

Prediction of Merits of Potential Matings from Sire-Maternal Grand sire Models with Nonadditive Genetic Effects

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ABSTRACT

Models for BLUP of matings under a nonadditive genetic model were derived for two equivalent models. These models were, first, an animal model with missing data on dams and, second, a sire-maternal grandsire model. The second model results in a marked decrease in the order of the mixed model equations and produces predictions identical to those of the animal model. The sire-maternal grandsire model first predicts merits of mating groups. Then a back solution can be used to predict individuals within mating groups. Also, minimum variance quadratic unbiased estimation for the sire-maternal grandsire model was found to produce the same estimates as those obtained employing the animal model for minimum variance quadratic unbiased estimation.

INTRODUCTION

Two quite different problems in the design of mating strategies exist. First, there are several traits of interest, and some or all of these have an intermediate optimum. In the simplest case, nonadditive genetic effects are negligible, and the goal is to choose matings that will maximize the genetic merit of progeny for some nonlinear merit function. This problem has been discussed elsewhere (1). A second problem, addressed in this paper, is the selection of matings to maximize genetic merit of progeny with respect to a single trait when the goal is maximum milk yield, for example. Further, nonadditive genetic effects are assumed to be nonnegligible.

Some methods that utilize the animal model

(AM) with nonadditive genetic effects have been described (7, 8). Only noninbred populations with negligible linkage effects can be dealt with in a simple manner, because Cockerham's (3) model can be invoked. For this paper I shall consider only one record per animal on the single trait of interest. The method can be extended with considerable difficulty to incorporate multiple traits, repeated records, and maternal effects.

In the strictly additive genetic effects model, the reduced animal model (RAM) of Quaas and Pollak (10) can be employed advantageously. There appears to be no comparable method for nonadditive genetic effects, because joint sire-dam effects need to be employed rather than separate sire and dam effects as in the additive model. A model often used in dairy cattle breeding is either a sire or a sire-maternal grandsire (sire-MGS) model. The purpose of this paper is to present a method for prediction of production of the progeny of a mating of a sire with a random daughter of an unrelated sire from an analysis under a sire-maternal grandsire model. The method is based on the equivalence of the sire-MGS model to AM with missing data on the dams. If nonadditive genetic effects are important and variances of these effects can be estimated accurately, then predictors will have smaller prediction error variances than predictors based on additive effects only. The latter prediction is simply predicted sire effect plus half the predicted maternal grandsire effect. If it can be assumed legitimately that the mates of a sire (the daughters of their maternal grandsires) are a random sample from their respective sires, the resulting predictors are unbiased and in a good AI program have prediction error variances that probably are not much greater than in an AM with recorded mates. The number of mixed model equations can be markedly fewer than in an AM. Further, such predictors are less biased than those from an AM where bull dams have received preferential treatment.

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$$\begin{bmatrix} X'X & X'Z \\ Z'X & Z'Z+T^{-1}\sigma_e^2 \end{bmatrix} \begin{bmatrix} \beta^\circ \\ \hat{t} \end{bmatrix} = \begin{bmatrix} X'y \\ Z'y \end{bmatrix} \tag{3}$$

where \hat{t} is BLUP of $a + d + aa + ad$. Under the Cockerham model:

$$\text{var}(t) \equiv T = A\sigma_a^2 + D\sigma_d^2 + A\#A\sigma_{aa}^2 + A\#D\sigma_{ad}^2$$

Then if we are interested in \hat{a} , \hat{d} , etc. of this individual,

$$\hat{a} = A\sigma_a^2 T^{-1} \hat{t}$$

$$\hat{d} = D\sigma_d^2 T^{-1} \hat{t}, \text{ etc.}$$

The basis for this result is given by Henderson (5).

Prediction of Future Matings

The primary purpose of the foregoing formulation is the prediction of genetic merit of future matings. Let t_f be the genetic merit of a single progeny of each of several potential matings that were not in the equations of [3]. Let:

$$\text{var} \begin{bmatrix} t \\ t_f \end{bmatrix} = \begin{bmatrix} T_{pp} & T_{pf} \\ T'_{pf} & T_{ff} \end{bmatrix} \tag{4}$$

where $T_{pp} = T$ of [3], T_{pf} is the covariance between t and t_f , and T_{ff} is the variance of these t_f .

$$\hat{t}_f = T'_{pf} T_{pp}^{-1} \hat{t} \tag{5}$$

Then the prediction of the mean of any number of progeny of a mating is the appropriate element of \hat{t}_f that pertains to a single progeny of that mating. This section is intended only to introduce a more efficient computing strategy presented in the next section.

SIRE-MATERNAL GRANDSIRE METHODS

If the mates of sires can be regarded as a random sample of the female progeny of their

respective sires, and if records of these mates are not utilized, a sire-MGS model can be written that is equivalent to the AM. Equivalence means that the first and second moments of y are the same in the two models (9). In the nonadditive genetic effects model this is not the RAM (10) often used for additive effects. Rather, it is a model that includes progeny group effects, where a group represents the progeny of a sire mated with random progeny of an unrelated sire.

Model

Partition the data vector as:

$$y' = [y'_1 : y'_2 : y'_3] \tag{6}$$

where:

- y_1 represents records of progeny of a known sire by a known maternal grandsire mating,
- y_2 represents records on progeny of a known sire by unknown maternal grandsire, and
- y_3 represents records on progeny of an unknown sire by a known maternal grandsire.

The records in y_1 are ordered within sire by maternal grandsire progeny groups, and similarly for ordering of y_2 and y_3 . The model is:

$$y = X\beta + Zp + \epsilon \tag{7}$$

where

$$p' = [p'_1 : p'_2 : p'_3] \tag{8}$$

The elements of p_1 refer to sire by maternal grandsire effects, and similarly for p_2 and p_3 . The elements of p are sums of a , d , etc.

$\text{Var}(p)$ is computed from A , D , etc. that are derived as though there is only one progeny of each mating of sire by random daughter of a maternal grandsire. Then the diagonals are modified as will be described.

Recursive Computation of A in a Sire-Maternal Grandsire Model

Start with a $b \times b$ A matrix representing base population animals. That is, $A_{bb} = I$. Then the matrix is expanded one row (and column) at a time. Suppose A now has order $j-1$. Then $a_{ij}(i = 1, \dots, j-1) = .5a_{is} + k a_{id}$, where s represents sire and d the dam or maternal grandsire of the j^{th} animal, and $k = .5$ if d is a dam and $k = .25$ if d is a maternal grandsire. If the sire is unknown, set a_{is} to 0, and if d is unknown set a_{id} to 0. Also $a_{ij} = 1 + k a_{sd}$ and $a_{sd} = 0$ if either s or d is unknown. For the Cockerham model to hold, all a_{sd} must be 0, that is, all animals must be noninbred.

Computation of D

Given an A matrix with all diagonals = 1, we can now compute the D matrix for the same animals. All diagonals of D = 1, and off-diagonal elements are computed as follows for i with j (j with i). Let the parents of i be s_i, d_i and of j be s_j, d_j . The d_i and d_j also can represent maternal grandsires. Now

$$d_{ij} = b [a_{s_i, s_j} a_{d_i, d_j} + a_{s_i, d_j} a_{d_i, s_j}]$$

where $b = .25$ if d_i and d_j are both dams, $b = .125$ if d_i is a maternal grandsire and d_j is a dam, $b = .125$ if d_j is a maternal grandsire and d_i is a dam, and $b = .0625$ if d_i and d_j are both maternal grandsires, and $b = 0$ if one or more of s_i, d_i, s_j, d_j is unknown.

The foregoing algorithms can be used to compute A and D for base animals, sires and maternal grandsires, and one progeny of the sire by maternal grandsire groups that has tested progeny. Note that a sire can also be a maternal grandsire of some other group. For A and D to be valid the sire and maternal grandsire of every tested progeny must be unrelated.

Now delete base animals that are not sires or maternal grandsires of tested progeny from A and D and call these matrices A_t and D_t . Next delete sires and maternal grandsires and call these matrices A_r and D_r . Then the diagonals of A_r and D_r are modified to form A_m and D_m

that are used in the reduced mixed model equations [9]. The changes in diagonals are now described.

Changes to Diagonals of A_r

The diagonals of the p_1 part of A_r are the a_{ij} for any 2 progeny of the mating of a sire by maternal grandsire. The diagonals of the p_2 part are a_{ij} for 2 progeny of the same sire and unknown maternal grandsire. The diagonals of the p_3 part are a_{ij} for 2 progeny of the same maternal grandsire with unknown sires. These values are 5/16, 1/4, 1/16 for p_1, p_2, p_3 , respectively.

Change of Diagonals of D_r

Again, partitions correspond to p_1, p_2 , and p_3 , and the diagonal values are 1/16, 0, 0 for p_1, p_2, p_3 , respectively.

Computation of Var(p)

Denote modified A_r by A_m and modified D_r by D_m . Then $\text{var}(p) \equiv P = \sigma_a^2 A_m + \sigma_d^2 D_m + \sigma_{aa}^2 A_m \# A_m + \sigma_{ad}^2 A_m \# D_m + \text{etc.}$ Thus, the diagonals of $A_m \# A_m$ are $(5/16)^2, (1/4)^2, (1/16)^2$ and of $A_m \# D_m$ are 5/256, 0, 0.

Modification of R

Remember that $\text{Var}(\epsilon)$ for the AM is assumed to be $I\sigma_e^2$. If that is used for the sire-MGS model, the variance of each y is not $\sigma_e^2 + \sigma_a^2 + \sigma_d^2 + \dots$ as with AM but rather is smaller. Consequently, we define the error vector as ϵ and it should have variance:

$$I\sigma_e^2 + R_a \sigma_a^2 + R_d \sigma_d^2 + \dots \equiv R_m$$

where R_a, R_d, \dots are diagonal with elements described below.

Let $\epsilon' = [\epsilon'_1 \ \epsilon'_2 \ \epsilon'_3]$, corresponding to $[y'_1 \ y'_2 \ y'_3]$. Thus ϵ_1 has elements numbering the same as the total number of tested progeny of known sire by known maternal grandsire.

$$\text{Var}(\epsilon_1) = \mathbf{R}_{a1}\sigma_a^2 + \mathbf{R}_{d1}\sigma_d^2 + \mathbf{R}_{aa1}\sigma_{aa}^2 + \mathbf{R}_{ad1}\sigma_{ad}^2 + \dots$$

$$\text{Var}(\epsilon_2) = \mathbf{R}_{a2}\sigma_a^2 + \mathbf{R}_{d2}\sigma_d^2 + \mathbf{R}_{aa2}\sigma_{aa}^2 + \mathbf{R}_{ad2}\sigma_{ad}^2 + \dots$$

and;
$$\text{Var}(\epsilon_3) = \mathbf{R}_{a3}\sigma_a^2 + \mathbf{R}_{d3}\sigma_d^2 + \mathbf{R}_{aa3}\sigma_{aa}^2 + \mathbf{R}_{ad3}\sigma_{ad}^2 + \dots$$

All these matrices are diagonal.

The diagonal elements of \mathbf{R}_{a1} , \mathbf{R}_{a2} , \mathbf{R}_{a3} are 11/16, 3/4, and 15/16, respectively. Note that these are 1 - 5/16, 1 - 1/4, and 1 - 1/16, where 5/16, 1/4, and 1/16 are diagonals of \mathbf{A}_m . The diagonals of \mathbf{R}_{d1} , \mathbf{R}_{d2} , \mathbf{R}_{d3} are 15/16, 1, and 1, respectively, corresponding to one minus diagonals of \mathbf{D}_m , that is, 1/16, 0, 0. The diagonals of \mathbf{R}_{aa1} , \mathbf{R}_{aa2} , \mathbf{R}_{aa3} are 1 - (5/16)², 1 - (1/4)², 1

- (1/16)². The diagonals of \mathbf{R}_{ad1} , \mathbf{R}_{ad2} , \mathbf{R}_{ad3} are 1 - (5/256)², 1 - 0, 1 - 0.

Mixed Model Equations

The reduced \mathbf{Z} matrix, say \mathbf{Z}_m , is \mathbf{I} of order equal to number of elements in \mathbf{p}_1 , \mathbf{p}_2 , \mathbf{p}_3 and with rows repeated to correspond to the number of progeny in a mating. Now the mixed model equations are:

$$\begin{bmatrix} \mathbf{X}'\mathbf{R}_m^{-1}\mathbf{X} & \mathbf{X}'\mathbf{R}_m^{-1}\mathbf{Z}_m \\ \mathbf{Z}'_m\mathbf{R}_m^{-1}\mathbf{X} & \mathbf{Z}'_m\mathbf{R}_m^{-1}\mathbf{Z}_m + \mathbf{P}^{-1} \end{bmatrix} \begin{bmatrix} \beta^* \\ \hat{\mathbf{p}} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{R}_m^{-1}\mathbf{y} \\ \mathbf{Z}'_m\mathbf{R}_m^{-1}\mathbf{y} \end{bmatrix} \quad [9]$$

The solution to β^* is the same as in [3] if \mathbf{X} is full rank. If \mathbf{X} is not full rank, and $\mathbf{K}'\beta$ is estimable, $\mathbf{K}'\beta^*$ is the same for the two solutions.

Other Predictions Derived from $\hat{\mathbf{p}}$ and $\hat{\epsilon}$

Several predictions can be obtained by computing appropriate linear functions of $\hat{\mathbf{p}}$ and $\hat{\epsilon}$ because these contain all of the information in the data. Too little experience is available from use of nonadditive genetic variance to state unequivocally what is optimum. Consequently, a number of predictors are presented that can be examined with specific incidence matrices and range of parameter values.

Separate Genetic Effects for Groups. Let the genetic effects for groups be \mathbf{a}_g , \mathbf{d}_g , . . . , where $\mathbf{a}_g + \mathbf{d}_g + \mathbf{aa}_g . . . = \mathbf{p}$ of [7].

$$\begin{aligned} \hat{\mathbf{a}}_g &= \sigma_a^2 \mathbf{A}_m \mathbf{P}^{-1} \hat{\mathbf{p}} \\ \hat{\mathbf{d}}_g &= \hat{\sigma}_d^2 \mathbf{D}_m \mathbf{P}^{-1} \hat{\mathbf{p}} \\ \hat{\mathbf{aa}}_g &= \sigma_{aa}^2 \mathbf{A}_m \# \mathbf{A}_m \mathbf{P}^{-1} \hat{\mathbf{p}} \end{aligned} \quad [10]$$

Then:
$$\hat{\mathbf{a}}_g + \hat{\mathbf{d}}_{gg} + \dots = \hat{\mathbf{p}} \text{ of [9]} \quad [11]$$

Producing Abilities and Separate Genetic Effects for Female Progeny. Equation [3] shows how to compute $\hat{\mathbf{t}}$, producing abilities of individuals. Identical results can be obtained from $\hat{\mathbf{p}}$ of [9] and from:

$$\hat{\epsilon} = \mathbf{y} - \mathbf{X}\beta^* - \mathbf{Z}\hat{\mathbf{p}}$$

This is:

$$\hat{\mathbf{t}} = \mathbf{Z}_m \hat{\mathbf{p}} + (\sigma_a^2 \mathbf{R}_a + \sigma_d^2 \mathbf{R}_d + \dots) \mathbf{R}_m^{-1} \hat{\epsilon} \quad [12]$$

If individual effects are wanted, and these are identical to the solution to [2], compute:

$$\begin{aligned} \hat{\mathbf{a}} &= \mathbf{Z}_m \hat{\mathbf{a}}_g + \sigma_a^2 \mathbf{R}_a \mathbf{R}_m^{-1} \hat{\epsilon}, \\ \hat{\mathbf{d}} &= \mathbf{Z}_m \hat{\mathbf{d}}_g + \sigma_d^2 \mathbf{R}_d \mathbf{R}_m^{-1} \hat{\epsilon}, \text{ etc.,} \end{aligned} \quad [13]$$

where $\hat{\mathbf{a}}_g$, $\hat{\mathbf{d}}_g$. . . are shown in [10].

Predictions for Potential Mating Groups with No Tested Progeny. Expand $\sigma_a^2 \mathbf{A}_m$, $\sigma_d^2 \mathbf{D}_m$, . . . to include these nontested groups. From these compute an expanded \mathbf{P} matrix. Denote the expanded matrices by:

Animal Model Solution

Now Z of AM is I with order, 25. The relationship matrix, A, for the 25 progeny is in Figure 1. The D matrix has this form:

$$\begin{bmatrix} B_1 & 0 & 0 & 0 \\ & B_2 & 0 & 0 \\ & & B_3 & 0 \\ \text{Symmetric} & & & B_4 \end{bmatrix}$$

where:

$$B_1 = \begin{bmatrix} 16 & 1 & 1 & 0 & 1 & 1 \\ & 16 & 1 & 0 & 1 & 1 \\ & & 16 & 0 & 1 & 1 \\ \text{Symmetric} & & & 16 & 0 & 0 \\ & & & & 16 & 1 \\ & & & & & 16 \end{bmatrix} /16$$

$$B_2 = \begin{bmatrix} 16 & 1 & 1 & 1 \\ & 16 & 1 & 1 \\ & & 16 & 1 \\ \text{Symmetric} & & & 16 \end{bmatrix} /16$$

$B_3 = B_2$, and $B_4 = I$ with order, 11.

Assuming that $\sigma_a^2 = 5$, $\sigma_{aa}^2 = 3$, $\sigma_d^2 = 4$, $\sigma_{ad}^2 = 2$, some of the elements of T are:

$$\begin{bmatrix} 3584 & 549 & 549 & \dots & 0 & 0 & 0 \\ & 3584 & 549 & \dots & 0 & 0 & 0 \\ & & 3584 & \dots & 0 & 0 & 0 \\ & & & & \vdots & \vdots & \vdots \\ & & & & \vdots & \vdots & \vdots \\ & & & & 3584 & 0 & 0 \\ & & & & & 3584 & 83 \\ & & & & & & 3584 \end{bmatrix} /256$$

The value of σ_e^2 is assumed to be 16. Then $\text{var}(y) = T + 16I$.

Now the mixed model solution is:

$$\begin{aligned} \beta^\circ &= [2.4870, .5965]' \\ \hat{t} &= [-.3023, -.1306, .2950, .5334, -.2023, -.8818, .3393, \\ & 1.0188, 1.6983, .2572, .0711, -.1006, .4146, .5864, \\ & .1472, -.0303, -.1871, -.3646, -.5421, -.3583, -.1723, \\ & .0136, .1996, .3379, -.9557]'. \end{aligned}$$

Sire and Maternal Grand sire Solution

$$Z_m = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

Note that Z_m has 25 rows corresponding to 25 progeny and 9 columns corresponding to 9 sib groups.

$$A_m = \frac{1}{16} \begin{bmatrix} 5 & 4 & 4 & 2 & 0 & 4 & 2 & 0 & 0 \\ & 5 & 2 & 1 & 2 & 4 & 0 & 1 & 0 \\ & & 5 & 4 & 0 & 2 & 4 & 0 & 0 \\ & & & 5 & 2 & 0 & 4 & 1 & 0 \\ Symmetric & & & & 5 & 0 & 0 & 2 & 1 \\ & & & & & 4 & 0 & 0 & 0 \\ & & & & & & 4 & 0 & 0 \\ & & & & & & & 1 & 0 \\ & & & & & & & & 1 \end{bmatrix}$$

$$D_m = \frac{1}{16} \begin{bmatrix} 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & 1 & 0 & 0 & 0 & 0 & 0 \\ Symmetric & & & & 1 & 0 & 0 & 0 & 0 \\ & & & & & 0 & 0 & 0 & 0 \\ & & & & & & 0 & 0 & 0 \\ & & & & & & & 0 & 0 \\ & & & & & & & & 0 \end{bmatrix}$$

$$R_d = \begin{bmatrix} 240I_{(14)} & 0 \\ 0 & 256I_{(11)} \end{bmatrix} /256$$

$$R_{ad} = \begin{bmatrix} 251I_{(14)} & 0 \\ 0 & 256I_{(11)} \end{bmatrix} /256$$

With $\sigma_a^2 = 5$, $\sigma_{aa}^2 = 3$, $\sigma_d^2 = 4$, $\sigma_{ad}^2 = 2$, $\sigma_e^2 = 16$ these give:

$$R_m = \begin{bmatrix} 7131I_{(14)} & & 0 \\ & 7312I_{(5)} & \\ 0 & & 7597I_{(6)} \end{bmatrix} /256$$

The numbers in parenthesis denote the order of the corresponding I matrix. Note that there are 14 progeny with known sire and maternal grandsire, 5 with known sires, and 6 with known maternal grandsire.

Then the solution to the mixed model equations is:

$$\beta^\circ = [2.4870, .5965]', \text{ which is the same as the AM solution,}$$

$$\hat{p} = [-.0225, .0936, -.0044, .1977, .1727, -.0023, .0345, .0817, -.0067].$$

We can compute \hat{a} , \hat{d} , etc. for the 9 groups from the \hat{p} as described in [10]. These are:

$$\hat{a} = [.092, .0725, .0269, .1080, .1499, -.0057, .0298, .0782, -.0064]',$$

$$\begin{aligned} \hat{d} &= [-.0719, -.0221, \dots, .1117, -.3317]' \\ \hat{aa} &= [-.1127, -.0584, \dots, .1048, -.2776]' \\ \text{and } \hat{ad} &= [-.0684, -.0292, \dots, .0751, -.2076]' \end{aligned}$$

$$\begin{aligned} \hat{d} &= [-.0242, .0093, -.0242, .0532, .0059, \\ & 0, 0, 0, 0]', \\ \hat{aa} &= [-.0045, .0104, -.0035, .0282, .0159, \\ & .0034, .0047, .0035, -.0002]', \text{ and} \\ \hat{ad} &= [-.0031, .0014, -.0037, .0083, .0009, \\ & 0, 0, 0, 0]'. \end{aligned}$$

Note that $\hat{a} + \hat{d} + \hat{aa} + \hat{ad} = \hat{p}$ reported above. Next we verify that \hat{t} of AM can be computed from \hat{p} and \hat{e} by [12].

$$\hat{e} = [-.6575, -.2540, .7460, \dots, .2559, .7477, -2.0593]'$$

The resulting \hat{t} are identical to those of AM. Further, the individual genetic effects computed by [13] are:

Suppose these matings for which there are no data need to be estimated.

Sire	MGS
3	1
4	2
4	3

by the method of [15]:

$$A'_{12} = \begin{bmatrix} .125 & .25 & .0625 & .125 & .25 & .125 & 0 & .125 & 0 \\ .0625 & 0 & .125 & .125 & .125 & 0 & .125 & 0 & .125 \\ 0 & .0625 & 0 & .0625 & .25 & 0 & 0 & .0625 & .125 \end{bmatrix}$$

$$D'_{12} = \begin{bmatrix} 0 & .0625 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & .0625 & 0 & 0 & 0 & 0 \end{bmatrix}$$

Then \hat{a} = [.1535, .0021, .0654]'

\hat{d} = [.0093, 0, .0059]'

\hat{aa} = [.0183, .0002, .0047]'

\hat{ad} = [.0012, 0, 0]

\hat{p} for the 3 groups = $\hat{a} + \hat{d} + \hat{aa} + \hat{ad}$ = [.1822, .0023, .0768]'

Finally, a, d, aa, ad are predicted for the 4 sires (maternal grandsires) by [16] and [17].

$$A'_{12} = \begin{bmatrix} .5 & .5 & .25 & 0 & 0 & .5 & 0 & 0 & 0 \\ .25 & 0 & .5 & .5 & 0 & 0 & .5 & 0 & 0 \\ 0 & .25 & 0 & .25 & .5 & 0 & 0 & .25 & 0 \\ 0 & 0 & 0 & 0 & .25 & 0 & 0 & 0 & .25 \end{bmatrix}$$

$D_{12} = 0$

Then \hat{a}_s = [-.0113, .0596, .3127, -.0257]'

\hat{d}_s = 0

\hat{aa}_s = [.0136, .0190, .0553, -.0038]'

\hat{ad}_s = 0.

We verify that \hat{t} of AM can be computed from the sire-maternal grandsire solution:

$$\hat{t} = Z_m \hat{p} + (5R_a + 3R_{aa} + 4R_d + 2R_{ad})R_m^{-1} \hat{\epsilon}$$

where $\hat{\epsilon}$ = [-.6575, -.2540, .7460, 1.0334, -.4651, -2.0615, .3329, 1.9294, 3.5259, .1399, -.2387, -.6422, .5684, .9719, .3398, -.0637, -.5040, -.9075, -1.3110, -.9546, -.5511, -.1476, .2559, .7477, -2.0593]'. The resulting \hat{t} are the same as in the AM solution.

MIVQUE OF VARIANCES

Any quadratic, unbiased, translation invariant estimator of variance and covariances can be computed from an equivalent model to obtain the same solutions obtained from the original model. This is illustrated by MIVQUE for our example.

Animal Model Estimation

Using the notation of Henderson (6) the example is:

$G_1^* = A$

$G_2^* = A\#A$

$G_3^* = D$

$G_4^* = A\#D$

$R_1^* = I$

Then:

$Q_1 = \hat{G}^{-1} G_1^* \hat{G}^{-1}$

$Q_2 = \hat{G}^{-1} G_2^* \hat{G}^{-1}$

$Q_3 = \hat{G}^{-1} G_3^* \hat{G}^{-1}$

$Q_4 = \hat{G}^{-1} G_4^* \hat{G}^{-1}$

and:

$$P_1 = \tilde{R}^{-1} R^*_1 \tilde{R}^{-1}$$

where:

$$\tilde{G} = 5G_1^* + 3G_2^* + 4G_3^* + 2G_4^*$$

and:

$$\tilde{R} = 16R_1^*$$

Then $\hat{y}'Q_1\hat{y}$, $\hat{y}'Q_2\hat{y}$, $\hat{y}'Q_3\hat{y}$, $\hat{y}'Q_4\hat{y}$, and $\hat{e}'P_1\hat{e}$ are computed and equated to their expectations:

$$E(\hat{y}'Q_i\hat{y}) = \text{tr } Q_i [C_u \text{Var}(y)C_u']$$

where:

$$\begin{aligned} \text{Var}(y) &= ZG^*_1 Z'\sigma_a^2 + ZG^*_2 Z'\sigma_{aa}^2 + ZG^*_3 Z'\sigma_d^2 + ZG^*_4 Z'\sigma_{ad}^2 + R^*_1 \sigma_e^2 \\ E(\hat{e}'P_1\hat{e}) &= \text{tr } P_1 [C_e \text{Var}(y) C_e'] \end{aligned}$$

Let C be a g-inverse of mixed model equations. Then C_u is C with rows 1 and 2 deleted and then post-multiplied by W' R⁻¹ where W = [X:Z]. Note that C_u y = \hat{y} . Also, C_e = I - WCW' R⁻¹, and note that C_e y = \hat{e} .

Using $\sigma_a^2 = 5$, $\sigma_{aa}^2 = 3$, $\sigma_d^2 = 4$, $\sigma_{ad}^2 = 2$, $\sigma_e^2 = 16$, the equations to be solved are:

$$\begin{bmatrix} .022046 & .022839 & .022892 & .022928 & .022942 \\ & .025402 & .025905 & .026047 & .026109 \\ & & .026571 & .026710 & .026772 \\ \text{Symmetric} & & & .026907 & .026993 \\ & & & & .027089 \end{bmatrix} \begin{bmatrix} \sigma_a^2 \\ \sigma_{aa}^2 \\ \sigma_d^2 \\ \sigma_{ad}^2 \\ \sigma_e^2 \end{bmatrix} = \begin{bmatrix} .035066 \\ .041047 \\ .043772 \\ .042700 \\ .042219 \end{bmatrix}$$

Sire-Maternal Grand Sire Solution

Now there are more quadratics to compute than in AM. They are:

$$\hat{p}'Q_1\hat{p}, \dots, \hat{p}'Q_4\hat{p}, \hat{e}'P_1\hat{e}, \dots, \hat{e}'P_4\hat{e}, \text{ and } \hat{e}'P_5\hat{e}$$

$$Q_1 = \tilde{G}_m^{-1} A_m \tilde{G}_m^{-1}, \dots, Q_4 = \tilde{G}_m^{-1} A_m \# D_m \tilde{G}_m^{-1}$$

$$P_1 = \tilde{R}_m^{-1} R_a \tilde{R}_m^{-1}, \dots, P_4 = \tilde{R}_m^{-1} R_{ad} \tilde{R}_m^{-1}$$

$$P_5 = \tilde{R}_m^{-1} I \tilde{R}_m^{-1}$$

$$E[\hat{p}'Q_i\hat{p}] = \text{tr } Q_i [C_u \text{Var}(y)C_u']$$

$$\text{Var}(y) = Z_m A_m Z_m' \sigma_a^2 + Z_m A_m \# A_m Z_m' \sigma_{aa}^2 + \dots + R_a \sigma_a^2 + R_{aa} \sigma_{aa}^2 + \dots + I \sigma_e^2$$

Let C_m be a g-inverse of the mixed model coefficient matrix. Then C_u is C_m with the first two rows deleted and post-multiplied by $W_m \hat{R}_m^{-1}$ where $W_m = [X:Z_m]$. Then $\hat{p} = C_u y$. Also $C_e = I - W_m C_m W_m' \hat{R}_m^{-1}$ and $\hat{e} = C_e y$. Now the right-hand sides of the estimation equations are:

$$\begin{aligned} \hat{t}'Q_1\hat{t} + \hat{e}'P_1\hat{e} \\ \hat{t}'Q_2\hat{t} + \hat{e}'P_2\hat{e} \\ \hat{t}'Q_3\hat{t} + \hat{e}'P_3\hat{e} \\ \hat{t}'Q_4\hat{t} + \hat{e}'P_4\hat{e} \\ \hat{e}'P_5\hat{e} \end{aligned}$$

Equating these to their expectations gives exactly the same set of equations as described for AM.

The data of this example are inadequate to estimate all of these variances as indicated by the similarity of the five equations of expectations. Also, the ratio of the largest to smallest eigenvalue is approximately 2.8 million. This indicates that the matrix is extremely ill-conditioned.

DISCUSSION

Many unsolved problems exist that must be answered before recommending that nonadditive genetic methods be used to derive selection criteria. First, there is little knowledge concerning the magnitude of nonadditive genetic variances even for the extensively studied trait, milk production. Assuming that heritability = .25 and $r = .5$, it can be stated that σ_a^2 is less than 25% of phenotypic variance because methods of estimation that have been used are biased upward by σ_{aa}^2 , σ_{aaa}^2 , etc. in estimation by sire variance components or by regression of daughter on dam. Suppose this fact is ignored. Then $\sigma_{aa}^2 + \sigma_{ad}^2 + \dots + \sigma_p^2$ is 25% of phenotypic variance, where σ_p^2 is the variance of permanent environmental effects. If σ_p^2 is small, then nonadditive genetic effects are important. Of course, σ_p^2 could be assumed to be 25% of phenotypic variance, and then nonadditive genetic variance is negligible.

Is it possible to estimate nonadditive genetic effects? With rapidly improving computer power and software, such as parallel processing, vector processing, and sparse matrix methods, it could be worthwhile to attempt this. This estimation could probably be done much more efficiently with AI progeny data under the sire-MGS methods of this paper rather than

under an AM.

One approach to a decision regarding whether nonadditive components should be used in evaluation would be first to study, with a good subset of the incidence matrix for evaluation, differences in prediction error variances for a wide range of parameter values, for example, with all genetic variances being σ_a^2 versus σ_a^2 , σ_d^2 , σ_{aa}^2 in proportionality 1:2:2. If the differences in prediction error variances proved to be small, there would be little incentive to embark upon a study of parameter values. However, large differences should encourage estimation.

Undue pessimism concerning the difficulties of estimation hardly seem warranted. If earlier workers had been inclined that way, worldwide application of BLUP would not have occurred. This author's first application of mixed model BLUP was in 1949 (4) using a desk calculator, not even an electronic one. The first application to regional sire evaluation, the Northeast Sire Comparison, was done with an IBM 360, Model 40, which was much inferior to some present day personal computers.

Some strategies for applying the procedures of this paper to large problems are not presented. If estimates of the variances are good and interest is only in prediction, the equations of [9] can be modified so that the large matrix, P , need not be inverted.

Solve these equations:

$$\left\{ \begin{matrix} \mathbf{T} \left[\begin{matrix} \mathbf{X} \mathbf{R}_m^{-1} \mathbf{X} & \mathbf{X} \mathbf{R}_m^{-1} \mathbf{Z}_m \\ \mathbf{Z}_m^{-1} \mathbf{R}_m^{-1} \mathbf{X} & \mathbf{Z}_m^{-1} \mathbf{R}_m^{-1} \mathbf{Z}_m \end{matrix} \right] \mathbf{T} + \begin{bmatrix} \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{P} \end{bmatrix} \end{matrix} \right\} \begin{bmatrix} \beta^\circ \\ \alpha^\circ \end{bmatrix} = \mathbf{T} \begin{bmatrix} \mathbf{X} \mathbf{R}_m^{-1} \mathbf{y} \\ \mathbf{Z}_m^{-1} \mathbf{R}_m^{-1} \mathbf{y} \end{bmatrix} \quad [18]$$

Then:

$$\begin{pmatrix} \beta^\circ \\ \hat{\mathbf{p}} \end{pmatrix} = \mathbf{T} \begin{pmatrix} \beta^\circ \\ \alpha^\circ \end{pmatrix}$$

where:

$$\mathbf{T} = \begin{bmatrix} \mathbf{I} & \mathbf{0} \\ \mathbf{0} & \mathbf{P} \end{bmatrix}$$

The equations of [18] could be solved iteratively. The price to pay for this method is the requirement for extensive matrix multiplication, but with proper use of vector processing, matrix multiplication is very fast compared with scalar operations.

However, it should not be ignored that **P** of [9] is a relatively sparse matrix. In fact, it has exactly the same number of zero elements as **A_m**. Consequently, sparse matrix methods make feasible the inversion of a large **P**. Estimation of variances by most standard methods requires the inversion of the coefficient matrix. This is not sparse because **P**⁻¹ is not. Consequently, it may be necessary for the present to resort to some method that does not require inversion of the coefficient matrix, for example, approximate MIVQUE or iterated approximate MIVQUE (6).

REFERENCES

- 1 Allaire, F. R., and C. R. Henderson. 1965. Specific combining abilities among dairy sires. *J. Dairy Sci.* 48:1096.
- 2 Allaire, F. R. 1980. Mate selection by selection index theory. *Theor. Appl. Genet.* 57:267.
- 3 Cockerham, C. C. 1954. An extension of the concept of partitioning hereditary covariance for analyses of covariance among selections when epistasis is present. *Genetics* 39:859.
- 4 Henderson, C. R. 1949. Estimation of changes in herd environment. *J. Dairy Sci.* 32:706. (Abstr.)
- 5 Henderson, C. R. 1977. Best linear unbiased predictions of breeding values not in the model for records. *J. Dairy Sci.* 60:783.
- 6 Henderson, C. R. 1984. ANOVA, MIVQUE, REML, and ML algorithms for estimation of variances and covariances. *Statistics: An appraisal. Proc. 50th Anniv. Conf. H. A. David and H. T. David, ed. Iowa State Univ. Press, Ames.*
- 7 Henderson, C. R. 1984. Best linear unbiased prediction of nonadditive genetic merits in noninbred populations. *J. Anim. Sci.* 60:111.
- 8 Henderson, C. R. 1985. MIVQUE and REML estimation of additive and nonadditive genetic variances. *J. Anim. Sci.* 61:113.
- 9 Henderson, C. R. 1985. Equivalent linear models to reduce computations. *J. Dairy Sci.* 68:2267.
- 10 Quaas, R. L., and E. J. Pollak. 1980. Mixed model methodology for farm and ranch beef cattle testing programs. *J. Anim. Sci.* 51:1277.
- 11 Rao, C. R. 1971. Minimum variance quadratic unbiased estimation of variance components. *J. Multivar. Anal.* 2:445.
- 12 Wright, S. 1922. Coefficients of inbreeding and relationship. *Am. Nat.* 56:330.