RECURSIVE PROCEDURES TO COMPUTE THE INVERSE OF THE MULTIPLE TRAIT ADDITIVE GENETIC COVARIANCE MATRIX IN INBRED AND NONINBRED MULTIBREED POPULATIONS[1]

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ABSTRACT

Multiple-trait, multibreed mixed model procedures require the inverse of a multiple-trait heterogeneous covariance matrix of direct and maternal additive genetic effects (G^{-1}). Because of the heterogeneity of variances and covariances across breed groups, recursive procedures used in single-breed populations cannot be used. Thus, recursive procedures to directly compute G^{-1} in multibreed populations were developed. These procedures account for inbreeding, heterogeneity of additive genetic variances and covariances in different breed groups and permit animals to be evaluated for different sets of traits. In addition, computational methods to recursively obtain G were developed. These strategies simplify the computation of best linear unbiased predictors by mixed model procedures, which are used to predict the genetic worth of animals and to make mating plans in cases of semen importation, stratified breeding schemes, formation of new breeds and sire evaluation for crossbreeding purposes.
(Key Words: Mixed Models, Sire Evaluation, Additive Effects, Maternal Effects, Crossbreeding, Beef Cattle.)

Introduction

A multibreed population can be defined as one composed of breeding animals of several breed groups. Breed groups can be formed by straightbred animals or by crossbred animals. For instance, the Simbrah population can be considered to be multibreed because it is composed of Simmental, Brahman and several Simmental × Brahman breed groups. Elzo and Famula (1985) and Elzo and Bradford (1985) developed single-trait and multiple-trait mixed model procedures to evaluate straightbred and crossbred bulls using straightbred and crossbred progeny in multibreed populations. Unequal variances and covariances across breed groups and unequal sets of traits evaluated per bull were accounted for. To build the mixed model equations for these procedures, the inverse of the matrix of covariances of additive genetic effects (G^{-1}) is needed. Because of the heterogeneity of additive genetic covariances across breed groups, G^{-1} cannot be expressed as $A^{-1}*G_0^{-1}$, where A^{-1} is the inverse of the numerator relationship matrix, G_0^{-1} is the matrix of additive genetic covariances among traits and * indicates a direct product. Hence, recursive procedures to compute G^{-1} within a breed (Henderson, 1975a,b, 1976a,b,c) cannot be used in multibreed populations. Direct computation of G^{-1} in large populations will be difficult and costly, even with mainframe computers. Thus, the objectives of this research were 1) to develop recursive procedures to compute G^{-1} for multiple-trait mixed model procedures in inbred and in noninbred multibreed populations when the matrix in additive genetic covariances among traits differs across breed groups and animals are allowed to be evaluated for different sets of traits and 2) to develop recursive procedures to compute G, under the same conditions specified for G^{-1}.

RECURSIVE METHOD TO COMPUTE G

The recursive procedure to compute G will be presented first, then procedures to compute G^{-1}. Finally, these recursive methods will be illustrated with a small numerical example. Animals from different breeds and from different subpopulations within a breed are dealt with in a similar fashion by these procedures. Thus, the term "breed" will be used throughout this paper to imply "breed or subpopulation within a breed." In addition, the word "traits" will be used to imply measurements of several characters in the usual sense (e.g., birth weight, weaning weight, milk yield, etc.) and to indicate measurements of this same trait in different countries that are treated as separate characters (e.g., weaning weight in Montana, U.S. vs Venezuela). The expression "considered for trait j" will be used to indicate that an animal is "identified in the pedigree and its set of traits contains trait j."

The recursive method to compute G is based on Van Vleck's (1974) and Henderson's (1976a) versions of Emik and Terrill's (1949) method to calculate A. Cases in which both sire and dam, only sire and maternal grandsire, only sire or dam, only maternal grandsire and none of the above ancestors of an individual are identified in the pedigree will be considered. The recursive procedure for G has two major steps. First, data must be organized in chronological order and, second, additive genetic covariances among animals are computed starting with the base animals and continuing with the pedigree animals. Some definitions must now be made.

Let n be the total number of animals and J_i the number of traits in the set for animal i. Define $\mathbf{a}$ to be the $\sum_{i=1}^{n} J_i \times 1$ vector of additive genetic effects ordered by trait within animal. Thus, the matrix of covariances among the elements of vector $\mathbf{a}$ can be written as:

$$G = \{g_{ii'}\} \ , \ 1 \leq i, \ i' \leq n \tag{1}$$

where

$g_{ii'} = \{g_{ij,i'j'}\}$ = matrix of covariances among the additive genetic values of the J_i traits for animal i and the $J_{i'}$ traits for animal i'.

The ith row-block (column-block) of G is defined to be the $J_i \times \sum_{i=1}^{n} J_i$ ($\sum_{i=1}^{n} J_i \times J_i$) submatrix formed by the rows (columns) of G associated with the J_i traits in the set of animal i.

The recursive method to compute G is as follows. First, identify 1) animals to be considered in descending chronological order from 1 (oldest) to n (youngest), 2) the sire, dam and maternal grandsire of each individual; write zero when any of them is unknown, 3) the genetic group of each animal, 4) the expected breed composition of each genetic group, and 5) the set of traits considered for each animal. Second, compute the additive genetic covariance ($g_{ij,i'j'}$) between the traits considered for the ith base animal (j) and those considered for the i'^{th} base animal (j'), over all base animals. Base animals can be straightbred and(or) crossbred, and they are (or are assumed to be) unrelated and noninbred.

Let $(\sigma_{jj'})_I$ be the additive genetic covariance between traits j and j' for genetic group I, the genetic group to which the ith animal belongs. Thus, the $g_{ij,i'j'}$ are equal to $(\sigma_{jj'})_I$, when i = i' and base animal i is considered for traits j and j', and equal to zero otherwise. Under the assumptions of independence of loci and constant additive genetic covariances over time, it can be shown that

$$(\sigma_{jj'})_I = \sum_{K} f_{IK}(\sigma_{jj'})_K \tag{2}$$

where f_{IK} is the expected fraction of breed K alleles in genetic group I, $(\sigma_{jj'})_K$ is the additive genetic covariance between traits j and j' in breed K and the sum is over all breeds present in the multibreed population.

Third, compute the additive genetic covariances ($g_{ij,i'j'}$) between the sets of traits for the ith

(base or pedigree) animal (j) and set of traits for the i'^{th} pedigree animal (j'), over all pedigree animals. Computations can be performed either one row-block or one column-block at a time. The value of the $g_{ij,i'j'}$ will depend on the ancestors identified for the pedigree animals and on the traits contained in the set for each animal. Thus,

(a) when $i \neq i'$ and traits j and j' are in the set for animal i, $g_{ij,i'j'}$ is equal to:

$$\text{(i)} \quad .5 \ g_{ij,s'j'} + .5 \ g_{ij,d'j'} \tag{3}$$

if the sire (s') and the dam (d') of individual i' are considered for traits j and j',

$$\text{(ii)} \quad .5 \ g_{ij,s'j'} + .25 \ g_{ij,m'j'} \tag{4}$$

if only s' and m' (maternal grandsire of animal i') are considered for traits j and j',

$$\text{(iii)} \quad .5 \ g_{ij,x'j'} \tag{5}$$

if only x' is considered for traits j and j', where x' = s' or d',

$$\text{(iv)} \quad .25 \ g_{ij,m'j'} \tag{6}$$

if only m' is considered for traits j and j', and

(v) 0, if animal i' has no ancestors considered for either trait j or j';

(b) when $i = i'$ and traits j and j' are in the set for animal i, $g_{ij,i'j'}$ is equal to:

$$\text{(i)} \quad (\sigma_{jj'})_I + .5 \ g_{sj,dj'} \tag{7}$$

if the sire (s) and dam (d) of animal i are considered for traits j and j',

$$\text{(ii)} \quad (\sigma_{jj'})_I + .25 \ g_{sj,mj'} \tag{8}$$

if only s and m (maternal grandsire of animal i) are considered for traits j and j', and

$$\text{(iii)} \quad (\sigma_{jj'})_I \tag{9}$$

if only one ancestor of animal i (s, d or mgs) or no ancestor of animal i (s, d and mgs) is considered for traits j and j'.

The above recursive procedure to compute G reduces to the one to compute A, as described by Emik and Terrill (1949), Henderson (1976a) or Van Vleck (1974), when the set of traits is the same for all animals and a common additive genetic covariance matrix (G_0) is assumed across genetic groups. Under these conditions G_0 can be factored out so that A is computed separately and G is computed as the direct product of A times G_0.

RECURSIVE METHODS TO COMPUTE G^{-1}

The objective of these recursive methods is to compute G^{-1} without previous knowledge of G. These methods require the same type and ordering of the data specified for computing G. Also, base animals must be assumed to be unrelated and noninbred. The rules to write G^{-1} are the same for multibreed populations with and without inbreeding, but the coefficients used by these rules are different and so are the procedures to compute them. Thus, the rules used to form G^{-1} in multibreed populations with and without inbred animals are presented.

Deriving the Computational Rules to Obtain $\mathbf{G}^{-1}$

The vector of additive genetic effects, **a**, expressed as a genetic model (Quaas and Pollak, 1980), can be written as:

$$\mathbf{a} = .5 \ \mathbf{Pa} + \Theta \tag{10}$$

where

P = lower triangular incidence matrix relating sires and dams or sires and maternal grandsires to progeny within traits. The row of P for the jth trait of the ith animal contains two 1's when the sire (s) and dam (d) of animal i are considered for trait j, a 1 and a .5 when s and m (maternal grandsire of animal i) are considered for trait j, a .5 when m is considered for trait j and all zeroes when no ancestor of animal i is considered for trait j; and

Θ = vector of residual random additive genetic effects.

The covariance matrix of vector **a** is:

$$\mathbf{G} = (\mathbf{I} - .5 \ \mathbf{P})^{-1}\mathbf{B}(\mathbf{I} - .5 \ \mathbf{P'})^{-1} \tag{11}$$

where $\mathbf{B} = \text{diag} (b_{ij,ij'})$. The ith block of **B** is a $J_i \times J_i$ matrix containing the covariances among the residual additive genetic effects of the traits contained in the set for animal i. The residual additive genetic covariances ($b_{ij,ij'}$) can be shown to be equal to:

$$\text{(i)} \quad (\sigma_{jj'})_I - .25 \ g_{sj,sj'} - .25 \ g_{dj,dj'} \tag{12}$$

when s and d are considered for traits j and j',

$$\text{(ii)} \quad (\sigma_{jj'})_I - .25 \ g_{sj,sj'} - .0625 \ g_{mj,mj'} \tag{13}$$

when only s and m are considered for traits j and j',

$$\text{(iii)} \quad (\sigma_{jj'})_I - .25 \ g_{xj,xj'} \tag{14}$$

when only ancestor x (s or d) is considered for traits j and j',

$$\text{(iv)} \quad (\sigma_{jj'})_I - .0625 \ g_{mj,mj'} \tag{15}$$

when only m is considered for traits j and j', and

$$\text{(v)} \quad (\sigma_{jj'})_I \tag{16}$$

when neither s, d nor m are considered for traits j and j' (i.e., traits j and j' are both contained only in the set for animal i).

The additive genetic covariance for ancestor z (z = s, d or m), $g_{zj,zj'}$, in formulas (12) through (15), is equal to:

$$\text{(i)} \quad (\sigma_{jj'})_Z + .5 \ g_{szj,dzj'} \tag{17}$$

when sz (sire of z) and dz (dam of z) are considered for traits j and j', where $(\sigma_{jj'})_Z$ is the additive genetic covariance between traits j and j' in the genetic group of animal z,

$$\text{(ii)} \quad (\sigma_{jj'})_Z + .25 \ g_{szj,mzj'} \tag{18}$$

when only sz and mz (maternal grandsire of z) are considered for traits j and j', and

$$\text{(iii)} \quad (\sigma_{jj'})_Z \tag{19}$$

when neither sz, dz nor mz are considered for traits j and j'.

The inverse of **G** is:

$$G^{-1} = (I - .5P')B^{-1} (I - .5P) \tag{20}$$

where $B^{-1} = \text{diag } \{b^{ij,ij'}\}$. The $b^{ij,ij'}$ are the elements of the inverse of the ith block of **B**. The rules to write G^{-1} directly can be derived by noting the contributions of the $b^{ij,ij'}$ to it, when s and d, s and m, only s (or only d) and only m are considered for traits j and j'. Define $g^{yj,zj'}$ to be the jj'^{th} element of the yz^{th} submatrix of G^{-1}, where y, z = s, or m. Thus,

(i) when animal i, its sire and its dam are considered for traits j and j', add

$b^{ij,ij'}$ to $g^{ij,ij'}$

.25 $b^{ij,ij'}$ to $g^{sj,sj'}$

.25 $b^{ij,ij'}$ to $g^{dj,dj'}$

.25 $b^{ij,ij'}$ to $g^{sj,dj'}$, $g^{dj,sj'}$

−.5 $b^{ij,ij'}$ to $g^{ij,sj'}$, $g^{sj,ij'}$

−.5 $b^{ij,ij'}$ to $g^{ij,dj'}$, $g^{dj,ij'}$

(ii) when only animal i, its sire and its maternal grandsire are considered for traits j and j', add

$b^{ij,ij'}$ to $g^{ij,ij'}$

.25 $b^{ij,ij'}$ to $g^{sj,sj'}$

.0625 $b^{ij,ij'}$ to $g^{mj,mj'}$

.125 $b^{ij,ij'}$ to $g^{sj,mj'}$, $g^{mj,sj'}$

−.5 $b^{ij,ij'}$ to $g^{ij,sj'}$, $g^{sj,ij'}$

−.25 $b^{ij,ij'}$ to $g^{ij,mj'}$, $g^{mj,ij'}$

(iii) when only animal i and its ancestor x (x = s or d) are considered for traits j and j', add

$b^{ij,ij'}$ to $g^{ij,ij'}$

.25 $b^{ij,ij'}$ to $g^{xj,xj'}$

−.5 $b^{ij,ij'}$ to $g^{ij,xj'}$, $g^{xj,ij'}$

(iv) when only animal i and its maternal grandsire are considered for traits j and j', add

$b^{ij,ij'}$ to $g^{ij,ij'}$

.0625 $b^{ij,ij'}$ to $g^{mj,mj'}$

−.25 $b^{ij,ij'}$ to $g^{ij,mj'}$, $g^{mj,ij'}$

(v) and when only animal i is considered for traits j and j', add

$b^{ij,ij'}$ to $g^{ij,ij'}$.

The rules to build G^{-1} in multibreed populations reduce to the rules to compute A^{-1}, given by Henderson in various publications (Henderson, 1975a,b, 1976a,b,c), when 1) a common additive covariance matrix (G_0) is assumed across genetic groups, 2) the set of traits is the same for all animals and, 3) G_0 is factored out such that G^{-1} is computed as the direct product of A^{-1} and G_0^{-1}. Under these assumptions, matrix B^{-1} becomes matrix D^{-2} of Henderson (1976a). This emphasizes the fact that matrices B^{-1} (here) and D^{-2} (Henderson, 1976a), although structurally different, are equivalent in terms of function because both of them contribute with coefficients used by recursive rules to simplify computations for G^{-1}, in multibreed populations and in single breed populations, respectively.

Computing G^{-1} *in Inbred and Noninbred Multibreed Populations*

The procedure used to compute the $b^{ij,ij'}$ in multibreed populations with no inbred animals will be different from the one used in multibreed populations with inbred animals. Thus, the computation of G^{-1} for each type of population will be treated separately.

Noninbred Multibreed Populations. In the absence of inbreeding, all covariance terms between ancestors of s, d and m in equations (12) through (15) vanish. Hence, the $b_{ij,ij'}$ can be calculated with knowledge only of the additive genetic covariances of the genetic groups involved. The $b_{ij,ij'}$ are computed as follows:

(i) $\quad (\sigma_{jj'})_I \; - \; .25 \; (\sigma_{jj'})_S \; - \; .25 \; (\sigma_{jj'})_D$ (21)

when s and d are considered for traits j and j', where $(\sigma_{jj'})_S$ $[(\sigma_{jj'})_D]$ is the additive genetic covariance between traits j and j' in the genetic group which s[d] belongs to,

(ii) $\quad (\sigma_{jj'})_I \; - \; .25 \; (\sigma_{jj'})_S \; - \; .0625 \; (\sigma_{jj'})_M$ (22)

when only s and m are considered for traits j and j', where $(\sigma_{jj'})_M$ is the additive genetic covariance between traits j and j' in the genetic group which m belongs to,

(iii) $\quad (\sigma_{jj'})_I \; - \; .25 \; (\sigma_{jj'})_X$ (23)

when only ancestor x (s or d) is considered for traits j and j', where X = S if x = s and X = D if x = d,

(iv) $\quad (\sigma_{jj'})_I \; - \; .0625 \; (\sigma_{jj'})_M$ (24)

when only m is considered for traits j and j', and

(v) $\quad (\sigma_{jj'})_I$ (25)

when neither s, d nor m are considered for traits j and j'.

Subsequently the $b^{ij,ij'}$ are obtained by inversion of the $\{b_{ij,ij'}\}$ submatrices, for $1 \leq i \leq n$. Finally, application of rules (i) through (v) for $1 \leq i \leq n$, yields G^{-1}.

Inbred Multibreed Populations. When some animals in a multibreed population are inbred, the additive genetic covariances between the ancestors considered for each inbred animal are needed to compute the residual random additive genetic effects. However, these covariances will be unknown because G^{-1} is being formed without previously computing G. Hence, equations (12) to (15) cannot be used to compute the residual random additive genetic covariances ($b_{ij,ij'}$) for those inbred animals. A procedure that computes the $b_{ij,ij'}$ for all animals (inbred and noninbred) in a multibreed population, without requiring previous knowledge of the additive genetic covariances among ancestors of the inbred animals, is described below. Steps to compute the coefficients used by the recursive rules to construct G^{-1} are also included in this procedure. This method is a modification of the one described by Henderson (1976a) to form A^{-1} using the diagonal elements of a lower triangular matrix L ($A^{-1} = (LL')^{-1}$) and of Quaas' (1976) algorithm to computer these elements rapidly.

Let J be the maximum number of traits contained in the set for animal i, $1 \leq i \leq n$. Define matrix $(I - .5 \; P')C$ to be L, where C is a matrix obtained by Cholesky decomposition (Golub and Van Loan, 1983) of B (i.e., $B = CC'$). Let U be an nJ × J matrix that stores the sum of squares of the submatrices of each row-block of L. Let V be an nJ × J matrix that stores the block diagonal elements of L and, temporarily, the offdiagonal submatrices of the ith column block. The recursive procedure involves computing the elements of matrix L as well as those of matrices B and its inverse, one animal at a time, starting with the oldest one (animal 1). Thus, for the ith animal:

(a)   compute $\mathbf{b_i} = \{b_{ij,ij'}\}_{J \times J}$

where

$$b_{ij,ij'} = (\sigma_{jj'})_I - .25\ U_{sjj'} - .25\ U_{djj'} \tag{26}$$

when animal i, its sire (s) and its dam (d) are considered for traits j and j', where $(\sigma_{jj'})_I$ is the additive genetic covariance between traits j and j' in genetic group I, $U_{sjj'}$ is the jj'^{th} element of the submatrix of U for s and $U_{djj'}$ for the jj'^{th} element of the submatrix of U for d,

$$= (\sigma_{jj'})_I - .25\ U_{sjj'} - .0625\ U_{mjj'} \tag{27}$$

when only animals i, s and m (maternal grandsire of animal i) are considered for traits j and j', where $U_{mjj'}$ is the jj'^{th} element of the submatrix of U for m,

$$= (\sigma_{jj'})_I - .25\ U_{xjj'} \tag{28}$$

when only animals i and x are considered for traits j and j', where x = s or d,

$$= (\sigma_{jj'})_I - .0625\ U_{mjj'} \tag{29}$$

when only animals i and m are considered for traits j and j',

$$= (\sigma_{jj'})_I \tag{30}$$

when no ancestor of animal i is considered for traits j and j', and

$$= 0$$

when traits j and j' are not in the set for animal i.

Formulas (26) through (29) are simply computational expressions of formulas (12) through (15). By definition $\mathbf{LL'} = \mathbf{G}$, hence $U_{zjj'}$ is equal to $g_{zj,zj'}$, for z = s, d and m.

Then,

(i) invert $\mathbf{b_i}$ and add the contributions of the inverse elements ($b^{ij,ij'}$) corresponding to combinations of traits evaluated for animal i to $\mathbf{G^{-1}}$, according to the rules given above. If $\mathbf{G^{-1}}$ is too large to be stored in core, the nonzero contributions of the $b^{ij,ij'}$ can be stored on disk or tape accompanied by their row and column numbers.

(ii) calculate $\mathbf{L_{ii}}$ by Cholesky decomposition of $\mathbf{b_i}$ and store it in the submatrix of V corresponding to animal i ($\mathbf{V_i}$).

(b) compute $\mathbf{L_{i'i}}$ for $i + 1 \le i' \le n$. Temporarily store the $\mathbf{L_{i'i}}$ in the $\mathbf{V_{i'}}$, $i + 1 \le i' \le n$. The elements of the offdiagonal submatrices $\mathbf{L_{i'i}}$ (i.e., the $l_{i'j,ij'}$) are computed using the elements of the $\mathbf{V_{i'}}$ (i.e., the $v_{i'jj'}$). Thus,

(i) when animals i, i', s' (sire of i') and d' (dam of i') are considered for traits j and j', the $l_{i'j,ij'}$ are equal to:

$.5\ v_{s'jj'} + .5\ v_{d'jj'}$	if $i \le s' < d'$ or $i \le d' < s'$
$.5\ v_{s'jj'}$	if $d' < i \le s'$
$.5\ v_{d'jj'}$	if $s' < i \le d'$ and
0	if s' and $d' < i$ and if $j' > j$

where $v_{s'jj'}$ is the jj'^{th} elements of the submatrix of $\mathbf{V}$ for s' ($\mathbf{V}_{s'}$) and $v_{d'jj'}$ is the jj'^{th} element of the submatrix of $\mathbf{V}$ for d' ($\mathbf{V}_{d'}$),

(ii) when only animals i, i', s' and m' (maternal grandsire of i') are considered for traits j and j', the $l_{i'j,ij'}$ are equal to:

$.5\, v_{s'jj'} + .25\, v_{m'jj'}$	if $i \le m' < s'$ or $i \le s' < m'$
$.5\, v_{s'jj'}$	if $m' < i \le s'$
$.25\, v_{m'jj'}$	if $s' < i \le m'$ and
0	if s' and $m' < i$ and if $j' > j$

where $v_{m'jj'}$ is the jj'^{th} element of the submatrix of $\mathbf{V}$ for m' ($\mathbf{V}_{m'}$),

(iii) when only animals i, i' and x'(x' = s' or d') are considered for traits j and j', the $l_{i'j,ij'}$ are equal to:

$.5\, v_{x'jj'}$	if $i \le x'$ and
0	if $x' < i$ and if $j' > j$

(iv) when only animals i, i' and m' are considered for traits j and j', the $l_{i'j,ij'}$ are equal to:

$25\, v_{m'jj'}$	if $i \le m'$ and
0	if $m' < i$ and if $j' > j$

(v) and when only animals i and i' are considered for traits j and j', the $l_{i'j,ij'}$ are equal to zero.

(c) compute $v_{i'} v_{i'}^T$ (i.e., $\mathbf{L}_{i'i}$) and add it to $\mathbf{U}_{i'}$, the submatrix of $\mathbf{U}$ for the i'^{th} animal, for $i < i' < n$.

After finishing with the computations for the nth animal (youngest one), $\mathbf{G}^{-1}$ is complete. If the contributions of the $b^{jj,ij'}$ to $\mathbf{G}^{-1}$ were stored on disk or tape, they must now be sorted by column number within row number, or vice versa, and those terms with equal row and column number added. The resulting values are the nonzero elements of $\mathbf{G}^{-1}$.

DISCUSSION

The methods described to compute $\mathbf{G}^{-1}$ (and $\mathbf{G}$) are general in that they can be used to form these matrices under conditions of 1) unequal genetic covariances among animals from different genetic groups, 2) different sets of traits for each animal, 3) different pedigree information for each animal, and 4) both inbred and noninbred animals. Allowing for these four characteristics permits substantial flexibility in the modeling and computing strategies of multibreed BLUP procedures. The matrix $\mathbf{G}^{-1}$ can be constructed to include only the traits of interest for each animal; this is an advantage especially when animals are being evaluated using data from highly unbalanced designs. However, a constraint requiring that each animal and its relatives be connected through common traits in their sets must be imposed to avoid breaking pedigree ties. Also, $\mathbf{G}^{-1}$ must include all pedigree animals connecting the animals of interest to the base animals and to the animals with records. This implies that the methods to form $\mathbf{G}^{-1}$ cannot be used to compute the inverse of a submatrix of $\mathbf{G}$ (e.g., the inverse of $\mathbf{G}$ for animals of one generation only). Such inverses could be obtained using inversion by partitioning techniques (Searle, 1966), as suggested by Henderson (1976a) for the inverse of a submatrix of $\mathbf{A}$. Nevertheless, this approach might not be practical if the matrices to be inverted are too large and have no special pattern (e.g., block diagonal) to facilitate computations.

In some multibreed data sets, simplifications with respect to the four conditions specified above will be made as part of the computing strategy. For instance, in a cattle sire evaluation program based on progeny data, only sires and maternal grandsires could be included in $\mathbf{G}^{-1}$. If

these simplifications are such that all animals are evaluated for the same set of traits and a common additive genetic covariance matrix (G_0) for all genetic groups is assumed, then G can be expressed as $A*G_0$, G^{-1} is equal to $A^{-1}*G_0^{-1}$ and the methods of this paper reduce to those of Henderson (1975a,b, 1976a,b,c), as indicated previously.

The methods to build G^{-1} (and G) allowed for combinations of sire and dam or maternal grandsire because, in practice, these are the ancestors most likely to be identified in the pedigree of an animal. However, these methods can be extended, using path coefficient principles (Wright, 1922), to account for the first paternal and maternal ancestors identified in the pedigree of an individual. This extension affects only the fractions that multiply the elements used by the methods to form G^{-1} and G. Let tp and tq be the numbers of generations between animal i and its first paternal (p) and maternal (q) ancestors considered for traits in the set for animal i. Let tp' and tq' be the numbers of generations between animal i' and its corresponding ancestors p' and q'. Thus, in the method to build G: 1) the $g_{ij,p'j'}$ and the $g_{ij,q'j'}$ are multiplied by $(.5)^{tp'}$ and $(.5)^{tq'}$, respectively, and 2) the $g_{pj,qj'}$ are multiplied by $(.5)^{tp+tq-1}$. In the method to build G^{-1}: 1) the $g_{pj,pj'}$ and the $g_{qj,qj'}$ are multiplied by $(.5)^{2tp}$ and $(.5)^{2tq}$, respectively, 2) the $b^{ij,ij'}$ are multiplied by 1 if added to $g^{ij,ij'}$, by $(.5)^{2tp}$ if added to $g^{pj,pj'}$, by $(.5)^{2tq}$ if added to $g^{qj,qj'}$, by $(.5)^{tp+tq}$ if added to $g^{pj,qj'}$ and $g^{qj,pj'}$, by $-(.5)^{tp}$ if added to $g^{ij,pj'}$ and $g^{pj,ij'}$ and by $-(.5)^{tq}$ if added to $g^{ij,qj'}$ and $g^{qj,ij'}$, 3) the $U_{pjj'}$ and the $U_{qjj'}$ are multiplied by $(.5)^{2tp}$ and $(.5)^{2tq}$, respectively, and 4) the $v_{p'jj'}$ and the $v_{q'jj'}$ are multiplied by $(.5)^{tp}$ and $(.5)^{tq}$, respectively. The methods to form G^{-1} (and G) will have rules for the cases when both first ancestors, only the first maternal ancestor, only the first paternal ancestor and none of them are considered for traits in the set of an individual. The procedures of this paper can be modified to account for these cases by substituting p', q', p and q for s', m', s and m, and ignoring the cases involving d.

IMPLICATIONS

The recursive procedures of this research greatly facilitate the computation of the mixed model equations of multibreed evaluation procedures. These procedures permit the simultaneous evaluation of bulls for direct and maternal additive and nonadditive genetic effects for one or more traits. Multibreed procedures allow breeders flexibility in their selection goals. For example, if short-term results were important, then bulls should be chosen based on the sum of their additive and nonadditive genetic values, but for long-term improvements, additive values should be emphasized. Also, crossbred mating strategies can be planned more accurately. These features make multibreed procedures useful to evaluate animal in cases of recurrent rounds of semen importation, stratified breeding schemes, formation of new breeds and sire evaluation for crossbreeding purposes.

TABLE 1. PEDIGREE, BREED COMPOSITION AND ADDITIVE GENETIC COVARIANCES
AMONG ALL TRAITS CONSIDERED PER ANIMAL

Animal	Sire	Maternal grandsire	Expected breed composition[a]		Trait number	Additive covariances		
						11	12	22
1			A		1,2	16	6	36
2			B		1	9	5	25
3	2		.5A	.5B	1,2	12.5	5.5	30.5
4	1		A		1	16	6	36
5		1	.5A	.5B	1,2	12.5	5.5	30.5
6		2	.25A	.75B	2	10.75	5.25	27.75
7	3	2	.5A	.5B	1,2	12.5	5.5	30.5
8	3	1	.75A	.25B	2	14.25	5.75	33.25

[a]A = breed 1; B = breed 2.

$$
\begin{bmatrix}
16 & 6 & 0 & 0 & 0 & 8 & 4 & 1.5 & 0 & 0 & 0 & 1.5 \\
6 & 36 & 0 & 0 & 0 & 3 & 1.5 & 9 & 0 & 0 & 0 & 9 \\
0 & 0 & 9 & 4.5 & 0 & 0 & 0 & 0 & 0 & 4.5 & 0 & 0 \\
0 & 0 & 4.5 & 12.5 & 5.5 & 0 & 0 & 0 & 0 & 7.375 & 2.75 & 2.75 \\
0 & 0 & 0 & 5.5 & 30.5 & 0 & 0 & 0 & 0 & 2.75 & 15.25 & 15.25 \\
8 & 3 & 0 & 0 & 0 & 16 & 2 & .75 & 0 & 0 & 0 & .75 \\
4 & 1.5 & 0 & 0 & 0 & 2 & 12.5 & 5.5 & 0 & 0 & 0 & .375 \\
1.5 & 9 & 0 & 0 & 0 & .75 & 5.5 & 30.5 & 0 & 0 & 0 & 2.25 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 27.75 & 0 & 0 & 0 \\
0 & 0 & 4.5 & 7.375 & 2.75 & 0 & 0 & 0 & 0 & 13.625 & 5.5 & 1.375 \\
0 & 0 & 0 & 2.75 & 15.25 & 0 & 0 & 0 & 0 & 5.5 & 30.5 & 7.625 \\
1.5 & 9 & 0 & 2.75 & 15.25 & .75 & .375 & 2.25 & 0 & 1.375 & 7.625 & 33.25
\end{bmatrix}
$$

NUMERICAL EXAMPLE

To illustrate the methods described above, G and G^{-1} are computed for a hypothetical case, whose data are shown in Table 1. For simplicity only two breeds and two traits are considered. The additive genetic covariances of the crossbred groups were computed using equation (2) from the text. For instance, the additive genetic covariance between traits 1 and 2 for the genetic group of animal 6 is $.25(6) + .75(5)$. Animals 1 and 2 are base animals and animals 3 to 8 are pedigree animals. The set of traits for animals 3, 5 and 7 contains traits 1 and 2, the set for animals 2 and 4 only contains trait 1 and the set for animals 6 and 8 only contains trait 2. Only male ancestors are considered in the pedigree.

Matrix G is presented in Table 2. The rules used to compute G are illustrated using the first column-block (= first row-block).

$$
g_{11} = \begin{bmatrix} 16 & 6 \\ 6 & 36 \end{bmatrix}, \quad
g_{21} = \begin{bmatrix} 0 & 0 \end{bmatrix},
$$

$$
g_{31} = \begin{bmatrix} .5(0) & .5(0) \\ 0 & 0 \end{bmatrix}, \quad
g_{41} = \begin{bmatrix} .5(16) & .5(6) \end{bmatrix},
$$

$$
g_{51} = \begin{bmatrix} .25(16) & .25(6) \\ .25(6) & .25(36) \end{bmatrix}, \quad
g_{61} = \begin{bmatrix} .25(0) & .25(0) \end{bmatrix},
$$

$$
g_{71} = \begin{bmatrix} .5(0) + .25(0) & .5(0) \\ .5(0) + .25(0) & .5(0) \end{bmatrix}, \quad \text{and } g_{81} = \begin{bmatrix} .5(0) + .25(6) \\ .5(0) + .25(36) \end{bmatrix}.
$$

Matrix G^{-1} is shown in Table 3. Notice that neither the sire nor the maternal grandsire of any of the pedigree animals is inbred. Hence, the coefficients used by the rules to build G^{-1} ($b^{ij,ij'}$) can be computed using equations (12) through (16). The matrices of coefficients, b^i, for the eight animals in this example are:

TABLE 3. INVERSE OF THE MATRIX OF ADDITIVE GENETIC COVARIANCES (G⁻¹) ORDERED BY TRAIT WITHIN ANIMAL FROM OLDEST TO YOUNGEST

.09341283	-.01218379	0	0	0	-.04166667	-.02365130	.00429072	0	0	0	-.01069519
	.03461042	0	0	.00534759	0	.00429072	-.00962796	0	0	0	0
		.14586054	-.03851413	.00694517	0	0	0	-.03098413	-.03098413	0	0
			.13899652	-.02506494	0	0	0	-.06196286	.01117460	0	-.02139037
				.05893095	0	0	0	.01117460	-.02387302	0	0
					.0833333	0	0	0	0	0	0
						.09460250	-.01716289	0	0	0	0
Symmetric							.03851185	0	0	0	0
								.12396351	-.02234921	0	0
									.04774603	0	0
										.03603604	0
											.04278075

$$\mathbf{b^1} = \begin{bmatrix} 16 & 6 \\ 6 & 36 \end{bmatrix}^{-1} \quad , \quad \mathbf{b^2} = \begin{bmatrix} 9 \end{bmatrix}^{-1} \quad ,$$

$$\mathbf{b^3} = \begin{bmatrix} 12.5-.25(9) & 5.5 \\ 5.5 & 30.5 \end{bmatrix}^{-1} \quad , \quad \mathbf{b^4} = \begin{bmatrix} 16-.25(16) \end{bmatrix}^{-1} \quad ,$$

$$\mathbf{b^5} = \begin{bmatrix} 12.5-.0625(16) & 5.5-.0625(6) \\ 5.5-.0625(6) & 30.5-.0625(36) \end{bmatrix}^{-1} \quad , \quad \mathbf{b^6} = \begin{bmatrix} 27.75 \end{bmatrix}^{-1} \quad ,$$

$$\mathbf{b^7} = \begin{bmatrix} 12.5-.25(12.5)-.0625(9) & 5.5-.25(5.5) \\ 5.5-.25(5.5) & 30.5-.25(30.5) \end{bmatrix}^{-1} \quad , \text{and}$$

$$\mathbf{b^8} = \begin{bmatrix} 33.5-.25(30.5)-.0625(36) \end{bmatrix}^{-1} \quad .$$

The computations for the first column-block of matrix $\mathbf{L}$ (recall $\mathbf{G} = \mathbf{LL'}$) are used next to illustrate the procedure used to compute the matrices of coefficients ($\mathbf{b^i}$) when some animals in a multibred population are inbred. First, we obtain the additive genetic covariance of the genetic group for animal one ($\mathbf{b_1}$). Because animal 1 is a base animal,

$$\mathbf{b_1} = \begin{bmatrix} 16 & 6 \\ 6 & 36 \end{bmatrix} \quad .$$

Second, $\mathbf{b_1}$ is inverted to obtain the matrix of coefficients for animal 1 ($\mathbf{b_1}$),

$$\mathbf{b_1} = \begin{bmatrix} 16 & 6 \\ 6 & 36 \end{bmatrix}^{-1} \quad .$$

Third, $\mathbf{L_{11}}$ is computed by Cholesky decomposition of $\mathbf{b_1}$,

$$\mathbf{L_{11}} = \begin{bmatrix} (16)^{.5} & 0 \\ 1.5 & [36-(1.5)^2]^{.5} \end{bmatrix} \quad .$$

Fourth, $L_{i'1}$, $2 \leq i' \leq 8$, are computed,

$$L_{21} = \begin{bmatrix} 0 & 0 \end{bmatrix}, \quad L_{31} = \begin{bmatrix} .5(0) & 0 \\ 0 & 0 \end{bmatrix},$$

$$L_{41} = \begin{bmatrix} .5(4) & 0 \end{bmatrix}, \quad L_{51} = \begin{bmatrix} .25(4) & 0 \\ .25(1.5) & .25(5.809475) \end{bmatrix},$$

$$L_{61} = \begin{bmatrix} 0 & .25(0) \end{bmatrix}, \quad L_{71} = \begin{bmatrix} .5(0)+.25(0) & 0 \\ .5(0) & .5(0) \end{bmatrix}, \text{ and}$$

$$L_{81} = \begin{bmatrix} .5(0)+.25(1.5) & .5(0)+.25(5.809475) \end{bmatrix}.$$

Fifth, $L_{i'1}L_{i'1}'$ is computed and added to $U_{i'}$, for $1 \leq i' \leq 8$. For instance,

$$L_{81}L_{81}' = \begin{bmatrix} 2.25 \end{bmatrix} \text{ and } \quad U_8 = \begin{bmatrix} 0 & 0 \\ 0 & 2.25 \end{bmatrix}.$$

If these computations are carried out for all column-blocks of L, coefficient matrices b^1 through b^8 are obtained. The use of the rules to form G^{-1} will be exemplified using b^7, where

$$b^7 = \begin{bmatrix} .12393651 & -.22349210 \\ -.22349210 & .04774603 \end{bmatrix} = \begin{bmatrix} b^{71,71} & b^{71,72} \\ b^{72,71} & b^{72,72} \end{bmatrix}.$$

Animal 7 has both its sire (animal 3) and its maternal grandsire (animal 2) identified. Thus, we must add

$$\mathbf{b}^7 \text{ to } \begin{bmatrix} g^{71,71} & g^{71,72} \\ g^{72,71} & g^{72,72} \end{bmatrix}$$

$$.5\,\mathbf{b}^7 \text{ to } \begin{bmatrix} g^{31,31} & g^{31,32} \\ g^{32,31} & g^{32,32} \end{bmatrix}$$

$.0625\ b^{71,71}$ to $g^{21,21}$

$.125\ \ b^{71,71}$ to $g^{21,31}, g^{31,21}$

$.125\ \ b^{71,72}$ to $g^{21,32}, g^{32,21}$

$$-.5\,\mathbf{b}^7 \text{ to } \begin{bmatrix} g^{31,71} & g^{31,72} \\ g^{32,71} & g^{32,72} \end{bmatrix}, \begin{bmatrix} g^{71,31} & g^{71,32} \\ g^{72,31} & g^{72,32} \end{bmatrix}$$

$-.25\ b^{71,71}$ to $g^{21,71}, g^{71,21}$ and

$-.25\ b^{71,72}$ to $g^{21,72}, g^{72,21}$.

Application of the rules for $\mathbf{G}^{-1}$ to the $\mathbf{b}^i$, $1 \le i \le 8$, yields matrix $\mathbf{G}^{-1}$ in Table 3. Notice that animal 6 is completely disconnected from animal 2 (animal 2 is the maternal grandsire of animal 6) because they do not share a common trait in their sets and there is no other animal linking them. On the other hand, animals 8 and 2, even though they have no trait in common in their sets, are connected through animal 3 (related to both animal 2 and animal 8), because the set for animal 3 has trait 1 in common with animal 2 and trait 2 in common with animal 8. These two cases illustrate the need for the constraint requiring common traits in the sets of relatives to connect them.

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