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Genetic Groups in an Animal Model

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ABSTRACT

Rules are presented for assigning coefficients to the genetic group portion(s) of the mixed model equations after transformation to solve directly for total genetic value (group plus animal solutions) simultaneously for sires and cows using an animal model. Inclusion of all known relationships seems to reduce the need for groups to account for genetic selection and genetic trend. Migration of animals into a population, however, results in a need for grouping to account for genetic merit of the migrants. Selection of parents on which records are not available also creates a need for grouping. Group solutions represent the average genetic merit of phantom (unidentified, or represented by only one descendant) animals selected to be parents that do not have records available. Groups can be cross-classified with time and the genetic path of selection. The total genetic value for every animal includes a function of genetic groups. The function of genetic groups is specific for each individual animal and depends on the number of generations to the base phantom ancestors and on the genetic groups to which those phantom ancestors are assigned. The group coefficients presented account for genetic selection that cannot be defined by known genetic relationships.

INTRODUCTION

Historically, animals have been allocated to genetic groups to account for selection that cannot be accounted for by known genetic

relationships. Sires have been assigned to groups based on arbitrary criteria such as year of birth, stud, year of entry into service, geographical region, or pedigree information (7). Pollak and Quaas (6) demonstrated that the need for grouping decreases as the genetic relationships among animals become more complete. Simultaneous sire and cow evaluation including all known relationships minimizes the necessity of grouping (3, 6, 10). Nevertheless, some animals entering the population (e.g., from herds starting test or from other countries) could have extensive pedigrees but would not have recognized parents that contribute ties and records to the data.

Group effects can be thought of as accounting for selection not accounted for by records of relatives. Under this concept, groups would be assigned only if animals were missing genetic relationships. The genetic merit of all descendants of any animal that has a missing parent would then include a function of the genetic group of the missing ancestor. Thompson (10) suggested a similar approach to genetic grouping in the accumulated groups model.

Inclusion of groups in the animal model has proved computationally challenging (8, 11). The purpose of this paper is to describe simple rules for calculating the coefficients associated with group effects of the mixed model equations for an animal model.

THE ANIMAL MODEL WITH GENETIC GROUPS

The mixed model equations (MME) for the animal model provide direct solutions for animals with records (4). Genetic values of animals without records, such as sires or dams for which there are no records, are predicted by augmenting the MME with a function of the inverse of the relationship matrix (5).

In most models for animal evaluation previously used, only a single group effect was included as the total genetic group effect for an

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animal. If, however, groups are to account for unknown genetic selection, consideration of precisely what information is unknown is necessary.

An alternative to including a single group effect for each animal is to define groups only for phantom (unknown, with only a single descendant) parents that do not have a record. The use of the term phantom is to emphasize that those animals are not themselves of interest. Phantom animals are considered only to facilitate computing solutions to the MME for the animal model. The group genetic effects represent the average genetic contribution of phantom animals selected to be parents to their descendants that do have records. Under the assumption that knowing relationships accounts for the effect of selection on the related ancestors, there is no need to assign groups when both parents are known. Genetic groups must be assigned if one or more parents are unknown by assigning phantom parents to replace each of the unknown animals. The phantom parents are assumed to be average representatives of the genetic groups of similar animals selected to be parents at the same time. Selection differentials may be different for phantom males and females. Thus, two parallel sets of groups could represent phantom sires and phantom dams selected to be parents. Four parallel sets of groups could represent phantom sires of sires, phantom sires of cows, phantom dams of sires, and phantom dams of cows corresponding to the four paths of selection allowing for each path to have different genetic selection differentials. Genetic groups could be cross-classified by sex of animal and sex of phantom parent to account for four selection paths (9). If only two sets of groups are used, phantom sires and phantom dams, then consideration should be taken of the different generation intervals for each of the four paths of selection when allocating genetic groups by time and sex of phantom parent. A phantom dam of a bull would not necessarily be a representative of the same time group as a phantom dam of a cow even though the bull and cow were born in the same year because the dam of the bull is likely to have been born before the dam of the cow (14). The time period for the genetic group could be defined by subtracting the average genetic interval from the year of birth of the animal

with the missing parent to estimate the year of birth of the missing parent (11, 14).

EXAMPLE OF ALLOCATION TO GROUPS

Consider the pedigree in Figure 1. Different amounts of pedigree information are available on the identified animals. Both parents are unknown for S_1 , D_1 , and D_2 ; one parent is unknown for each of D_3 , D_4 , D_5 , and S_2 ; and both parents of S_3 and S_4 are known. Figure 2 shows the phantom parents that would be assigned for the example of Figure 1. A projected year (or time period) of birth for each phantom parent can be estimated from average generation intervals. One-half of the effect of the phantom parent genetic group is attributed to its progeny.

EQUIVALENT MIXED MODEL EQUATIONS WITH GROUPS INCLUDED

To develop notation for the MME including equations for phantom parents, let:

y be a vector of records,

X be an incidence matrix associating records with fixed effects represented in h ,

h be a vector of fixed effects, e.g., herd-year-season (HYS) effects,

g be the vector of order n of effects of groups to which phantom parents have been assigned,

Z be an incidence matrix associating records with elements in a_1 (if an identified animal does not have a record, e.g., a bull with daughters with records, the corresponding row in Z is null),

a_0 be a vector of genetic values of the phantom parents,

a_1 be a vector of genetic values corresponding to identified animals with the variance of $(a_0 \ a_1)' = A\sigma_a^2$,

e be a vector of residual effects with variance $R\sigma_e^2$, which in this development is assumed to be $I\sigma_e^2$,

Q_0 be the incidence matrix assigning phantom animals to groups,

Q_1 be the coefficient matrix relating identified animals to group effects,

A_{10} be the submatrix of the numerator relationship matrix corresponding to relationships

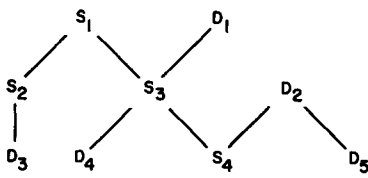


Figure 1. Sample pedigree.

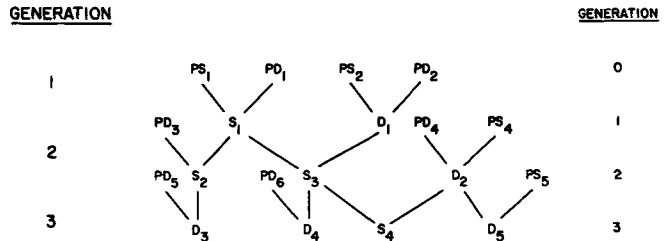


Figure 2. Assignment of phantom parents.

between identified animals and phantom parents,

A^{00} be the submatrix of the inverse of the relationship matrix corresponding to relationships among base (phantom) animals,

A^{01} be the submatrix of the inverse of the relationship matrix corresponding to relationships between phantom parents and identified animals, and

A^{11} be the submatrix of the inverse of the relationship matrix corresponding to relationships among identified animals.

In matrix notation, the model for animals with records can be expressed as:

$$y = Xh + Za + ZQ_1g + e$$

Note that elements of Q_1 , q_{jr} , are fractions re-

lating the contribution of the r^{th} genetic group to the total genetic value of the j^{th} animal. The total of genetic group effects for the j^{th} animal is:

$$\sum_{r=1}^n q_{jr} \xi_r$$

which is a weighted average of specific genetic group effects where the sum of the weights is one. The estimate of total genetic value for the j^{th} animal is:

$$\hat{u}_j = \hat{a}_j + \sum_{r=1}^n q_{jr} \hat{g}_r$$

The phantom parents can be included in the augmented MME (5) to give with $k = \sigma_e^2/\sigma_a^2$:

$$\begin{bmatrix} A^{00}k & A^{01}k & 0 & 0 \\ A^{10}k & Z'Z + A^{11}k & Z'ZQ_1 & Z'X \\ 0 & Q_1'Z'Z & Q_1'Z'ZQ_1 & Q_1'Z'X \\ 0 & X'Z & X'ZQ_1 & X'X \end{bmatrix} \begin{bmatrix} \hat{a}_0 \\ \hat{a}_1 \\ \hat{g} \\ \hat{h} \end{bmatrix} = \begin{bmatrix} 0 \\ Z'y \\ Q_1'Z'y \\ X'y \end{bmatrix}$$

The vector of total group effects for the identified animals is represented by Q_1g . A single genetic group effect is assigned only to each phantom parent. Every descendant of a phantom parent is assigned a fraction of the phantom parent's genetic group effect with the fraction depending on the genetic relationship of the descendant to the phantom animal. Therefore, the vector of total group effects is $Q_1g = A_{10}Q_0g$; that is, identified animals are related back to the genetic groups of the phantom ancestors with $A_{10}Q_0 = Q_1$. The MME can now be re-expressed as:

$$\begin{bmatrix} A^{00}k & A^{01}k & -Q_0k & 0 \\ A^{10}k & Z'Z + A^{11}k & 0 & Z'X \\ -Q'_0k & 0 & Q'_0Q_0k & 0 \\ 0 & X'Z & 0 & X'X \end{bmatrix} \begin{bmatrix} \hat{a}_0 + Q_0\hat{g} \\ \hat{a}_1 + A_{10}Q_0\hat{g} \\ \hat{g} \\ \hat{h} \end{bmatrix} = \begin{bmatrix} 0 \\ Z'y \\ 0 \\ X'y \end{bmatrix}$$

Inclusion of phantom parents in the equations increases the number of equations to solve. The solutions, however, for phantom parents are never needed. Absorption of the equations for the phantom parents provides an alternative set of equations that are more tractable, and for which rules for accumulation of coefficients associated with group effects and additive genetic values can be defined easily.

Absorption of the equations for phantom parents into the QP transformed equations yields:

$$\begin{bmatrix} Z'Z + [A^{11} - A^{10}(A^{00})^{-1}A^{01}]k & A^{10}(A^{00})^{-1}Q_0k & Z'X \\ Q'_0(A^{00})^{-1}A^{01}k & [Q'_0Q_0 - Q'_0(A^{00})^{-1}Q_0]k & 0 \\ X'Z & 0 & X'X \end{bmatrix} \begin{bmatrix} \hat{a}_1 + A_{10}Q_0\hat{g} \\ \hat{g} \\ \hat{h} \end{bmatrix} = \begin{bmatrix} Z'y \\ 0 \\ X'y \end{bmatrix}$$

RULES FOR GROUPING

Examination of the coefficients of the mixed model equations after absorption of the equations for phantom parents proves illuminating. Let:

$$W_{11} = A^{11} - A^{10}(A^{00})^{-1}A^{01}$$

$$W_{12} = A^{10}(A^{00})^{-1}Q_0$$

$$W_{22} = Q'_0Q_0 - Q'_0(A^{00})^{-1}Q_0$$

The coefficient matrix after absorption resembles the coefficient matrix for equations augmented by animals without records with terms in W replacing terms in A⁻¹:

$$\begin{bmatrix} Z'Z + W_{11}k & W_{12}k & Z'X \\ W'_{12}k & W_{22}k & 0 \\ X'Z & 0 & X'X \end{bmatrix}$$

The four submatrices have been changed by absorption of equations for the phantom parents.

Rules for Construction of the (Animal, Animal) Submatrix

Submatrix W₁₁ = A¹¹ - A¹⁰(A⁰⁰)⁻¹A⁰¹. Because phantom parents are absorbed, the terms allocated to W₁₁ are identical to those that would be calculated for A⁻¹ according to Henderson's rules (2) had phantom parents not been included in the calculations.

Rules for Construction of the (Animal, Group) Submatrix

Submatrix W₁₂ = A¹⁰(A⁰⁰)⁻¹Q₀. W₁₂ relates identified animals to groups of phantom parents and also can be easily computed with Henderson's rules (2) for calculating the inverse of the relationship matrix. All identified animals in the data set have two parents, either identified or phantom. Henderson's rules for

assigning off-diagonal coefficients when both parents are known are used for such animals. A^{00} is the portion of the inverse of the relationship matrix that pertains to phantom animals. By definition each phantom parent has only one progeny. A mate (m) of a phantom parent (j) is either another phantom parent (if progeny, i, has two phantom parents) or an identified animal (if i has one identified parent). According to Henderson's rules, the diagonal of A^{00} is always 1.5. All off-diagonals for the jth row of A^{00} will be 0 if m is an identified animal. The (j,m)th element of A^{00} will be .5 if m is a phantom parent. The block diagonal structure of A^{00} permits easy definition of $(A^{00})^{-1}$, which will also be block diagonal. For a phantom parent (j) mated to a phantom parent (m), the diagonal terms, (j,j) and (m,m), for $(A^{00})^{-1}$ will be .75 and the off-diagonal terms, (j,m) and (m,j), will be -.25. All other off-diagonals will be zero. For phantom parent (j) mated to an identified animal (m) the diagonal term (j,j) of $(A^{00})^{-1}$ will be .66 and all off-diagonals in the corresponding row and column will be 0. For example, if:

$$A^{00} = \begin{bmatrix} 1.5 & .5 & 0 \\ .5 & 1.5 & 0 \\ 0 & 0 & 1.5 \end{bmatrix}$$

then:

$$(A^{00})^{-1} = \begin{bmatrix} .75 & -.25 & 0 \\ -.25 & .75 & 0 \\ 0 & 0 & .66 \end{bmatrix}$$

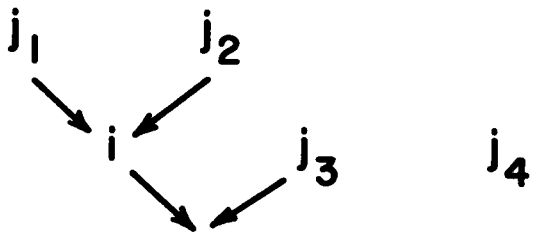
A^{10} relates identified progeny to phantom parents and identified parents to their phantom mates. There will be an off-diagonal coefficient for every phantom mate of i and one for

every phantom parent of i. The number of non-zero off-diagonal coefficients in the ith row of A^{10} is limited by the number of phantom mates of the ith identified animal. If i and j are mates, then the (i,j)th coefficient of A^{10} will be .5. If i and j are parent-progeny, the (i,j)th coefficient will be -1.0. The possible nonzero elements of W_{12} will be shown by example.

RULES BY EXAMPLE

Example 1

Let a subset of the animals being evaluated in a population be i, j₁, j₂, j₃, and j₄. The relationships between i and the phantom animals are defined by the following pedigree.



where:

i is an identified animal, the progeny of phantom parents j₁ and j₂,

i is mated to phantom parent j₃ (the offspring of i and j₃ is not shown in the pedigree), and

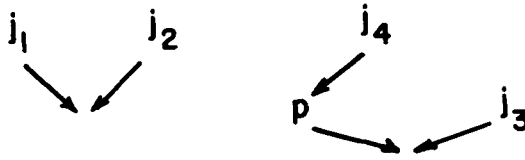
j₄ is a phantom animal mated to another identified animal.

Then the ith row of $A^{10}(A^{00})^{-1}Q_0$ is:

$$(-1 \quad -1 \quad .5 \quad 0) \begin{bmatrix} .75 & -.25 & 0 & 0 \\ -.25 & .75 & 0 & 0 \\ 0 & 0 & .66 & 0 \\ 0 & 0 & 0 & .66 \end{bmatrix} Q_0 = (-.5 \quad -.5 \quad .33 \quad 0) Q_0$$

Example 2

Let a subset of the animals being evaluated in a population be $p, j_1, j_2, j_3,$ and j_4 with relationships between identified animal p and phantom animals (j) be defined by:



In this example, j_1 and j_2 are phantom mates but are not related to p , p is an identified animal and a progeny of phantom animal j_4 , and j_3 is a phantom mate of p . Then the p th row $A^{10}(A^{00})^{-1}Q_0$ is:

$$\begin{pmatrix} 0 & 0 & .5 & -1.0 \end{pmatrix} \begin{bmatrix} .75 & -.25 & 0 & 0 \\ -.25 & .75 & 0 & 0 \\ 0 & 0 & .\overline{66} & 0 \\ 0 & 0 & 0 & .\overline{66} \end{bmatrix} Q_0 \\
 = \begin{pmatrix} 0 & 0 & .\overline{33} & -.\overline{66} \end{pmatrix} Q_0$$

The only nonzero coefficients in W_{12} (the animal, group coefficient submatrix) result from phantom parent-offspring relationships or from matings to phantom animals. The Q_0 is a matrix of 1's and 0's assigning each phantom parent to a group. Postmultiplication of A_{10} by Q_0 designates the specific group effects of the phantom animals that contribute to total genetic value of the identified animals.

Thus, the rules for constructing coefficients for $W_{12}k$ are as follows. For i , the progeny of j and m , the mate of l , when both parents, j and m , are phantom, add the following to the indicated coefficients of $W_{12}k$,

- add $-.5k$ to (i, group of j)
- add $-.5k$ to (i, group of m).

- If a single parent, j , is phantom,
- add $.66k$ to (i, group of j),
- and if a mate l is phantom,
- add $.33k$ to (i, group of l).

Rules for Construction of the (Group, Group) Submatrix

$W_{22} = Q_0'Q_0 - Q_0'(A^{00})^{-1}Q_0$. $Q_0'Q_0$ is a

diagonal matrix summing the number of phantom animals in each group. Because of the nature of $(A^{00})^{-1}$ the (group, group) coefficients may be defined for i , which is the progeny of j and m , and also the mate of l . Thus, the rules for constructing coefficients for $W_{22}k$ are:

- If both parents j and m are phantom then,
- add $(1 - .75)k = .25k$ to the diagonal coefficient corresponding to the j th group.
- add $(1 - .75)k = .25k$ to the diagonal coefficient corresponding to the m th group.
- add $.25k$ to the (j th group, m th group coefficient).
- add $.25k$ to the (m th group, j th group coefficient).
- If l is a phantom mate,
- add $(1 - .66)k = .33k$ to the diagonal corresponding to the l th group.

SUMMARY OF RULES

Summary of Rules for Calculating Coefficients due to Groups

The rules can be summarized. For *i*, the progeny of *j* and *m*, add the coefficients to the appropriate row and column locations when

a) one parent (*m*) is phantom:

	<i>i</i>	<i>j</i>	group of <i>m</i>
<i>i</i>	0	0	-2 <i>k</i> /3
<i>j</i>	0	0	<i>k</i> /3
group of <i>m</i>	-2 <i>k</i> /3	<i>k</i> /3	<i>k</i> /3

b) both parents (*j,m*) are phantom:

	<i>i</i>	group of <i>j</i>	group of <i>m</i>
<i>i</i>	0	- <i>k</i> /2	- <i>k</i> /2
group of <i>j</i>	- <i>k</i> /2	<i>k</i> /4	<i>k</i> /4
group of <i>m</i>	- <i>k</i> /2	<i>k</i> /4	<i>k</i> /4

Summary of Computing Rules for Calculating Coefficients due to Groups and Relationships

An alternate presentation indicates the relationship between the rules for incorporation of the A^{-1} matrix and rules for coefficients due to groups after absorption of phantom parents.

Let the QP transformed MME be represented as:

$$\begin{bmatrix} Z'Z + Wk & Z'X \\ X'Z & X'X \end{bmatrix} \begin{bmatrix} \hat{u} \\ \hat{b} \end{bmatrix} = \begin{bmatrix} Z'y \\ X'y \end{bmatrix}$$

where \hat{u} includes both \hat{g} and $\hat{a} + A_{10}Q_0\hat{g}$ (group and animal merit) and $Z'Z$ has null rows and columns corresponding to groups. The matrix *W* is computed from the following rules. For each identified animal let:

- IA = animal's number,
- IS = sire's number (if identified) or sire's group number (if sire is phantom),
- ID = dam's number (if identified) or dam's group number (if dam is phantom),
- D = 1 if both parents are phantom, 4/3 if one parent is phantom, and 2 if both parents are identified, and
- $k = \sigma_e^2/\sigma_a^2$ as defined previously.

Then add:

- D*k* to (IA,IA)
- .5D*k* to (IA,IS), (IS,IA), (ID,IA), (IA,ID)
- .25D*k* to (IS,IS), (IS,ID), (ID,IS), and (ID,ID).

The coefficients added to *W* are as indicated such that for animal *i* with a) both parents (*j,m*) known (*D* = 2):

	<i>i</i>	<i>j</i>	<i>m</i>
<i>i</i>	2 <i>k</i>	-1 <i>k</i>	-1 <i>k</i>
<i>j</i>	-1 <i>k</i>	<i>k</i> /2	<i>k</i> /2
<i>m</i>	-1 <i>k</i>	<i>k</i> /2	<i>k</i> /2

b) one parent (*m*) unknown (*D* = 4/3):

	<i>i</i>	<i>j</i>	group of <i>m</i>
<i>i</i>	4 <i>k</i> /3	-2 <i>k</i> /3	-2 <i>k</i> /3
<i>j</i>	-2 <i>k</i> /3	<i>k</i> /3	<i>k</i> /3
group of <i>m</i>	-2 <i>k</i> /3	<i>k</i> /3	<i>k</i> /3

c) two parents (*j,m*) unknown (*D* = 1):

	<i>i</i>	group of <i>j</i>	group of <i>m</i>
<i>i</i>	1 <i>k</i>	- <i>k</i> /2	- <i>k</i> /2
group of <i>j</i>	- <i>k</i> /2	<i>k</i> /4	<i>k</i> /4
group of <i>m</i>	- <i>k</i> /2	<i>k</i> /4	<i>k</i> /4

Any column of *W* will sum to zero.

EXAMPLE WITH RECORDS

An example of computation of group coefficients is given for simultaneous sire and cow evaluation using mixed model equations which have been QP transformed. In this example there are two herds, each with two HYS and representing two sires (*s_j*) and two groups (*g_k*). The cows' records are in brackets.

Herd 1

- HYS₁₁: C₁₃ (8), C₁₄ (7)
- HYS₁₂: C₁₁ (-2), C₁₂ (7)

Herd 2

- HYS₂₁: C₂₃ (11), C₂₄ (0), C₂₅ (10)
- HYS₂₂: C₂₁ (-8), C₂₂ (-9)

Let the genetic relationships be defined by the following pedigree.

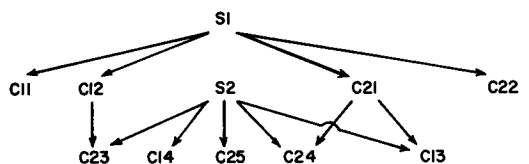


TABLE 1. The QP transformed mixed model equations.

5	0	0	0	0	1	0	0	0	0	0	0	0	0	-2	0	-2	0	\hat{c}_{11}	-2
0	6.5	0	0	0	1	0	0	-3	0	0	0	0	0	-2	1.5	-2	0	\hat{c}_{12}	7
0	0	7	0	1	0	-3	0	0	0	0	0	0	0	0	-3	0	0	\hat{c}_{13}	8
0	0	0	5	1	0	0	0	0	0	0	0	0	0	0	-2	0	-2	\hat{c}_{14}	7
0	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	\hat{h}_{11}	15
1	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	\hat{h}_{12}	5
0	0	-3	0	0	0	8	0	0	-3	0	0	1	-2	3	-2	0	0	\hat{c}_{21}	-8
0	0	0	0	0	0	0	5	0	0	0	0	1	-2	0	-2	0	0	\hat{c}_{22}	-9
0	-3	0	0	0	0	0	0	7	0	0	1	0	0	-3	0	0	0	\hat{c}_{23}	11
0	0	0	0	0	0	-3	0	0	7	0	1	0	0	-3	0	0	0	\hat{c}_{24}	0
0	0	0	0	0	0	0	0	0	0	5	1	0	0	-2	0	-2	0	\hat{c}_{25}	10
0	0	0	0	0	0	0	0	1	1	1	3	0	0	0	0	0	0	\hat{h}_{21}	21
0	0	0	0	0	0	1	1	0	0	0	0	2	0	0	0	0	0	\hat{h}_{22}	-17
-2	-2	0	0	0	0	-2	-2	0	0	0	0	0	7	0	2.5	-1.5	0	\hat{s}_1	0
0	1.5	-3	-2	0	0	3	0	-3	-3	-2	0	0	0	9.5	-1.5	.5	0	\hat{s}_2	0
-2	-2	0	0	0	0	-2	-2	0	0	0	0	0	2.5	-1.5	5.5	1.5	0	\hat{g}_1	0
0	0	0	-2	0	0	0	0	0	0	-2	0	0	-1.5	.5	1.5	3.5	0	\hat{g}_2	0

Let two genetic groups account for selection. One parent each of S₁ and S₂ is from group 1 and one is from group 2; all phantom mates of S₁ are assumed to be representatives of group 1, and all phantom mates of S₂ are assumed to be average representatives of those cows selected to be dams from group 2. For heritability of .25, $k = \sigma_e^2/\sigma_a^2 = 3.0$. The QP transformed MME, where the c's and s's correspond to genetic merit (deviation plus function of group effects), are in Table 1.

CONCLUSION

The rules defined in this paper are applicable for solving QP transformed equations for an animal model where all known relationships are included. They have been presented before in oral presentation and abstract (12) and have been used in a simultaneous sire and cow evaluation in the Northeast (11, 13, 14). With minor alterations they can be extended to equations for the QP transformed reduced animal model. The reduced animal model has been described previously (1).

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