$$

The two-locus interaction variances and covariances for bull 1 were obtained as follows:

$$\begin{aligned} \text{cov}(11,11)_2 &= (1) [(t_{1121} + t_{1123}) \sigma_{21}^2 + t_{1122} \sigma_{22}^2] \text{ by formula [1],} \\ &= (1 + 0) 10 + (0) 14, \\ &= 10, \end{aligned}$$

where  $t_{1121}$  was obtained by formula [6],  $t_{1123}$  by formula [11] and  $t_{1122} = (1 - t_{1121} - t_{1123})$ , and the subscript 2 of  $\text{cov}(11,11)_2$  denotes 2 loci,

$$\begin{aligned} \text{cov}(12,12)_2 &= (1) [(t_{1221} + t_{1223}) \sigma_{21}^2 + t_{1222} \sigma_{22}^2] \text{ by formula [1],} \\ &= (0 + .25) 10 + (.75) 14, \\ &= 13, \end{aligned}$$

where  $t_{1221}$  and  $t_{1223}$  were calculated by formulas [6] and [11], respectively, and  $t_{1222} = (1 - t_{1221} - t_{1223})$ ,

$$\begin{aligned} \text{cov}(11,12)_2 &= (1) [\min(t_{1121}, t_{1221}) + \min(t_{1123}, t_{1223})] \sigma_{21}^2 + \min(t_{1122}, t_{1222}) \sigma_{22}^2 \text{ by} \\ &\quad \text{formula [1],} \\ &= (.25 + 0) 10 + (0) 14, \\ &= 2.5. \end{aligned}$$

The matrix  $V_S$  (Table 2) is block diagonal with two blocks:  $V_{1S}$  and  $V_{2S}$ . To construct  $V_S$ : 1) fill up the  $2 \times 2$  diagonal blocks of  $V_{1S}$  and  $V_{2S}$  with the variances and covariances computed in Table 1, as indicated in step 2.a) of the rules to compute  $V_{mS}$ , 2) calculate the off-diagonal blocks

of  $V_{1S}$  and  $V_{2S}$  using steps 2.b) i) to iv) of the procedure to compute  $V_{mS}$ . For instance, the offdiagonal blocks of bull 1 were computed as follows:

1) for  $V_{1S}$ :

$$(V_{1S})_{12} = \begin{bmatrix} 0 & 0 \\ 0 & 0 \end{bmatrix} \text{ by rule 2.b) iv),}$$

$$(V_{1S})_{13} = (.5) \begin{bmatrix} 0 & 0 \\ 0 & 0 \end{bmatrix} = \begin{bmatrix} 0 & 0 \\ 0 & 0 \end{bmatrix} \text{ by rule 2.b) ii),}$$

$$(V_{1S})_{14} = (.25) \begin{bmatrix} 0 & 0 \\ 0 & 0 \end{bmatrix} = \begin{bmatrix} 0 & 0 \\ 0 & 0 \end{bmatrix} \text{ by rule 2.b) iii), and}$$

$$(V_{1S})_{15} = (.5) \begin{bmatrix} 0 & 0 \\ 0 & 0 \end{bmatrix} + (.25) \begin{bmatrix} 12 & 6 \\ 6 & 14 \end{bmatrix} = \begin{bmatrix} 3 & 1.5 \\ 1.5 & 3.5 \end{bmatrix}$$

by rule 2.b) i); and

2) for  $V_{2S}$ :

$$(V_{2S})_{12} = \begin{bmatrix} 0 & 0 \\ 0 & 0 \end{bmatrix} \text{ by rule 2.b) iv),}$$

$$(V_{2S})_{13} = (.5)^2 \begin{bmatrix} 0 & 0 \\ 0 & 0 \end{bmatrix} = \begin{bmatrix} 0 & 0 \\ 0 & 0 \end{bmatrix} \text{ by rule 2.b) ii),}$$

$$(V_{2S})_{14} = (.25)^2 \begin{bmatrix} 0 & 0 \\ 0 & 0 \end{bmatrix} = \begin{bmatrix} 0 & 0 \\ 0 & 0 \end{bmatrix} \text{ by rule 2.b) iii), and}$$

$$(V_{2S})_{15} = (.5)^2 \begin{bmatrix} 0 & 0 \\ 0 & 0 \end{bmatrix} + (.25)^2 \begin{bmatrix} 10 & 2.5 \\ 2.5 & 13 \end{bmatrix} = \begin{bmatrix} .625 & .15625 \\ .15625 & .8125 \end{bmatrix}$$

by rule 2.b) i).

The inverse of  $V_S$  (Table 3) was obtained by computing the inverse of each block, i.e.,  $(V_{1S})^{-1}$  and  $(V_{2S})^{-1}$ , individually. The first step was to calculate the matrices  $D_{mu}^{-1}$ , for intralocus ( $m = 1$ ) and two-locus ( $m = 2$ ) interactions for the five bulls ( $u = 1, \dots, 5$ ).

The  $D_{1u}^{-1}$ ,  $u = 1, \dots, 5$ , were:

$$D_{11}^{-1} = \begin{bmatrix} 12 & 6 \\ 6 & 14 \end{bmatrix}^{-1} = \begin{bmatrix} .10606506 & -.04545454 \\ -.04545454 & .09090909 \end{bmatrix} \text{ by formula [21],}$$

$$D_{12}^{-1} = \begin{bmatrix} 16 & 8 \\ 8 & 14 \end{bmatrix}^{-1} = \begin{bmatrix} .875 & -.05 \\ -.05 & .1 \end{bmatrix} \text{ by formula [21],}$$

$$D_{13}^{-1} = \left[ \begin{bmatrix} 14 & 11 \\ 11 & 14 \end{bmatrix} - (.25) \begin{bmatrix} 16 & 8 \\ 8 & 14 \end{bmatrix} \right]^{-1} = \begin{bmatrix} .4375 & -.375 \\ -.375 & .41666667 \end{bmatrix} \text{ by formula [19],}$$

$$D_{14}^{-1} = \left[ \begin{bmatrix} 15 & 9.5 \\ 9.5 & 14 \end{bmatrix} - (.0625) \begin{bmatrix} 16 & 8 \\ 8 & 14 \end{bmatrix} \right]^{-1} \\ = \begin{bmatrix} .12773723 & -.08759124 \\ -.08759124 & .13625304 \end{bmatrix} \text{ by formula [20], and}$$

TABLE 3. INVERSE OF THE MATRIX OF COVARIANCES AMONG SIRE  $\times$  BREED-GROUP-OF-DAM INTERACTION EFFECTS ( $V_S^{-1}$ )

$V_S^{-1} = \text{diagonal } \{V_{1S}^{-1} \ V_{2S}^{-1}\}$											
$V_{1S}^{-1} =$											
.11693324	-.05152628	.0	.02174527	-.01214346	.0	.0	-.03193431	.0	-.04349054	.02428692	.02428692
.0	.10079330	.0	-.01214346	.01976843	.0	.0	.1875	.0	.02428692	-.03953685	-.03953685
.20485858	-.14922445	-.0485858	-.21875	.1875	-.03193431	-.02189781	-.03193431	.02189781	.0	.0	.0
.21268248	.21268248	.21268248	.1875	-.20833333	.02189781	-.03193431	.02189781	-.03193431	.0	.0	.0
	.48099054	.48099054	.48099054	-.39928692	.0	.0	.0	.0	-.08698108	.04857385	.04857385
			.45620352	.45620352	.0	.0	.0	.0	.04857385	-.07907371	-.07907371
					.12773723	-.08759124	.12773723	-.08759124	.0	.0	.0
						.13625304		.13625304	.17396216	-.0971477	-.0971477
										.15814742	.15814742
Symmetric											
$V_{2S}^{-1} =$											
.10559570	-.02050021	.0	.00218078	-.00119277	.0	.0	-.02071114	.0	-.00872311	.00477109	.00477109
.08128417	.08128417	.0	-.00119277	.00190434	.0	.0	.01854045	.0	.00477109	-.00761737	-.00761737
.20040287	-.16228955	-.16228955	-.07169503	.05915723	-.02071114	-.02071114	.01854045	.01854045	.0	.0	.0
	.21358156	.21358156	.05915723	-.06851643	.01854045	-.02128797	.01854045	-.02128797	.0	.0	.0
			.29550324	-.24140001	.0	.0	.0	.0	-.03489245	.01908437	.01908437
				.28168310	.33137822	-.29664714	.33137822	-.29664714	.01908437	-.03046946	-.03046946
						.34060746		.34060746	.0	.0	.0
									.13956980	-.07633747	-.07633747
										.12187785	.12187785
Symmetric											



$$D_{15}^{-1} = \left[ \begin{array}{cc} [13 & 8.5] \\ [8.5 & 13] \end{array} \right] - (.25) \left[ \begin{array}{cc} [14 & 11] \\ [11 & 14] \end{array} \right] - (.0625) \left[ \begin{array}{cc} [12 & 6] \\ [6 & 14] \end{array} \right]^{-1}$$

$$= \begin{bmatrix} .17396216 & -.09714770 \\ -.09714770 & .15814742 \end{bmatrix} \text{ by formula [18].}$$

The  $D_{2u}^{-1}$ ,  $u = 1, \dots, 5$ , were:

$$D_{21}^{-1} = \begin{bmatrix} 10 & 2.5 \\ 2.5 & 13 \end{bmatrix}^{-1} = \begin{bmatrix} 1.0505050 & -.02020202 \\ -.02020202 & .08080808 \end{bmatrix} \text{ by formula [21],}$$

$$D_{22}^{-1} = \begin{bmatrix} 14 & 10.5 \\ 10.5 & 14 \end{bmatrix}^{-1} = \begin{bmatrix} .18118467 & -.14634146 \\ -.14634146 & .19512195 \end{bmatrix} \text{ by formula [21],}$$

$$D_{23}^{-1} = \left[ \begin{array}{cc} [13 & 11.1] \\ [11.1 & 13.5] \end{array} \right] - (.25)^2 \left[ \begin{array}{cc} [14 & 10.5] \\ [10.5 & 13] \end{array} \right]^{-1}$$

$$= \begin{bmatrix} .28343073 & -.23330678 \\ -.23330678 & .27086484 \end{bmatrix} \text{ by formula [19],}$$

$$D_{24}^{-1} = \left[ \begin{array}{cc} [13.8 & 12] \\ [12 & 13.4] \end{array} \right] - (.0625)^2 \left[ \begin{array}{cc} [14 & 10.5] \\ [10.5 & 13] \end{array} \right]^{-1}$$

$$= \begin{bmatrix} .32983939 & -.29548876 \\ -.29548876 & .33962627 \end{bmatrix} \text{ by formula [20], and}$$

$$D_{25}^{-1} = \left[ \begin{array}{cc} [11.8 & 7.5] \\ [7.5 & 13.4] \end{array} \right] - (.25)^2 \left[ \begin{array}{cc} [13 & 11.1] \\ [11.1 & 13.5] \end{array} \right] - (.0625)^2 \left[ \begin{array}{cc} [10 & 2.5] \\ [2.5 & 13] \end{array} \right]^{-1}$$

$$= \begin{bmatrix} .13784209 & -.07491456 \\ -.07491456 & .12067965 \end{bmatrix} \text{ by formula [18].}$$

The matrices  $D_{mu}^{-1}$ ,  $m = 1, 2$ ,  $u = 1, \dots, 5$ , are now added to the appropriate locations of the inverse of  $V_{mS}$ ,  $m = 1, 2$ , according to the rules specified here. The use of these rules will be illustrated with bull 5. Bull 5 has its sire (bull 3) and its maternal grandsire (bull 1) identified. Thus, 1) its contributions to  $C_{1S}$  are:  $D_{15}^{-1}$  to  $(C_{1S})_{55}$ ,  $(.25) D_{15}^{-1}$  to  $(C_{1S})_{33}$ ,  $(.0625) D_{15}^{-1}$  to  $(C_{1S})_{11}$ ,  $(.125) D_{15}^{-1}$  to  $(C_{1S})_{31}$  and  $(C_{1S})_{13}$ ,  $-.5) D_{15}^{-1}$  to  $(C_{1S})_{53}$  and  $(C_{1S})_{35}$  and  $-.25) D_{15}^{-1}$  to  $(C_{1S})_{51}$  and  $(C_{1S})_{15}$ , and 2) its contributions to  $C_{2S}$  are:  $D_{25}^{-1}$  to  $(C_{2S})_{55}$ ,  $(.25)^2 D_{25}^{-1}$  to  $(C_{2S})_{33}$ ,  $(.0625)^2 D_{25}^{-1}$  to  $(C_{2S})_{11}$ ,  $(.125)^2 D_{25}^{-1}$  to  $(C_{2S})_{31}$  and  $(C_{2S})_{13}$ ,  $-.5)^2 D_{25}^{-1}$  to  $(C_{2S})_{53}$  and  $(C_{2S})_{35}$  and  $-.25)^2 D_{25}^{-1}$  to  $(C_{2S})_{51}$  and  $(C_{2S})_{15}$ . When the contributions of all bulls have been added, the resulting matrix (Table 3) is the inverse of  $V_S$ .

#### Computation of $V_R$ and $V_R^{-1}$ for Regression Models

Each bull is evaluated for the four nonadditive effects defined above (i.e., intralocus intrabreed, intralocus interbreed, two-locus intrabreed and two-locus interbreed interaction effects). The matrices  $V_{m0}$ ,  $m = 1, 2$ , are:

$$V_{10} = \text{diagonal } \{12 \quad 16\} \text{ and,}$$

$$V_{20} = \text{diagonal } \{10 \quad 14\}.$$

The matrix  $V_R$  (Table 4) is block diagonal, with blocks  $V_{1R}$  and  $V_{2R}$ . Each block can be written as a direct product of two matrices:  $V_{1R} = A_1 * V_{10}$  and  $V_{2R} = A_2 * V_{20}$ . As defined in

TABLE 4. MATRIX OF NONADDITIVE GENETIC COVARIANCES DUE TO INTRALOCUS AND TWO-LOCUS INTERACTION EFFECTS ( $V_R$ )

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$V_S = \text{block diagonal } \{V_{1R} \ V_{2R}\}$

$$V_{1R} = \begin{bmatrix} 12 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 3 & 0 \\ & 16 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 4 \\ & & 12 & 0 & 6 & 0 & 3 & 0 & 3 & 0 \\ & & & 16 & 0 & 8 & 0 & 4 & 0 & 4 \\ & \text{Symmetric} & & & 12 & 0 & 1.5 & 0 & 6 & 0 \\ & & & & & 16 & 0 & 2 & 0 & 8 \\ & & & & & & 12 & 0 & .75 & 0 \\ & & & & & & & 16 & 0 & 1 \\ & & & & & & & & 12 & 0 \\ & & & & & & & & & 16 \end{bmatrix}$$

$$V_{2R} = \begin{bmatrix} 10 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & .625 & 0 \\ & 14 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & .875 \\ & & 10 & 0 & 2.5 & 0 & .625 & 0 & .625 & 0 \\ & & & 14 & 0 & 3.5 & 0 & .875 & 0 & .875 \\ & \text{Symmetric} & & & 10 & 0 & .15625 & 0 & 2.5 & 0 \\ & & & & & 14 & 0 & .21875 & 0 & 3.5 \\ & & & & & & 10 & 0 & .0390625 & 0 \\ & & & & & & & 14 & 0 & .0546875 \\ & & & & & & & & 10 & 0 \\ & & & & & & & & & 14 \end{bmatrix}$$


---

formula [1], the elements of  $A_m$  are probabilities that two bulls received the same alleles at  $m$  loci considering all common ancestors. The matrix  $V_R$  was computed in two steps. In step 1, matrices  $A_1$  and  $A_2$  were formed by using rules 2.a. and 2.b. i) to iv) of the procedure to construct  $A_m$ . For example: 1) the elements of the first row of  $A_1$  were:  $(a_1)_{11} = 1$ ,  $(a_1)_{12} = 0$ ,  $(a_1)_{13} = 0$ ,  $(a_1)_{14} = 0$ ,  $(a_1)_{15} = .25$ , and 2) the elements of the first row of  $A_2$  were:  $(a_2)_{11} = 1$ ,  $(a_2)_{12} = 0$ ,  $(a_2)_{13} = 0$ ,  $(a_2)_{14} = 0$ ,  $(a_2)_{15} = .0625$ . After the five bulls were processed, the resulting matrices were  $A_1$  and  $A_2$ . In step 2,  $V_{1R}$  and  $V_{2R}$  were computed as direct products of  $A_1 * V_{10}$  and  $A_2 * V_{20}$ , respectively. For instance, the nonzero  $2 \times 2$  submatrices of bull 1 contributing to  $V_{1R}$  and  $V_{2R}$  were:

1) between bull 1 and itself,

$$(V_{1R})_{11} = (1) \begin{bmatrix} 12 & 0 \\ 0 & 16 \end{bmatrix} = \begin{bmatrix} 12 & 0 \\ 0 & 16 \end{bmatrix},$$

$$(V_{2R})_{11} = (1)^2 \begin{bmatrix} 10 & 0 \\ 0 & 14 \end{bmatrix} = \begin{bmatrix} 10 & 0 \\ 0 & 14 \end{bmatrix},$$

and 2) between bulls 1 and 5,

$$(V_{1R})_{15} = (.25) \begin{bmatrix} 12 & 0 \\ 0 & 16 \end{bmatrix} = \begin{bmatrix} 3 & 0 \\ 0 & 4 \end{bmatrix},$$

$$(V_{2R})_{15} = (.25)^2 \begin{bmatrix} 10 & 0 \\ 0 & 14 \end{bmatrix} = \begin{bmatrix} .625 & 0 \\ 0 & .875 \end{bmatrix}.$$

The computation of the inverse of  $V_R$  (Table 5), that is,  $C_R$ , also proceeded in two steps. The first step consisted of obtaining the inverses of  $A_1$  and  $A_2$  (i.e.,  $B_1$  and  $B_2$ ) using the recursive

procedure to compute  $B_m$ , for  $m = 1, 2$ . To illustrate this procedure, bull 5 will be used again. Because the sire (bull 3) and the maternal grandsire (bull 1) of bull 5 are known, rules i) of the procedure to build  $B_m$  apply. The contributions of bull 5 to: 1)  $B_1$  were:  $d_{15}^{-1}$  to  $(b_1)_{55}$ ,  $(.25) d_{15}^{-1}$  to  $(b_1)_{33}$ ,  $(.0625) d_{15}^{-1}$  to  $(b_1)_{11}$ ,  $(.125) d_{15}^{-1}$  to  $(b_1)_{31}$  and  $(b_1)_{13}$ ,  $-.5) d_{15}^{-1}$  to  $(b_1)_{53}$  and  $(b_1)_{35}$  and  $-.25) d_{15}^{-1}$  to  $(b_1)_{51}$  and  $(b_1)_{15}$ , where  $d_{15}^{-1} = (1 - .25 - .0625)^{-1}$ , and 2)  $B_2$  were:  $d_{25}^{-1}$  to  $(b_2)_{55}$ ,  $(.25)^2 d_{25}^{-1}$  to  $(b_2)_{33}$ ,  $(.0625)^2 d_{25}^{-1}$  to  $(b_2)_{11}$ ,  $(.125)^2 d_{25}^{-1}$  to  $(b_2)_{31}$  and  $(b_2)_{13}$ ,  $-.5)^2 d_{25}^{-1}$  to  $(b_2)_{53}$  and  $(b_2)_{35}$  and  $-.25)^2 d_{25}^{-1}$  to  $(b_2)_{51}$  and  $(b_2)_{15}$ , where  $d_{25}^{-1} = (1 - (.25)^2 - (.0625)^2)^{-1}$ . The complete  $B_1$  and  $B_2$  matrices are:

$$B_1 = \begin{bmatrix} 1.09090909 & .0 & .18181818 & .0 & -.36363636 \\ & 1.4 & -.66666667 & -.26666667 & .0 \\ & & 1.6969697 & .0 & -.72727273 \\ \text{Symmetric} & & & 1.06666667 & .0 \\ & & & & 1.45454545 \end{bmatrix}$$

and,

$$B_2 = \begin{bmatrix} 1.0041841 & .0 & .0167364 & .0 & -.06694561 \\ & 1.07058824 & -.26666667 & -.0627451 & .0 \\ & & 1.13361227 & .0 & -.26778243 \\ \text{Symmetric} & & & 1.00392157 & .0 \\ & & & & 1.07112971 \end{bmatrix}$$

In the second step to form  $C_R$ , the direct products by  $B_m * V_{m0}^{-1}$ ,  $m = 1, 2$ , were computed. The matrices  $V_{m0}^{-1}$ ,  $m = 1, 2$ , were obtained by direct inversion of  $V_{m0}$ ,  $m = 1, 2$ . The  $V_{m0}^{-1}$  matrices were:

$$V_{10}^{-1} = \text{diagonal } \{.08333333 \ .0625\} \text{ and} \\ V_{20}^{-1} = \text{diagonal } \{.1 \ .07142867\}.$$

As an example, the nonzero submatrices of  $C_R$  for bull 1 were:

1) between bull 1 and itself,

$$(C_R)_{11} = 1.09090909 * \text{diagonal } \{.08333333 \ .0625\} \\ = \text{diagonal } \{.09090909 \ .06818182\}$$

and

$$(C_{2R})_{11} = 1.0041841 * \text{diagonal } \{.1 \ .07142857\} \\ = \text{diagonal } \{.10041841 \ .07172744\},$$

2) between bull 1 and bull 3,

$$(C_{1R})_{13} = .18181818 * \text{diagonal } \{.08333333 \ .0625\} \\ = \text{diagonal } \{.00167364 \ .00119546\},$$

and

$$(C_{2R})_{13} = .0167364 * \text{diagonal } \{.1 \ .07142857\} \\ = \text{diagonal } \{.00167364 \ .001194546\},$$

and 3) between bull 1 and bull 5,

$$(C_{1R})_{15} = -.36363636 * \text{diagonal } \{.08333333 \ .0625\} \\ = \text{diagonal } \{-.03030303 \ -.02272727\}$$

and

$$(C_{2R})_{15} = -.06694561 * \text{diagonal } \{.1 \ .07142857\} \\ = \text{diagonal } \{-.00669456 \ -.00478183\}.$$

TABLE 5. INVERSE OF THE MATRIX OF COVARIANCES DUE TO INTRALOCUS AND TWO-LOCUS INTERACTION EFFECTS ( $V_R^{-1}$ )

$V_R^{-1} = \text{block diagonal } \{V_{1R}^{-1} \ V_{2R}^{-1}\}$											
$V_{1R}^{-1} =$											
.09090909	.0	.0	.01515152	.0	.0	.0	.0	.0	.0	-.03030303	.0
.06818182	.0	.0	.0	.01136364	.0	.0	.0	.0	.0	.0	-.02272727
.11666667	.0	.0	-.05555556	.0	-.02222222	.0	.0	.0	.0	.0	.0
.0875	.0	.0	.0	-.04166667	.0	-.16666667	.0	.0	.0	.0	.0
	.14141414	.0	.10606061	.0	.0	.0	.0	.0	.0	.0	-.04545455
		.08888889	.0	.0	.0	.0	.0	.0	.0	.0	.0
		.06666667	.0	.0	.0	.0	.0	.0	.0	.0	.0
		.12121212	.0	.0	.0	.0	.0	.0	.0	.0	.0
			.09090909								
Symmetric											
$V_{2R}^{-1} =$											
.10041841	.0	.0	.00167364	.0	.0	.0	.0	.0	.0	-.00669456	.0
.07172744	.0	.0	.0	.00119546	.0	.0	.0	.0	.0	.0	-.00478183
.10691824	.0	.0	-.002641509	.0	-.00503145	.0	.0	.0	.0	.0	.0
.07637017	.0	.0	.0	-.01886792	.0	-.00359389	.0	.0	.0	.0	.0
	.1136128	.0	.1136128	.0	-.00503145	.0	.0	.0	.0	.0	.0
		.081152	.0	.081152	.0	-.00359389	.0	.0	.0	.0	.0
		.10062893	.0	.10062893	.0	.0	.0	.0	.0	.0	.0
		.07187781	.0	.07187781	.0	.0	.0	.0	.0	.0	.0
		.10711297	.0	.10711297	.0	.0	.0	.0	.0	.0	.0
		.07650926	.0	.07650926	.0	.0	.0	.0	.0	.0	.0
Symmetric											

IMPLICATIONS

Additive as well as nonadditive genetic effects are important sources of variation in multibreed populations. However, straightbred and crossbred bulls used for crossbreeding purposes currently are evaluated using intrabreed sire evaluation procedures. Sire × breed group of dam interaction effects are ignored in intrabreed procedures. The genetic interpretation of sire × breed group of dam interactions given in this research makes it computationally feasible to evaluate large numbers of bulls for these nonadditive genetic effects. Because covariances among sire × breed group of dam interactions are accounted for, sires also can be evaluated for matings not made through progeny from relatives that have them. Mating and selection decisions as well as economic projections can be made more accurately.

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APPENDIX

Derivation of Formula [1]

$$V_{mS} = \{cov(s_{ik} \times BGD_j, s_{i'k'} \times BGD_j)\}.$$

Conditioning each covariance term in  $V_{mS}$  on the interaction effects present among alleles at  $m$  loci, and applying Theorem 7, page 159 in Mood et al. (1974), we obtain:

$$V_{mS} = \{E[cov(s_{ik} \times BGD_j, s_{i'k'} \times BGD_j) | n] + cov(s_{ik} \times BGD_j | n), E[s_{i'k'} \times BGD_j | n])\},$$

where  $n$  represents the  $n^{th}$  interaction among alleles at  $m$  loci,  $E$  denotes expectation and  $|$  means given. The second term of this expression is zero because all random interaction effects were assumed to have mean equal to zero. Thus,

$$V_{mS} = \{ \sum_{n=1}^{N_m} P(s_{ik} \times BGD_j \cap s_{i'k'} \times BGD_j | n) \sigma_{mn}^2 \}$$

$$V_{mS} = \{ \sum_{c=1}^C (a_{ik,i'k',ck''})^m \sum_{n=1}^{N_m} \min (P(s_{ck''} \times BGD_j | n), P(s_{ck''} \times BGD_j | n)) \sigma_{mn}^2 \}$$

$$V_{mS} = \{ \sum_{c=1}^C (a_{ik,i'k',ck''})^m \sum_{c=1}^c \min (t_{ck''jmn'} t_{ck''j'mn}) \sigma_{mn}^2 \}$$

where  $P$  means probability and  $\cap$  means intersection.