Inverse of Single Trait Additive Genetic Covariance Matrix with Unequal Variances Across Additive Genetic Groups[1]

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ABSTRACT

Recursive procedures are presented to compute the additive genetic covariance matrix and its inverse for a single trait when additive genetic variances differ across genetic groups. They are extensions of well-known recursive methods that assume equal additive variances for all genetic groups in a population. These procedures facilitate animal evaluation with mixed model analysis when animals being evaluated belong to different subpopulations within a breed or to different breeds and crossbred groups, especially when animals belonging to different genetic groups are related. Models should include additive and nonadditive fixed (group) and random effects depending on the trait being evaluated.

INTRODUCTION

In mixed model single trait animal evaluation methods, the additive genetic covariance matrix among individuals being evaluated (G), or more particularly its inverse (G^{-1}), is required (5, 6, 7, 8). When animals being evaluated belong to several additive genetic groups within a breed, G is defined as σ_A^2 A, where σ_A^2 is the additive genetic variance and A is the numerator relationship matrix (7). This expression (σ_A^2 A) assumes a common σ_A^2 over all additive genetic groups in a population where additive genetic groups usually are defined as a function of time to account for genetic trend not explained by G. However, when additive genetic groups are also a function of geographic location of animals within a breed (e.g., country of origin)

or breed composition of animals (i.e., animals are from various breeds and crossbred groups), the assumption of a common σ_A^2 over all additive genetic groups may be untenable (3, 4). If additive genetic variances differ across additive genetic groups, G cannot be written as σ_A^2 A. Thus, neither G nor G^{-1} can be formed by existing methods (5, 6, 7, 8, 11, 13). Objectives of this research are to modify Henderson's rules to compute A^{-1} and Emik and Terril's procedure to build A to write G^{-1} and G recursively, accounting for unequal variances across additive genetic groups, for the one trait case. The presence and absence of inbreeding are considered in these procedures when only male ancestors or both male and female ancestors are included in the pedigree. The resulting G and G^{-1} can be used in single trait mixed model procedures that account for additive and nonadditive fixed (group) and random effects, such as those developed in (3, 4) and in models with negligible nonadditive random effects or nonadditive fixed and random effects.

Recursive Method to Compute G for a Single Trait with Unequal σ_A^2 Across Genetic Groups

The recursive procedure to build G has two main steps. First, some pedigree and breed composition information on each animal is obtained. Second, additive genetic covariances among all animals in the pedigree are computed one row (or one column) at a time.

Rules of the recursive procedure to build G are to:

1. Identify i) animals to be evaluated from 1 to n in chronological order, oldest first; ii) sire, dam, and maternal grandsire (MGS) of each individual (write zero if any of them is unknown); iii) genetic group of each individual, iv) expected breed composition of each genetic group.

2). Compute a) g_{ii}', for all base animals, i.e., $1 \leqslant i$, $i' \leqslant b$, where g_{ii}' is the additive covariance

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between individuals i and i' (i.e., the ii'th element of G) and b is the number of base animals. If base animals are noninbred and unrelated, $g_{ii}' = 0$, $1 \leq i, i' \leq b$, $i \neq i'$, and $g_{ii} = (\sigma_A^2)_i^I$, i.e., the additive genetic variance of breed group I, the breed group of the ith individual. Under no linkage and constancy of variances over time:

$$(\sigma_A^2)_i^I = \left[\sum_{m=1}^{M} p_m (\sigma_A^2)_m \right]_i^I \qquad [1]$$

where p_m is the expected fraction of alleles of breed m in breed group I and $(\sigma_A^2)_m$ is the additive genetic variance of breed m (3). Thus, under these conditions, the additive genetic variance of any crossbred group can be computed with knowledge of the base breed additive genetic variances and the expected breed composition of crossbred groups.

Compute b) g_{ii}', for all pedigree animals, i.e., $b + 1 \leq i, i' \leq n$. The expression for g_{ii}' will depend on the ancestors considered in the pedigree of the i'th individual. Hence: i) when the sire (S') and the dam (D') of the i'th individual are considered, the diagonal elements of G are computed as:

$$g_{i'i'} = (\sigma_A^2)_i^{I'} + .5 \, g_{S'D'}$$

and the off-diagonal elements of G as:

$$g_{ii}' = .5 \, g_{iS}' + .5 \, g_{iD}'$$

ii) when S' and the MGS (MGS') of the i'th individual are considered, the diagonal elements of G are computed as:

$$g_{i'i'} = (\sigma_A^2)_i^{I'} + .25 \, g_{S' \, MGS'}$$

and the off-diagonal elements of G as:

$$g_{ii}' = .5 \, g_{iS}' + .25 \, g_{i \, MGS'}$$

iii) when only S' or D' is considered, the diagonal elements of G are computed as:

$$g_{i'i'} = (\sigma_A^2)_i^{I'}$$

and the off-diagonal elements of G as:

$$g_{ii}' = .5 \, g_{iS}' \text{ if } S' \text{ is considered}$$
$$= .5 \, g_{iD}' \text{ if } D' \text{ is considered}$$

iv) when only MGS' is considered; the diagonal elements of G are computed as:

$$g_{i'i'} = (\sigma_A^2)_i^{I'}$$

and the off-diagonal elements of G as:

$$g_{ii}' = .25 \, g_{i \, MGS'}$$

v) when no ancestor is considered, the diagonal elements of G are computed as:

$$g_{i'i'} = (\sigma_A^2)_i^{I'}$$

and the off-diagonal elements of G are zero, i.e., $g_{ii}' = 0$.

Notice that inbreeding of a straightbred or a crossbred animal depends exclusively on how related its parents are. The only difference between an inbred straightbred and an inbred crossbred animal is that some of the alleles identical by descent in a crossbred animal may belong to different breeds.

Recursive Method for Compute G^{-1}
for a Single Trait with Unequal σ_A^2
Across Genetic Groups

This procedure also involves two steps. The first is the same used to compute G. The second computes elements of G^{-1}, i.e., the g^{ii}, based on the contributions of each animal in the pedigree to itself and its ancestors. Thus, repeat step 1) of the method to build G, and compute G^{-1} by the following rules.

i) When the sire (S) and the dam (D) of the ith individual are considered, add:

$$b^i \text{ to } g^{ii}$$
$$.25 \, b^i \text{ to } g^{SS}, g^{DD}, g^{SD}, g^{DD}$$
$$-.5 \, b^i \text{ to } g^{iS}, g^{Si}, g^{iD}, g^{Di}$$

where:

$$b^i = \Big[(\sigma_A^2)_i^I - .25 \, (\sigma_A^2)_i^S - .25 \, (\sigma_A^2)_i^D$$
$$- .125 \, \text{cov} (a_i^{SS}, a_i^{DS})$$
$$- .125 \, \text{cov} (a_i^{SD}, a_i^{DD}) \Big]^{-1} \qquad [2]$$

In Equation [2], $a_i^X =$ additive value of ancestor X of i for the trait being evaluated, X = SS, DS,

SD, DD, SS(DS) = sire (dam) of S, and SD(DD) = sire (dam) of D. The additive genetic covariance represented by cov (a_i^{SS}, a_i^{DS}), for example, is the element of G for the particular ancestors of i.

ii) When the sire (S) and the maternal grandsire (MGS) of the ith individual are considered, add:

$$b^i \text{ to } g^{ii}$$

$$.25 \, b^i \text{ to } g^{SS}$$

$$.0625 \, b^i \text{ to } g^{MGS,MGS}$$

$$.125 \, b^i \text{ to } g^{S,MGS}, g^{MGS,S}$$

$$-.5 \, b^i \text{ to } g^{iS}, g^{Si}$$

$$-.25 \, b^i \text{ to } g^{i \, MGS}, g^{MGS \, i}$$

where:

$$b^i = \Big[(\sigma_A^2)_i^I - .25 \, (\sigma_A^2)_i^S - .0625 \, (\sigma_A^2)_i^{MGS}$$
$$- .0625 \, \text{cov} (a_i^{SS}, a_i^{MGSS})$$
$$- .015625 \, \text{cov} (a_i^{SMGS},$$
$$a_i^{MGSMGS}) \Big]^{-1} \qquad [3]$$

In Equation [3], SS (MGSS) = sire (MGS) of S, and SMGS (MGSMGS) = sire (MGS) of MGS.

iii) When only the sire or the dam of the ith individual is considered, add:

$$b^i \text{ to } g^{ii}$$

$$.25 \, b^i \text{ to } g^{XX}$$

$$-.5 \, b^i \text{ to } g^{iX}, g^{Xi}$$

where:

$$b^i = \Big[(\sigma_A^2)_i^I - .25 \, (\sigma_A^2)_i^X$$
$$- .125 \, \text{cov} (a_i^{SX}, a_i^{DX}) \Big]^{-1} \qquad [4]$$

SX (DX) = sire (dam) of X, X = S or D.

iv) When only the MGS of the ith individual is considered, add:

$$b^i \text{ to } g^{ii}$$

$$.0625 \, b^i \text{ to } g^{MGS, MGS}$$

$$-.25 \, b^i \text{ to } g^{i \, MGS}, g^{MGS \, i}$$

where:

$$b^i = \Big[(\sigma_A^2)_i^I - .125 \, (\sigma_A^2)_i^{MGS}$$
$$- .015625 \, \text{cov} (a_i^{SMGS},$$
$$a_i^{MGSMGS}) \Big]^{-1} \qquad [5]$$

v) When neither the sire, the dam, nor the MGS of the ith individual are considered, add:

$$b^i \text{ to } g^{ii}$$

where:

$$b^i = \Big[(\sigma_A^2)_i^I \Big]^{-1} \qquad [6]$$

Computation of the b^i's

With knowledge of additive genetic variances, b^i can be calculated both in the presence or absence of inbreeding. In a noninbred population the b^i are only a function of the additive genetic variances of the breed groups. Hence, they can be calculated by Equations [2] through [6]. If there is inbreeding, however, additive genetic covariances between ancestors will be required. Because the goal here is to compute G^{-1} without computing G first, these covariances will be unknown. A simple modification of the Quaas (11) procedure to find diagonal elements of A permits its use to compute the b^i when there is inbreeding. This modification consists of including the unequal additive genetic variances, required to explain the additive genetic covariances among animals of different breed groups or subpopulations within a breed, in the derivation of the Quaas algorithm as in (11). For completeness the entire algorithm will be described.

Let $G = LL'$, where L is a lower triangular matrix. Let u be an n X 1 vector where the sums of squares of the elements of each row of L are accumulated. Let v be an n X 1 vector that stores the diagonal elements of L and also temporarily the off-diagonal elements of L. This procedure requires n rounds of computations to produce G^{-1}, i.e., one round of computation per animal in the pedigree. Computations for the ith round (i.e., the ith animal) are:

i) $v_i (=l_{ii}) = \left[(\sigma_A^2)_i^I - .25(u_S + u_D)\right]^{.5}$

when both S and D are known

$$= \left[(\sigma_A^2)_i^I - .25(u_S + .25 u_{MGS})\right]^{.5}$$

if S and MGS known but D unknown

$$= \left[(\sigma_A^2)_i^I - .25 u_S\right]^{.5}$$

if S known but D and MGS unknown

$$= \left[(\sigma_A^2)_i^I - .25 u_D\right]^{.5}$$

if D known but S unknown

$$= \left[(\sigma_A^2)_i^I - .0625 u_{MGS}\right]^{.5}$$

if MGS known but S and D unknown

$$= \left[(\sigma_A^2)_i^I\right]^{.5}$$

if S, D and MGS unknown

where u_X is the element of the vector u corresponding to ancestor X, X = S, D, or MGS, and v_i is the element of vector v for the ith individual. The u in the preceding formulas account for inbreeding, e.g., $u_s = (\sigma_A^2)_i^S + .5 \text{ cov}$ (a_i^{SS}, a_i^{DS}) when both S and D are known.

ii) $v_{i'} = l_{i'i}$ for $i + 1 \leqslant i' \leqslant n$

where:

$v_{i'} = .5(v_S' + v_D')$

if $i \leqslant S'(D') < D'(S')$

$= .5v_S' + .25 v_{MGS}'$

if $i \leqslant MGS'(S') < S'(MGS')$

$= .5v_S'$

if D' or $MGS' < i \leqslant S'$

$= .5v_D'$

if $S' < i \leqslant D'$

$= .25v_{MGS}'$

if $S' < i \leqslant MGS'$

$= 0$

if $S', D',$ or $MGS' < i$

where v_X' is the element of vector v corresponding to individual X', $X' = i', S', D',$ MGS'.

iii) Add $(v_j)^2$ to u_j, for $i \leqslant j \leqslant n$.

iv) Obtain $b^i = (v_i)^{-2}$ and calculate its contributions to G^{-1} by rules i) through v) of the recursive method to form G^{-1} given previously.

If external storage is used to store contributions of the b^i to G^{-1}, the nonzero elements of G^{-1} are obtained by column within row (or vice versa) and added terms with equal row and column number.

The procedures described here greatly facilitate mixed model analysis when additive genetic variances differ across related additive genetic groups and inbreeding exists. Models that account for additive and nonadditive fixed effects as well as random additive genetic effects (sire, MGS) and random nonadditive effects associated with interactions of sire by genetic groups of dam are in (3, 4). Nonadditive fixed effects are defined to be associated with interactions of sire genetic group by dam genetic group. These models (3, 4) account for unequal additive and nonadditive variances across additive and nonadditive genetic fixed effects, respectively, and also can account for maternal additive and nonadditive effects. Models in (3, 4) use the rules to obtain G and G^{-1} given here when the evaluation is for a single trait. Although these models (3, 4) require specific residual variances for each straightbred and crossbred progeny group, they could be taken to be the same to ease computations. Furthermore, were several subsets of data (i.e., progeny groups) not connected to each other through sires or MGS, separate analyses of each subset would be simpler than a joint analysis.

Procedures of this paper will be useful for evaluation of animals in recurrent instances of semen importation. For example, in dairy cattle there is considerable exchange of semen between Canadian and United States populations. Because both populations have been under different selection pressures, their additive genetic variances for milk production traits are likely to differ. Thus, the procedure could be used to compute G^{-1} when young sires from both populations are evaluated within the United States or Canada. Also,

these procedures can be used in the analysis of crossbreeding experiments such as those in Beltsville, Illinois, Clemson, Georgia, Purdue, and British Columbia (2, 10, 12) when sires are included as random effects and unequal additive genetic variances across additive genetic groups are accounted for in the model. Such models may need to include nonadditive genetic fixed (group) and random effects and possibly maternal effects, depending on the trait being analyzed (3, 4). Finally, the procedures can be used to help analyze data from experiments to form new breeds, e.g., Kamaduk breed in India (1) and data from stratified crossbreeding programs such as in Sudan (9).

Numerical Example

The following hypothetical example will be used to illustrate the methods described to compute G and G^{-1} (Table 1).

TABLE 1. Data for the hypothetical example.

Individual	Sire	MGS[1]	Expected breed composition (2)		Additive variance
1	. . .	. . .		A	16
2	. . .	. . .		B	9
3	2	. . .	.5A	.5B	12.5
4	1	. . .		A	16
5	. . .	1	.5A	.5B	12.5
6	. . .	2	.25A	.75B	10.75
7	3	2	.5A	.5B	12.5
8	3	1	.75A	.25B	14.25

[1] Maternal grandsire.

[2] A = Breed A, B = Breed B.

TABLE 2. Matrix G for the example.

$$
\begin{bmatrix}
16 & 0 & 0 & 8 & 4 & 0 & 0 & 4 \\
0 & 9 & 4.5 & 0 & 0 & 2.25 & 4.5 & 2.25 \\
0 & 4.5 & 12.5 & 0 & 0 & 1.125 & 7.375 & 6.25 \\
8 & 0 & 0 & 16 & 2 & 0 & 0 & 2 \\
4 & 0 & 0 & 2 & 12.5 & 0 & 0 & 1 \\
0 & 2.25 & 1.125 & 0 & 0 & 10.75 & 1.125 & .5625 \\
0 & 4.5 & 7.375 & 0 & 0 & 1.125 & 13.625 & 3.6875 \\
4 & 2.25 & 6.25 & 2 & 1 & .5625 & 3.6875 & 14.25
\end{bmatrix}
$$

The complete G matrix is in Table 2. The first row of G will be used to show the calculations in building it. Here: $g_{11} = 16$, $g_{12} = 0$, $g_{13} = .5(0)$, $g_{14} = .5(16)$, $g_{15} = .25(16)$, $g_{16} = .25(0)$, $g_{17} = .5(0) + .25(0)$, $g_{18} = .5(0) + .25(16)$. Thus, the first row (= first column, by symmetry) is:

$$[16, 0, 0, 8, 4, 0, 0, 4]$$

TABLE 3. Matrix G^{-1} for the example.

$$
\begin{bmatrix}
.094941 & 0 & .012347 & -.041667 & -.021739 & 0 & 0 & -.024691 \\
0 & .148729 & -.034596 & 0 & 0 & -.024540 & -.028369 & 0 \\
.012347 & -.034596 & .150621 & 0 & 0 & 0 & -.056738 & -.049383 \\
-.041667 & 0 & 0 & .083333 & 0 & 0 & 0 & 0 \\
-.021739 & 0 & 0 & 0 & .086957 & 0 & 0 & 0 \\
0 & -.024540 & 0 & 0 & 0 & .098160 & 0 & 0 \\
0 & -.028369 & -.056738 & 0 & 0 & 0 & .113475 & 0 \\
-.024691 & 0 & -.049383 & 0 & 0 & 0 & 0 & .098765
\end{bmatrix}
$$

The complete matrix G^{-1} is in Table 3. Neither the sire nor the MGS of any of the animals in this example is inbred. Hence, the b^i's can be calculated with only the additive variances. For instance, $b^7 = [12.5 - .25(.08) - .0625 (.111111)] - 1 = .080173$. The rules to build G^{-1} indicate that we must add: b^7 to g^{77}, $.25\, b^7$ to g^{33}, $.0625\, b^7$ to g^{22}, $.125\, b^7$ to g^{32} and g^{23}, $-.5\, b^7$ to g^{73} and g^{37} and $-.25\, b^7$ to g^{72} and g^{27}.

The first row of L will be used to exemplify calculations to obtain the b^i's when a population is inbred. The v_i, $1 \leqslant i \leqslant 8$, are: $v_1 = (16)^{.5}$, $v_2 = 0$, $v_3 = .5(0)$, $v_4 = .5(4)$, $v_5 = .25(4)$, $v_6 = .25(0)$, $v_7 = .5(0) + .25(0)$, $v_8 = .5(0) + .25(4)$. Each v_i, $1 \leqslant i \leqslant 8$, is squared and added to the corresponding u_i. The b^1 ($= .0625$) can be computed before or after v_1 is calculated. Because the sire and the dam or the MGS of animal 1 are unknown, its only contribution to G^{-1} is .0625.

ACKNOWLEDGMENTS

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