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Estimation of Nonadditive Genetic Variances for a Total-Merit Model Including Maternal Effects¹

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ABSTRACT: Henderson described a method to reduce the number of mixed-model equations when estimating additive and nonadditive genetic variances or predicting additive and nonadditive genetic merits. The extension to a maternal effects model is straightforward. When maternal genetic effects are strictly additive, an algebraic identity was found that reduces by a factor of two the order of a matrix that must be inverted each round to account for the genetic covariances among direct and maternal genetic effects. An algorithm for derivative-free restricted maximum likelihood was developed based on Henderson's total-merit model that is the basis for a reduced number of equations. The same values for the logarithm of the

likelihood can be calculated from components of the equations for the total-merit model and from components of the equations for the individual effects model. The computational properties of the equations for the total-merit model, however, do not lend themselves to sparse-matrix methods. Both memory and time requirements were much greater for the total-merit model than for the individual-effects model for a data set of 871 animals and a model with additive, dominance, and additive \times additive direct and additive maternal genetic effects. Approximately 14 times more memory was required, although the number of equations decreased from 3,773 to 2,031. Computing time per round increased by a factor of 50.

Key Words: Genetic Algebras, REML, Genetic Effects

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Introduction

Henderson (1985a) described a method of predicting additive and nonadditive genetic values from a total-merit model with a reduced number of equations. A succeeding paper (Henderson, 1985b) described minimum variance quadratic unbiased estimation (**MIVQUE**) and REML estimation of additive and nonadditive genetic variances from the reduced set of equations. At approximately the same time, Smith and Graser (1986) and Graser et al. (1987) described a derivative-free algorithm for REML (**DFREML**). The purposes of this paper are 1) to extend Henderson's total-merit model to a model including maternal effects and 2) to describe a derivative-free algorithm for estimation of additive and nonadditive genetic variances from the total-merit model. Of special interest is a simplification when the maternal genetic effects are strictly additive.

The Total-Merit Model

For simplicity, only additive (**a**), dominance (**d**), and additive \times additive (**a:a**) genetic effects will be included in an animal model. The full or individual effects model including direct and maternal effects can be written as follows:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Sc} + \mathbf{Za}_d + \mathbf{Zd}_d + \mathbf{Za:a}_d + \mathbf{Wa}_m + \mathbf{Wd}_m + \mathbf{Wa:a}_m + \mathbf{e},$$

where

- y** = vector of observations,
- β** = vector of fixed effects,
- X** = matrix associating **β** with **y**,
- c** = vector of random permanent environmental effects,
- S** = matrix associating **c** with **y**,
- a_d**, **d_d**, **a:a_d** = vectors of additive, dominance, and additive \times additive direct genetic effects,
- Z** = matrix associating direct genetic effects with **y**,
- a_m**, **d_m**, **a:a_m** = vectors of additive, dominance, and additive \times additive maternal genetic effects,

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\mathbf{W} = matrix associating maternal genetic effects with \mathbf{y} , and

\mathbf{e} = vector of random residual (temporary environmental) effects.

$\mathbf{E}[\mathbf{y}] = \mathbf{X}\boldsymbol{\beta}$ and

$$\mathbf{V} \begin{bmatrix} \mathbf{c} \\ \mathbf{a}_d \\ \mathbf{d}_d \\ \mathbf{a}:\mathbf{a}_d \\ \mathbf{a}_m \\ \mathbf{d}_m \\ \mathbf{a}:\mathbf{a}_m \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{I}_c \sigma_c^2 & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ & \mathbf{A} \sigma_{a_d}^2 & \mathbf{0} & \mathbf{0} & \mathbf{A} \sigma_{a_{dm}} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ & & \mathbf{D} \sigma_{d_d}^2 & \mathbf{0} & \mathbf{0} & \mathbf{D} \sigma_{d_{dm}} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ & & & \mathbf{A}:\mathbf{A} \sigma_{a:a_d}^2 & \mathbf{0} & \mathbf{0} & \mathbf{A}:\mathbf{A} \sigma_{a:a_{dm}} & \mathbf{0} & \mathbf{0} \\ & & & & \mathbf{A} \sigma_{a_m}^2 & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ & & & & & \mathbf{D} \sigma_{d_m}^2 & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ & & & & & & \mathbf{A}:\mathbf{A} \sigma_{a:a_m}^2 & \mathbf{0} & \mathbf{0} \\ & & & & & & & \mathbf{I}_N \sigma_e^2 & \mathbf{0} \end{bmatrix}$$

Symmetric

Henderson (1985a,b) demonstrated that solutions for total merit, $\mathbf{t} = \mathbf{a} + \mathbf{d} + \mathbf{a}:\mathbf{a}$, from iterating on a set of reduced mixed-model equations (**MME**) based on the total-merit model could be used to obtain estimates of σ_a^2 , σ_d^2 , and $\sigma_{a:a}^2$. He stated that the methodology could be extended to models with maternal effects. The extension, however, involves inversion of a matrix of order twice the number of animals to set up the MME for an animal model. For example, if $\mathbf{t}_d = \mathbf{a}_d + \mathbf{d}_d + \mathbf{a}:\mathbf{a}_d$ and $\mathbf{t}_m = \mathbf{a}_m + \mathbf{d}_m + \mathbf{a}:\mathbf{a}_m$ are the vectors of direct and maternal total genetic values, then in the MME, \mathbf{G}^{-1} for

$$\mathbf{G} = \mathbf{V} \begin{pmatrix} \mathbf{t}_d \\ \mathbf{t}_m \end{pmatrix} = \begin{bmatrix} \mathbf{G}_{dd} & \mathbf{G}_{dm} \\ \mathbf{G}'_{dm} & \mathbf{G}_{mm} \end{bmatrix}$$

is needed where

$$\begin{aligned} \mathbf{G}_{dd} &= \mathbf{A} \sigma_{a_d}^2 + \mathbf{D} \sigma_{d_d}^2 + \mathbf{A}:\mathbf{A} \sigma_{a:a_d}^2, \\ \mathbf{G}_{mm} &= \mathbf{A} \sigma_{a_m}^2 + \mathbf{D} \sigma_{d_m}^2 + \mathbf{A}:\mathbf{A} \sigma_{a:a_m}^2, \text{ and} \\ \mathbf{G}'_{dm} &= \mathbf{G}_{dm} = \mathbf{A} \sigma_{a_{dm}} + \mathbf{D} \sigma_{d_{dm}} + \mathbf{A}:\mathbf{A} \sigma_{a:a_{dm}}, \end{aligned}$$

with \mathbf{A} and \mathbf{D} the matrices of numerator and dominance relationships and $\mathbf{A}:\mathbf{A}$ the Hadamard product of \mathbf{A} with itself (i.e., $\{\mathbf{a}:\mathbf{a}\}_{ij} = \{\mathbf{a}_{ij}^2\}$). Any simplification of \mathbf{G}^{-1} is not obvious to avoid inverting \mathbf{G} for each round, a matrix of order $2q$ where q is the number of animals in the equations. With derivative methods for REML, elements from the inverse of the coefficient matrix of order $2q$ + number of levels of fixed and other random effects also would be required. Thus, for each round of iteration, inverse elements of two matrices of order $2q$ or greater would be required. If the individual effects model were used, the order of each matrix would be greater than $2 \times (\text{number of genetic effects}) \times (\text{number of animals})$ but many off-diagonal blocks of these matrices would be especially sparse.

With the total-merit model, an important simplification can be found when only additive genetic effects contribute to maternal genetic value. The inverse of \mathbf{G}^{-1} will involve inverting only a matrix of order the number of animals, as will be shown. In this case:

$$\mathbf{G} = \begin{bmatrix} \mathbf{G}_{dd} & \mathbf{A} \sigma_{am} \\ \mathbf{A} \sigma_{am} & \mathbf{A} \sigma_m^2 \end{bmatrix},$$

where

σ_m^2 = additive genetic variance of maternal effects and
 σ_{am} = additive genetic covariance between direct and maternal effects.

Note now that with $\sigma_a^2 = \sigma_{a_d}^2$, $\sigma_d^2 = \sigma_{d_d}^2$, and $\sigma_{a:a}^2 = \sigma_{a:a_d}^2$, the partitioned inverse of \mathbf{G} is as follows:

$$\mathbf{G}^{-1} = \begin{bmatrix} \mathbf{G}^{11} & \mathbf{G}^{12} \\ \mathbf{G}^{21} & \mathbf{G}^{22} \end{bmatrix} = \begin{bmatrix} \mathbf{T}^{-1} & -\mathbf{T}^{-1}\boldsymbol{\alpha} \\ -\mathbf{T}^{-1}\boldsymbol{\alpha} & \mathbf{A}^{-1}\boldsymbol{\delta} + \mathbf{T}^{-1}\boldsymbol{\alpha}^2 \end{bmatrix}$$

where

$$\begin{aligned} \mathbf{T} &= \mathbf{G}_{dd} - \mathbf{A} \sigma_{am} \sigma_{am} / \sigma_m^2 \\ &= \mathbf{A} (\sigma_a^2 - \sigma_{am} \sigma_{am} / \sigma_m^2) + \mathbf{D} \sigma_d^2 + \mathbf{A}:\mathbf{A} \sigma_{a:a}^2 \\ &= \mathbf{A} [(\sigma_a^2 \sigma_m^2 - \sigma_{am}^2) / \sigma_m^2] + \mathbf{D} \sigma_d^2 + \mathbf{A}:\mathbf{A} \sigma_{a:a}^2, \\ \boldsymbol{\alpha} &= \sigma_{am} / \sigma_m^2, \text{ and} \\ \boldsymbol{\delta} &= 1 / \sigma_m^2. \end{aligned}$$

Thus, only \mathbf{T} , of order the number of animals, needs to be inverted each round because updated elements of \mathbf{G}^{-1} are functions of updated \mathbf{T}^{-1} and updated variances and covariances. The elements of \mathbf{A}^{-1} need to be calculated only once for each data set by rules of Henderson (1976) or Quaas (1976) with \mathbf{Z} and \mathbf{W}

augmented by columns of zeros for animals without records (Henderson, 1977).

For the equations for the total-merit model with additive genetic maternal effects and permanent environmental effects (which could be on the animal with records or on the mother of the animal as visualized here), the model can be written as follows:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{S}\mathbf{c} + \mathbf{Z}\mathbf{t} + \mathbf{W}\mathbf{m} = \mathbf{e}$$

where all terms are as defined previously except

\mathbf{t} = the vector of sums of vectors of additive, dominance, and additive \times additive direct genetic effects,

\mathbf{Z} = the matrix associating \mathbf{t} with \mathbf{y} ,

\mathbf{m} = the vector of maternal additive genetic effects,

\mathbf{W} = the matrix associating \mathbf{m} with \mathbf{y} ,

$\mathbf{E}[\mathbf{y}] = \mathbf{X}\boldsymbol{\beta}$, and

$$\mathbf{V} \begin{bmatrix} \mathbf{c} \\ \mathbf{t} \\ \mathbf{m} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{I}_c \sigma_c^2 & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{G}_{dd} & \mathbf{A}\sigma_{am} & \mathbf{0} \\ \mathbf{0} & \mathbf{A}\sigma_{am} & \mathbf{A}\sigma_m^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{I}_N \sigma_e^2 \end{bmatrix}.$$

The MME ($\times \sigma_e^2$) for the total merit model are:

$$\begin{bmatrix} \mathbf{X}'\mathbf{X} & \mathbf{X}'\mathbf{S} & \mathbf{X}'\mathbf{Z} & \mathbf{X}'\mathbf{W} \\ \mathbf{S}'\mathbf{X} & \mathbf{S}'\mathbf{S} + \mathbf{I}_\lambda & \mathbf{S}'\mathbf{Z} & \mathbf{S}'\mathbf{W} \\ \mathbf{Z}'\mathbf{X} & \mathbf{Z}'\mathbf{S} & \mathbf{Z}'\mathbf{Z} + \sigma_e^2 \mathbf{G}^{11} & \mathbf{Z}'\mathbf{W} + \sigma_e^2 \mathbf{G}^{12} \\ \mathbf{W}'\mathbf{X} & \mathbf{W}'\mathbf{S} & \mathbf{W}'\mathbf{Z} + \sigma_e^2 \mathbf{G}^{21} & \mathbf{W}'\mathbf{W} + \sigma_e^2 \mathbf{G}^{22} \end{bmatrix} \begin{bmatrix} \hat{\boldsymbol{\beta}} \\ \hat{\mathbf{c}} \\ \hat{\mathbf{t}} \\ \hat{\mathbf{m}} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{y} \\ \mathbf{S}'\mathbf{y} \\ \mathbf{Z}'\mathbf{y} \\ \mathbf{W}'\mathbf{y} \end{bmatrix}$$

where $\lambda = \sigma_e^2 / \sigma_c^2$.

Derivative-Free Restricted Maximum Likelihood with Total-Merit Model

The procedures described by Henderson (1985a,b) can be used to obtain quadratics for derivative methods of estimating the variances and covariance. These procedures, however, require not only the inverse of \mathbf{G} but also matrix products to compute quadratic forms and traces, such as $\mathbf{T}^{-1}\mathbf{A}\mathbf{T}^{-1}$, that involve approximately q^3 multiplications each. The number of arithmetic operations for each such product is greater than for inverting a dense, symmetric matrix of the same order.

One way to avoid the multiplications involved with the quadratics and corresponding traces is to use a derivative-free algorithm to maximize the likelihood (Smith and Graser, 1986). The main question is whether the computations are any more feasible. The answer seems to be that with sparse-matrix methods, the number of arithmetic operations is much greater with the total-merit model than with the individual-effects model.

Harville (1977) and Searle (1979) derived identities that allow calculation of the logarithm of the normal likelihood given a set of data, \mathbf{y} , based on functions of the MME and the variance-covariance matrix of the data, $\mathbf{V}(\mathbf{y}) = \mathbf{V}$. Meyer (1989, 1991) described the quantities to be calculated for many models and an algorithm based on Gaussian elimination (Smith and Graser, 1986) and sparse-matrix storage. Boldman and Van Vleck (1991) used sparse-matrix methods based on Choleski factorization to obtain solutions to MME used to calculate the logarithm of the likelihood. The parts of the log likelihood to be maximized other than a constant are as follows:

$$\Lambda = -.5[\log|\mathbf{R}| + \log|\mathbf{G}| + \log|\mathbf{C}| + \mathbf{y}'\mathbf{P}\mathbf{y}],$$

where

$$\mathbf{R} = \mathbf{V}(\mathbf{e}),$$

$$\mathbf{G} = \mathbf{V}(\mathbf{u}) \text{ with } \mathbf{u} \text{ the vector of all random effects except } \mathbf{e},$$

$$\mathbf{C} = \text{coefficient matrix of a full rank set of the mixed-model equations, and}$$

$$\mathbf{y}'\mathbf{P}\mathbf{y} = \text{residual sum of squares from fitting the model with}$$

$$\mathbf{P} = \mathbf{V}^{-1} - \mathbf{V}^{-1} \mathbf{X}(\mathbf{X}'\mathbf{V}^{-1}\mathbf{X})^{-1} \mathbf{X}'\mathbf{V}^{-1} \text{ for full rank set of } \mathbf{X}.$$

For the total-merit model with additive genetic maternal effects and permanent environmental effects,

$$\mathbf{G} = \begin{bmatrix} \mathbf{G}_{dd} & \mathbf{A}\sigma_{am} & \mathbf{0} \\ \mathbf{A}\sigma_{am} & \mathbf{A}\sigma_m^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{I}_c \sigma_c^2 \end{bmatrix},$$

where

\mathbf{I}_c has order the number, n_c , of permanent environmental effects (e.g., number of dams with progeny with records) and

\mathbf{A} has order, q , the number of animals in \mathbf{A} .

Then $\log|\mathbf{G}| = \log|\mathbf{I}_c \sigma_c^2| + \log|\mathbf{H}|$ with

$$\log|\mathbf{I}_c \sigma_c^2| = n_c \log(\sigma_c^2) \text{ and}$$

$$\mathbf{H} = \begin{bmatrix} \mathbf{G}_{dd} & \mathbf{A}\sigma_{am} \\ \mathbf{A}\sigma_{am} & \mathbf{A}\sigma_m^2 \end{bmatrix}.$$

One way to determine $\log|\mathbf{H}|$ is as follows:

$$\begin{aligned} \log|\mathbf{H}| &= \log|\mathbf{A}\sigma_m^2| + \log|\mathbf{G}_{dd} - \mathbf{A}\mathbf{A}^{-1}\mathbf{A}\sigma_{am}^2/\sigma_m^2| \\ &= \log|\mathbf{A}\sigma_m^2| + \log|\mathbf{G}_{dd} - \mathbf{A}\sigma_{am}^2/\sigma_m^2| \\ &= \log|\mathbf{A}\sigma_m^2| + \log|\mathbf{T}|. \end{aligned}$$

The $\log|\mathbf{T}|$ can be calculated as a byproduct of inverting \mathbf{T} for each round and $\log|\mathbf{A}|$ is a constant that is not needed but can be computed, if desired, as a byproduct of Quaas' (1976) rules for \mathbf{A}^{-1} as realized by Meyer (1989).

When the MME are set up by multiplying both sides by σ_e^2 , then instead of adding \mathbf{H}^{-1} to the least squares part of the MME, $\sigma_e^2\mathbf{H}^{-1}$ is added. In fact, $\mathbf{T}^* = \mathbf{T}(1/\sigma_e^2)$ would be used so that $\mathbf{T}^{*-1} = \sigma_e^2\mathbf{T}^{-1}$. Then $\log|\mathbf{T}| = \log|\mathbf{T}^*| + q \log(\sigma_e^2)$, where $\log|\mathbf{T}^*|$ is obtained as a byproduct of inverting \mathbf{T}^* . Similarly, the coefficient matrix after multiplying by σ_e^2 is $\mathbf{C}^* = \sigma_e^2\mathbf{C}$, so that $\log|\mathbf{C}^*| = \log|\mathbf{C}| + \text{rank}(\mathbf{C}) \log(\sigma_e^2)$ and $\log|\mathbf{C}| = \log|\mathbf{C}^*| - \text{rank}(\mathbf{C}) \log(\sigma_e^2)$ with $\text{rank}(\mathbf{C}) = \text{rank}(\mathbf{X}) + n_c + 2q$. As emphasized by Meyer (1989), the usual residual sum of squares, $\mathbf{y}'\mathbf{y} - \mathbf{s}'\mathbf{r}^*$, where \mathbf{s} and \mathbf{r}^* are the solution and right-hand-side vectors, must be divided by σ_e^2 to obtain the generalized residual sum of squares, $\mathbf{y}'\mathbf{P}\mathbf{y}$.

Thus, the parts of the log of the likelihood are computed as follows:

$$\begin{aligned} \log|\mathbf{C}| &\leftarrow \log|\mathbf{C}^*| - \text{rank}(\mathbf{C}) \log(\sigma_e^2) \\ \mathbf{y}'\mathbf{P}\mathbf{y} &\leftarrow (\mathbf{y}'\mathbf{y} - \mathbf{s}'\mathbf{r}^*)/\sigma_e^2 \\ \log|\mathbf{R}| &\leftarrow N \log(\sigma_e^2) \\ \log(\mathbf{I}\sigma_c^2) &\leftarrow n_c \log(\sigma_c^2) \\ \log|\mathbf{H}| &\leftarrow \log|\mathbf{T}^*| + q \log(\sigma_e^2) + \log|\mathbf{A}| + q \log(\sigma_m^2) \\ \mathbf{T}^* &= \mathbf{A}(\sigma_a^2\sigma_m^2 - \sigma_{am}^2)/(\sigma_e^2\sigma_m^2) + \mathbf{D}(\sigma_d^2/\sigma_e^2) \\ &\quad + \mathbf{A}:\mathbf{A}(\sigma_{a:a}^2/\sigma_e^2), \end{aligned}$$

and at each round current values of σ_e^2 , σ_c^2 , σ_m^2 , σ_a^2 , σ_d^2 , σ_{am} , and $\sigma_{a:a}^2$ are used.

Note that $\text{rank}(\mathbf{C}) = \text{rank}(\mathbf{X}) + n_c + 2q$. Thus, $\Lambda = -0.5\{[\mathbf{N} - \text{rank}(\mathbf{X}) - n_c - q] \log(\sigma_e^2) + \log|\mathbf{C}^*| + n_c \log(\sigma_c^2) + \log|\mathbf{T}^*| + q \log(\sigma_m^2) + \log|\mathbf{A}| + (\mathbf{y}'\mathbf{y} - \mathbf{s}'\mathbf{r}^*)/\sigma_e^2\}$.

This log likelihood is the same as the log likelihood obtained with the same variance and covariance values when the MME are set up with the individual-effects model:

$$\mathbf{y} = \mathbf{X}\beta + \mathbf{S}\mathbf{c} + \mathbf{Z}\mathbf{a} + \mathbf{Z}\mathbf{d} + \mathbf{Z}\mathbf{a}:\mathbf{a} + \mathbf{W}\mathbf{m} + \mathbf{e}.$$

The MME $\times \sigma_e^2$ for the individual-effects model are as follows:

$$\begin{bmatrix} \mathbf{X}'\mathbf{X} & \mathbf{X}'\mathbf{S} & \mathbf{X}'\mathbf{Z} & \mathbf{X}'\mathbf{Z} & \mathbf{X}'\mathbf{W} \\ \mathbf{S}'\mathbf{X} & \mathbf{S}'\mathbf{S} + \mathbf{I}\lambda_c & \mathbf{S}'\mathbf{Z} & \mathbf{S}'\mathbf{Z} & \mathbf{S}'\mathbf{W} \\ \mathbf{Z}'\mathbf{X} & \mathbf{Z}'\mathbf{S} & \mathbf{Z}'\mathbf{Z} + \mathbf{A}^{-1}\mathbf{g}^{dd} & \mathbf{Z}'\mathbf{Z} & \mathbf{Z}'\mathbf{W} + \mathbf{A}^{-1}\mathbf{g}^{dm} \\ \mathbf{Z}'\mathbf{X} & \mathbf{Z}'\mathbf{S} & \mathbf{Z}'\mathbf{Z} & \mathbf{Z}'\mathbf{Z} + \mathbf{D}^{-1}\lambda_D & \mathbf{Z}'\mathbf{W} \\ \mathbf{Z}'\mathbf{X} & \mathbf{Z}'\mathbf{S} & \mathbf{Z}'\mathbf{Z} & \mathbf{Z}'\mathbf{Z} & \mathbf{Z}'\mathbf{W} \\ \mathbf{W}'\mathbf{X} & \mathbf{W}'\mathbf{S} & \mathbf{W}'\mathbf{Z} + \mathbf{A}^{-1}\mathbf{g}^{dm} & \mathbf{W}'\mathbf{Z} & \mathbf{W}'\mathbf{W} + \mathbf{A}^{-1}\mathbf{g}^{mm} \end{bmatrix} \begin{bmatrix} \hat{\beta} \\ \hat{\mathbf{c}} \\ \hat{\mathbf{a}} \\ \hat{\mathbf{d}} \\ \hat{\mathbf{a}}:\hat{\mathbf{a}} \\ \hat{\mathbf{m}} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{y} \\ \mathbf{S}'\mathbf{y} \\ \mathbf{Z}'\mathbf{y} \\ \mathbf{Z}'\mathbf{y} \\ \mathbf{Z}'\mathbf{y} \\ \mathbf{W}'\mathbf{y} \end{bmatrix}$$

Let $\mathbf{C}_{\mathbf{I}^*}$ be the full rank (after constraints on $\hat{\beta}$) coefficient matrix, $\mathbf{r}_{\mathbf{I}^*}$ be the right-hand-side vector after multiplying by σ_e^2 as shown above and $\mathbf{s}_{\mathbf{I}}$ be the solution vector. Also let:

$$\mathbf{H}_{\mathbf{I}^*} = \mathbf{H}_{\mathbf{I}}(1/\sigma_e^2) = \begin{bmatrix} \mathbf{A}\sigma_a^2/\sigma_e^2 & 0 & 0 & \mathbf{A}\sigma_{am}/\sigma_e^2 \\ 0 & \mathbf{D}\sigma_d^2/\sigma_e^2 & 0 & 0 \\ 0 & 0 & \mathbf{A}:\mathbf{A}\sigma_{a:a}^2/\sigma_e^2 & 0 \\ \mathbf{A}\sigma_{am}/\sigma_e^2 & 0 & 0 & \mathbf{A}\sigma_m^2/\sigma_e^2 \end{bmatrix}$$

and

$$\mathbf{H}_{\mathbf{I}^*}^{-1} = \sigma_e^2 \mathbf{H}_{\mathbf{I}}^{-1} = \begin{bmatrix} \mathbf{A}^{-1}\mathbf{g}^{dd} & 0 & 0 & \mathbf{A}^{-1}\mathbf{g}^{dm} \\ 0 & \mathbf{D}^{-1}\lambda_D & 0 & 0 \\ 0 & 0 & (\mathbf{A}:\mathbf{A})^{-1}\lambda_{\mathbf{A}:\mathbf{A}} & 0 \\ \mathbf{A}^{-1}\mathbf{g}^{dm} & 0 & 0 & \mathbf{A}^{-1}\mathbf{g}^{mm} \end{bmatrix},$$

where

$$\begin{bmatrix} \mathbf{g}^{dd} & \mathbf{g}^{dm} \\ \mathbf{g}^{dm} & \mathbf{g}^{mm} \end{bmatrix} = \sigma_e^2 \begin{bmatrix} \sigma_a^2 & \sigma_{am} \\ \sigma_{am} & \sigma_m^2 \end{bmatrix}^{-1},$$

$$\lambda_D = \sigma_e^2/\sigma_d^2 \text{ and}$$

$$\lambda_{A:A} = \sigma_e^2/\sigma_{a:a}^2.$$

The log likelihood calculation is as follows:

$$\begin{aligned} \log|\mathbf{C}_I| &\leftarrow \log|\mathbf{C}_{I*}| - \text{rank}(\mathbf{C}_I) \log(\sigma_e^2) \\ \mathbf{y}'\mathbf{P}\mathbf{y} &\leftarrow (\mathbf{y}'\mathbf{y} - \mathbf{s}_I'\mathbf{r}_{I*})/\sigma_e^2 \\ \log|\mathbf{R}| &\leftarrow N \log(\sigma_e^2) \\ \log|\mathbf{I}\sigma_c^2| &\leftarrow n_c \log(\sigma_c^2) \\ \log|\mathbf{H}_I| &\leftarrow \log|\mathbf{H}_{I*}| + 4 q \log(\sigma_e^2) \\ &= \log|\mathbf{D}| + q \log(\sigma_d^2) \\ &+ \log|\mathbf{A:A}| + q \log(\sigma_{a:a}^2) \\ &+ 2 \log|\mathbf{A}| + q \log(\sigma_a^2) + q \log(\sigma_m^2 - \sigma_{am}^2/\sigma_a^2) \\ &+ 4 q \log(\sigma_e^2). \end{aligned}$$

Note that $\log|\mathbf{D}|$, $\log|\mathbf{A:A}|$, and $\log|\mathbf{A}|$ are constants that are not needed unless a likelihood ratio test is used to compare the fit for full and reduced models. Note that $\text{rank}(\mathbf{C}_I) = \text{rank}(\mathbf{X}) + n_c + 4 q$. Thus,

$$\begin{aligned} \Lambda &= -5\{[N - \text{rank}(\mathbf{X}) - n_c]\log(\sigma_e^2) + \log|\mathbf{C}_{I*}| \\ &+ n_c \log(\sigma_c^2) + q[\log(\sigma_a^2) + \log(\sigma_d^2) + \log(\sigma_{a:a}^2) \\ &+ \log(\sigma_m^2 - \sigma_{am}^2/\sigma_a^2)] + 2 \log|\mathbf{A}| + \log|\mathbf{D}| + \log|\mathbf{A:A}| \\ &+ (\mathbf{y}'\mathbf{y} - \mathbf{s}_I'\mathbf{r}_{I*})/\sigma_e^2\} \end{aligned}$$

Although the models are equivalent and thus have the same likelihood, comparison of the two expressions to evaluate the log likelihood reveals few similarities. As an arithmetic check, the sums of the two parts of the log likelihood were found to be equal when calculated for two data sets and for two sets of parameter values with each data set. Thus, either set of equations should lead to the same estimates of variances and covariances. For the real data set summarized and presented in Table 1, computing time and memory requirements with the equations for the total-merit model led to the conclusion that the method is not competitive with the equations for the individual effects.

Computational Properties of Equations for Total-Merit Model

The reason for investigating the potential of the total-merit model was that the analysis of a set of beef cattle data with 1,837 animals generated 937,373 and 1,128,899 non-zero, half-stored coefficients, of a possible 1,688,203, for \mathbf{D}^{-1} and $\mathbf{A:A}^{-1}$, respectively. The individual effects model with sparse methods could not be handled on a computer with 32 Mbytes of memory.

The intent was to try to use the equations for the total-merit model. Testing involved a smaller data set of 871 animals from a different line of the same project. The disappointing comparison is summarized in Table 1. As expected, the number of equations and number of non-zero coefficients from the least squares portion of the MME were considerably less with the total-merit model. Although \mathbf{D}^{-1} and $\mathbf{A:A}^{-1}$ were not dense for this data set, the inverse of \mathbf{T} was very dense, which affected the memory requirements and timings. More than 12 times more non-zero coefficients were generated for the reduced equations than for the usual equations. That result suggested that the memory requirement for the larger data set would be too large for this method even if the computational operations were comparable. In fact, and as would be expected, the number of the computational steps mirrored the memory requirements. The reduced-equations method was not competitive for the example. The time per round with the total-merit model was essentially the sum of time to invert \mathbf{T} plus time to solve the MME by Choleski factorization, approximately 50 min per round compared with approximately 1 min for the individual-effects model. Obviously, the larger data set would require at least 8 to 10 times as long for the inversion.

Table 1. Summary of computations for derivative-free restricted maximum likelihood with sparse-matrix techniques for a model with additive, dominance, additive \times additive direct genetic effects, and additive genetic maternal effects: Individual-effects and total-merit models

Item	Individual effects ^{ab}	Total merit ^{ac}
Number		
Records	683	683
Animals	871	871
Equations	3,773	2,031
Memory (non-zero)		
Half-stored elements		
\mathbf{A}^{-1}	2,850	2,850
\mathbf{D}^{-1}	5,454	—
$\mathbf{A:A}^{-1}$	13,215	—
\mathbf{T}^{-1}	—	379,726
Least squares coefficients	18,385	8,140
Maximum storage ^d	224,449	3,050,320
Time (486/33 personal computer)		
Factor, s	10.3	585.3
Invert \mathbf{T} , s	—	768.7
Solve, s	59.0	2,280.6
Per round, s	59.0	3,049.3

^aIncluded three fixed factors with 4, 12, and 2 levels; maternal permanent environmental effects (273);

^bFootnote a plus 871 additive, 871 dominance, 871 additive \times additive direct genetic effects, and 871 additive maternal genetic effects.

^cFootnote a plus 871 total direct genetic and 871 additive maternal genetic effects.

^dStorage locations in \mathbf{S} vector of SPARSPAK that require 8 bytes each.

The final reason for the abandonment of the reduced-equations method was the unpredictability of which elements of \mathbf{T}^{-1} would be zero in each round. The original strategy that was not explored very deeply was the following. With an initial correlation of .5 between additive direct and maternal effects, initial elements of \mathbf{T}^{-1} with absolute value $< 1 \times 10^{-8}$ were set to zero to reduce the number of non-zero elements to make use of sparse-matrix methods for the symbolic reordering. The reordering is done only once to establish an order that minimizes fill during later numerical factorization. In succeeding rounds, elements of \mathbf{T}^{-1} with absolute value $< 1 \times 10^{-6}$ were set to zero. With a small example of 21 animals, no new non-zero elements were generated as the variance components changed from round to round in response to the simplex algorithm. With the larger example, new non-zero elements were generated. The non-zero elements of \mathbf{A}^{-1} , \mathbf{D}^{-1} , and $\mathbf{A:A}^{-1}$ are the same in every round so that an initial symbolic reordering can be done with the individual-effects model. With \mathbf{T} changing in each round, the same property does not hold. A non-sparse algorithm could be developed but does not seem to be competitive with a sparse algorithm based on the equations developed for the individual-effects model.

Conclusion

The total-merit model with reduced equations (Henderson, 1985a,b) is easily extended to a maternal-effects model. With only additive genetic maternal effects, a simplification reduces by one-half the size of the matrix, \mathbf{T} , that must be inverted during each round to obtain the inverse of the variance-covariance matrix of random effects needed to set up the MME. The inverse of \mathbf{T} for an example with actual data, however, was dense even though \mathbf{A}^{-1} , \mathbf{D}^{-1} , and $\mathbf{A:A}^{-1}$ were not dense. Denseness of \mathbf{T}^{-1} leads quickly to large memory requirements and to greatly increased computing time compared with the equations for the individual effects model for which sparse matrix methods are effective. Even with non-sparse techniques, the use of equations for the total-merit model is not likely to be competitive with sparse methods based on equations for the individual-effects model.

Implications

The method based on a total-merit model proposed by Henderson to predict nonadditive and additive genetic values is easily extended to include maternal effects. For estimating variance components with derivative-free restricted maximum likelihood with sparse-matrix methods, the increase in number of coefficients of the mixed-model equations and the necessity to invert the matrix of genetic covariances each round, neither of which benefit from sparse-matrix methods, results in increased computational requirements in each computational round. Thus, sparse-matrix algorithms are much more efficient based on individual-effects models than on total-merit models.

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