Chapter 29
Non-Additive Genetic Merit

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1 Model for Genetic Components

All of the applications in previous chapters have been concerned entirely with additive genetic models. This may be a suitable approximation, but theory exists that enables consideration to be given to more complicated genetic models. This theory is simple for non-inbred populations, for then we can formulate genetic merit of the animals in a sample as

$$\mathbf{g} = \sum_i \mathbf{g}_i.$$

$\mathbf{g}$ is the vector of total genetic values for the animals in the sample. $\mathbf{g}_i$ is a vector describing values for a specific type of genetic merit. For example, $\mathbf{g}_1$ represents additive values, $\mathbf{g}_2$ dominance values, $\mathbf{g}_3$ additive $\times$ additive, $\mathbf{g}_4$ additive by dominance, etc. In a non-inbred, unselected population and ignoring linkage

$$Cov(\mathbf{g}_i, \mathbf{g}_j') = \mathbf{0}$$

for all pairs of $i \neq j$.

$$Var(\text{additive}) = \mathbf{A}\sigma_a^2,$$

$$Var(\text{dominance}) = \mathbf{D}\sigma_d^2,$$

$$Var(\text{additive} \times \text{additive}) = \mathbf{A}\#\mathbf{A}\sigma_{aa}^2,$$

$$Var(\text{additive} \times \text{dominance}) = \mathbf{A}\#\mathbf{D}\sigma_{ad}^2,$$

$$Var(\text{additive} \times \text{additive} \times \text{dominance}) = \mathbf{A}\#\mathbf{A}\#\mathbf{D}\sigma_{aad}^2, \text{ etc.}$$

The # operation on $\mathbf{A}$ and $\mathbf{D}$ is described below. These results are due mostly to Cockerham (1954). $\mathbf{D}$ is computed as follows. All diagonals are 1. $d_{km} (k \neq m)$ is computed from certain elements of $\mathbf{A}$. Let the parents of k and m be g, h and i, j respectively. Then

$$d_{km} = .25(a_{gi}a_{hj} + a_{gj}a_{hi}). \tag{1}$$

In a non-inbred population only one at most of the products in this expression can be greater than 0. To illustrate suppose k and m are full sibs. Then $g = i$ and $h = j$.

Consequently

$$d_{km} = .25[(1)(1) + 0] = .25.$$

Suppose k and m are double first cousins. Then

$$d_{km} = .25[(.5)(.5) + 0] = .0625.$$

For non-inbred paternal sibs from unrelated dams is

$$d_{km} = .25[1(0) + 0(0)] = 0,$$

and for parent-progeny $d_{km} = 0$.

The # operation on two matrices means that the new matrix is formed from the products of the corresponding elements of the 2 matrices. Thus the ij^{th} element of $\mathbf{A}\#\mathbf{A}$ is a_{ij}^2, and the ij^{th} element of $\mathbf{A}\#\mathbf{D}$ is $a_{ij}d_{ij}$. These are called Hadamard products. Accordingly, we see that all matrices for $Var(\mathbf{g}_i)$ are derived from $\mathbf{A}$.

2 Single Record on Every Animal

We shall describe BLUP procedures and estimation of variances in this and subsequent sections of Chapter 29 by a model with additive and dominance components. The extension to more components is straightforward. The model for $\mathbf{y}$ with no data missing is

$$\mathbf{y} = (\mathbf{X} \;\; \mathbf{I} \;\; \mathbf{I}) \begin{pmatrix} \boldsymbol{\beta} \\ \mathbf{a} \\ \mathbf{d} \end{pmatrix} + \mathbf{e}\,.$$

$\mathbf{y}$ is n x 1, $\mathbf{X}$ is n x p, both $\mathbf{I}$ are n x n, and $\mathbf{e}$ is n x 1, $\boldsymbol{\beta}$ is p x 1, $\mathbf{a}$ and $\mathbf{d}$ are n x 1.

$$Var(\mathbf{a}) = \mathbf{A}\sigma_a^2,$$

$$Var(\mathbf{d}) = \mathbf{D}\sigma_d^2,$$

$$Var(\mathbf{e}) = \mathbf{I}\sigma_e^2.$$

$Cov(\mathbf{a}, \mathbf{d}')$, $Cov(\mathbf{a}, \mathbf{e}')$, and $Cov(\mathbf{d}, \mathbf{e}')$ are all $n \times n$ null matrices. Now the mixed model equations are

$$\begin{pmatrix} \mathbf{X}'\mathbf{X} & \mathbf{X}' & \mathbf{X}' \\ \mathbf{X} & \mathbf{I} + \mathbf{A}^{-1}\sigma_e^2/\sigma_a^2 & \mathbf{I} \\ \mathbf{X} & \mathbf{I} & \mathbf{I} + \mathbf{D}^{-1}\sigma_e^2/\sigma_d^2 \end{pmatrix} \begin{pmatrix} \boldsymbol{\beta}^o \\ \hat{\mathbf{a}} \\ \hat{\mathbf{d}} \end{pmatrix} = \begin{pmatrix} \mathbf{X}'\mathbf{y} \\ \mathbf{y} \\ \mathbf{y} \end{pmatrix}. \quad (2)$$

Note that if $\mathbf{a}, \mathbf{d}$ were regarded as fixed, the last n equations would be identical to the $p + 1, \ \ldots, \ p + n$ equations, and we could estimate only differences among elements of

$\mathbf{a}+\mathbf{d}$. An interesting relationship exists between $\hat{\mathbf{a}}$ and $\hat{\mathbf{d}}$. Subtracting the third equation of (29.2) from the second,

$$\mathbf{A}^{-1}\sigma_e^2/\sigma_a^2\hat{\mathbf{a}} - \mathbf{D}^{-1}\sigma_e^2/\sigma_d^2\hat{\mathbf{d}} = \mathbf{0}.$$

Therefore

$$\hat{\mathbf{d}} = \mathbf{D}\mathbf{A}^{-1}\sigma_d^2/\sigma_a^2\hat{\mathbf{a}}. \tag{3}$$

This identity can be used to reduce (29.2) to

$$\begin{pmatrix} \mathbf{X}'\mathbf{X} & \mathbf{X}'(\mathbf{I}+\mathbf{D}\mathbf{A}^{-1}\sigma_d^2/\sigma_a^2) \\ \mathbf{X} & \mathbf{I}+\mathbf{A}^{-1}\sigma_e^2/\sigma_a^2+\mathbf{D}\mathbf{A}^{-1}\sigma_d^2/\sigma_a^2 \end{pmatrix} \begin{pmatrix} \boldsymbol{\beta}^o \\ \hat{\mathbf{a}} \end{pmatrix} = \begin{pmatrix} \mathbf{X}'\mathbf{y} \\ \mathbf{y} \end{pmatrix}. \tag{4}$$

Note that the coefficient matrix of (29.4) is not symmetric. Having solved for $\hat{\mathbf{a}}$ in (29.4) compute $\hat{\mathbf{d}}$ by (29.3).

σ_a^2, σ_d^2, σ_e^2 can be estimated by MIVQUE. Quadratics needed to be computed and equated to their expectations are

$$\hat{\mathbf{a}}'\mathbf{A}^{-1}\hat{\mathbf{a}},\ \hat{\mathbf{d}}'\mathbf{D}^{-1}\hat{\mathbf{d}},\ \text{and}\ \hat{\mathbf{e}}'\hat{\mathbf{e}}. \tag{5}$$

To obtain expectations of the first two of these we need $Var(\mathbf{r})$, where $\mathbf{r}$ is the vector of right hand sides of (29.2). This is

$$\begin{pmatrix} \mathbf{X}'\mathbf{A}\mathbf{X} & \mathbf{X}'\mathbf{A} & \mathbf{X}'\mathbf{A} \\ \mathbf{A}\mathbf{X} & \mathbf{A} & \mathbf{A} \\ \mathbf{A}\mathbf{X} & \mathbf{A} & \mathbf{A} \end{pmatrix}\sigma_a^2 + \begin{pmatrix} \mathbf{X}'\mathbf{D}\mathbf{X} & \mathbf{X}'\mathbf{D} & \mathbf{X}'\mathbf{D} \\ \mathbf{D}\mathbf{X} & \mathbf{D} & \mathbf{D} \\ \mathbf{D}\mathbf{X} & \mathbf{D} & \mathbf{D} \end{pmatrix}\sigma_d^2 + \begin{pmatrix} \mathbf{X}'\mathbf{X} & \mathbf{X}' & \mathbf{X}' \\ \mathbf{X} & \mathbf{I} & \mathbf{I} \\ \mathbf{X} & \mathbf{I} & \mathbf{I} \end{pmatrix}\sigma_e^2. \tag{6}$$

From (29.6) we can compute $Var(\hat{\mathbf{a}})$, $Var(\hat{\mathbf{d}})$ as follows. Let some g-inverse of the matrix of (29.2) be

$$\mathbf{C} = \begin{pmatrix} \mathbf{C}_\beta \\ \mathbf{C}_a \\ \mathbf{C}_d \end{pmatrix}.$$

$\mathbf{C}_a$ and $\mathbf{C}_d$ each have n rows. Then

$$\hat{\mathbf{a}} = \mathbf{C}_a\mathbf{r},$$

and

$$\hat{\mathbf{d}} = \mathbf{C}_d\mathbf{r}.$$

$$Var(\hat{\mathbf{a}}) = \mathbf{C}_a\, Var(\mathbf{r})\mathbf{C}_a', \tag{7}$$

and

$$Var(\hat{\mathbf{d}}) = \mathbf{C}_d\, Var(\mathbf{r})\mathbf{C}_d'. \tag{8}$$

$$E(\hat{\mathbf{a}}'\mathbf{A}^{-1}\hat{\mathbf{a}}) = tr\mathbf{A}^{-1}\, Var(\hat{\mathbf{a}}). \tag{9}$$

$$E(\hat{\mathbf{d}}'\mathbf{D}^{-1}\hat{\mathbf{d}}) = tr\mathbf{D}^{-1}\, Var(\hat{\mathbf{d}}). \tag{10}$$

For the expectation of $\hat{\mathbf{e}}'\hat{\mathbf{e}}$ we compute $tr(Var(\hat{\mathbf{e}}))$. Note that

$$\begin{aligned}
\hat{\mathbf{e}} &= \left(\mathbf{I} - (\mathbf{X}\ \ \mathbf{I}\ \ \mathbf{I})\,\mathbf{C}\begin{pmatrix}\mathbf{X}'\\ \mathbf{I}\\ \mathbf{I}\end{pmatrix}\right)\mathbf{y} \\
&= (\mathbf{I} - \mathbf{X}\mathbf{C}_{11}\mathbf{X}' - \mathbf{X}\mathbf{C}_{12} - \mathbf{C}_{12}'\mathbf{X}' - \mathbf{X}\mathbf{C}_{13} - \mathbf{C}_{13}'\mathbf{X}' \\
&\quad -\mathbf{C}_{22} - \mathbf{C}_{23} - \mathbf{C}_{23}' - \mathbf{C}_{33})\mathbf{y} \\
&\equiv \mathbf{T}\mathbf{y}
\end{aligned} \tag{11}$$

where

$$\mathbf{C} = \begin{pmatrix}\mathbf{C}_{11} & \mathbf{C}_{12} & \mathbf{C}_{13}\\ \mathbf{C}_{12}' & \mathbf{C}_{22} & \mathbf{C}_{23}\\ \mathbf{C}_{13}' & \mathbf{C}_{23}' & \mathbf{C}_{33}\end{pmatrix}. \tag{12}$$

Then

$$Var(\hat{\mathbf{e}}) = \mathbf{T}\, Var(\mathbf{y})\mathbf{T}'. \tag{13}$$

$$Var(\mathbf{y}) = \mathbf{A}\sigma_a^2 + \mathbf{D}\sigma_d^2 + \mathbf{I}\sigma_e^2. \tag{14}$$

REML by the EM type algorithm is quite simple to state. At each round of iteration we need the same quadratics as in (29.5). Now we pretend that $Var(\hat{\mathbf{a}})$, $Var(\hat{\mathbf{d}})$, $Var(\hat{\mathbf{e}})$ are represented by the mixed model result with true variance ratios employed. These are

$$\begin{aligned}
Var(\hat{\mathbf{a}}) &= \mathbf{A}\sigma_a^2 - \mathbf{C}_{22}. \\
Var(\hat{\mathbf{d}}) &= \mathbf{D}\sigma_d^2 - \mathbf{C}_{33}. \\
Var(\hat{\mathbf{e}}) &= \mathbf{I}\sigma_e^2 - \mathbf{W}\mathbf{C}\mathbf{W}'.
\end{aligned}$$

$\mathbf{C}_{22}$, $\mathbf{C}_{33}$, $\mathbf{C}$ are defined in (29.12).

$$\mathbf{W} = (\mathbf{X}\ \ \mathbf{I}\ \ \mathbf{I}).$$

$\mathbf{W}\mathbf{C}\mathbf{W}'$ can be written as $\mathbf{I} - \mathbf{T} = \mathbf{X}\mathbf{C}_{11}\mathbf{X}' + \mathbf{X}\mathbf{C}_{12} +$ etc. From these "variances" we iterate on

$$\hat{\sigma}_a^2 = (\hat{\mathbf{a}}'\mathbf{A}^{-1}\hat{\mathbf{a}} + tr\mathbf{A}^{-1}\mathbf{C}_{22})/n, \tag{15}$$

$$\hat{\sigma}_d^2 = (\hat{\mathbf{d}}'\mathbf{D}^{-1}\hat{\mathbf{d}} + tr\mathbf{D}^{-1}\mathbf{C}_{33})/n, \tag{16}$$

and

$$\hat{\sigma}_e^2 = (\hat{\mathbf{e}}'\hat{\mathbf{e}} + tr\mathbf{W}\mathbf{C}\mathbf{W}')/n. \tag{17}$$

This algorithm guarantees that at each round of iteration all estimates are non-negative provided the starting values of σ_e^2/σ_a^2, σ_e^2/σ_d^2 are positive.

3 Single or No Record on Each Animal

In this section we use the same model as in Section 29.2, except now some animals have no record but we wish to evaluate them in the mixed model solution. Let us order the animals by the set of animals with no record followed by the set with records.

$$\mathbf{y} = (\mathbf{X} \;\; \mathbf{0} \;\; \mathbf{I} \;\; \mathbf{0} \;\; \mathbf{I}) \begin{pmatrix} \boldsymbol{\beta} \\ \mathbf{a}_m \\ \mathbf{a}_p \\ \mathbf{d}_m \\ \mathbf{d}_p \end{pmatrix} + \mathbf{e}\,. \tag{18}$$

The subscript, m, denotes animals with no record, and the subscript, p, denotes animals with a record. Let there be n_p animals with a record and n_m animals with no record. Then $\mathbf{y}$ is n_p x 1, $\mathbf{X}$ is n_p x p, the $\mathbf{0}$ submatrices are both n_p x n_m, and the $\mathbf{I}$ submatrices are both n_p x n_p. The OLS equations are

$$\begin{pmatrix} \mathbf{X}'\mathbf{X} & \mathbf{0} & \mathbf{X}' & \mathbf{0} & \mathbf{X}' \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{X} & \mathbf{0} & \mathbf{I} & \mathbf{0} & \mathbf{I} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{X}' & \mathbf{0} & \mathbf{I} & \mathbf{0} & \mathbf{I} \end{pmatrix} \begin{pmatrix} \boldsymbol{\beta}^o \\ \hat{\mathbf{a}}_m \\ \hat{\mathbf{a}}_p \\ \hat{\mathbf{d}}_m \\ \hat{\mathbf{d}}_p \end{pmatrix} = \begin{pmatrix} \mathbf{X}'\mathbf{y} \\ \mathbf{0} \\ \mathbf{y} \\ \mathbf{0} \\ \mathbf{y} \end{pmatrix}. \tag{19}$$

The mixed model equations are formed by adding $\mathbf{A}^{-1}\sigma_e^2/\sigma_a^2$ and $\mathbf{D}^{-1}\sigma_e^2/\sigma_d^2$ to the appropriate submatrices of matrix (29.19).

We illustrate these equations with a simple example. We have 10 animals with animals 1,3,5,7 not having records. 1,2,3,4 are unrelated, non-inbred animals. The parents of 5 and 6 are 1,2. The parents of 7 and 8 are 3,4. The parents of 9 are 6,7. The parents of 10 are 5,8. This gives

$$\mathbf{A} = \begin{pmatrix} 1 & 0 & 0 & 0 & .5 & .5 & 0 & 0 & .25 & .25 \\ & 1 & 0 & 0 & .5 & .5 & 0 & 0 & .25 & .25 \\ & & 1 & 0 & 0 & 0 & .5 & .5 & .25 & .25 \\ & & & 1 & 0 & 0 & .5 & .5 & .25 & .25 \\ & & & & 1 & .5 & 0 & 0 & .25 & .5 \\ & & & & & 1 & 0 & 0 & .5 & .25 \\ & & & & & & 1 & .5 & .5 & .25 \\ & & & & & & & 1 & .25 & .5 \\ & & & & & & & & 1 & .25 \\ & & & & & & & & & 1 \end{pmatrix}.$$

$\mathbf{D}$ = matrix with all 1's in diagonal,

$$d_{56} = d_{65} = d_{78} = d_{87} = .25,$$

$$d_{9,10} = d_{10,9} = .0625,$$

and all other elements = 0.

$$\mathbf{y}' = [6, 9, 6, 7, 4, 6].$$

$$\mathbf{X}' = (1\ 1\ 1\ 1\ 1\ 1).$$

Assuming that $\sigma_e^2/\sigma_a^2 = 2.25$ and $\sigma_e^2/\sigma_d^2 = 5$, the mixed model coefficient matrix with animals ordered as in the **A** and **D** matrices is in (29.20) . . . (29.22). The right hand side vector is [38, 0, 6, 0, 9, 0, 6, 0, 7, 4, 6, 0, 6, 0, 9, 0, 6, 0, 7, 4, 6]′. The solution is

$$\boldsymbol{\beta}^o = 6.400,$$

$$\hat{\mathbf{a}}' = [-.203,\ -.256,\ -.141,\ .600,\ -.259,\ -.403,\ .056,\ .262,\ -.521,\ -.058],$$

and

$$\hat{\mathbf{d}}' = (0,\ -.024,\ 0,\ .333,\ 0,\ 0,\ .014,\ .056,\ -.316,\ -.073).$$

Upper left 11 × 11

$$\begin{pmatrix}
6. & 0 & 1. & 0 & 1. & 0 & 1. & 0 & 1. & 1. & 1. \\
 & 4.5 & 2.25 & 0 & 0 & -2.25 & -2.25 & 0 & 0 & 0 & 0 \\
 & & 5.5 & 0 & 0 & -2.25 & -2.25 & 0 & 0 & 0 & 0 \\
 & & & 4.5 & 2.25 & 0 & 0 & -2.25 & -2.25 & 0 & 0 \\
 & & & & 5.5 & 0 & 0 & -2.25 & -2.25 & 0 & 0 \\
 & & & & & 5.625 & 0 & 0 & 1.125 & 0 & -2.25 \\
 & & & & & & 6.625 & 1.125 & 0 & -2.25 & 0 \\
 & & & & & & & 5.625 & 0 & -2.25 & 0 \\
 & & & & & & & & 6.625 & 0 & -2.25 \\
 & & & & & & & & & 5.5 & 0 \\
 & & & & & & & & & & 5.5
\end{pmatrix}. \quad (20)$$

Upper right 10 × 10 and (lower left 10 × 11)′

$$\begin{pmatrix}
0 & 1 & 0 & 1 & 0 & 1 & 0 & 1 & 1 & 1 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1
\end{pmatrix}. \quad (21)$$

Lower right 10 × 10

$$\begin{pmatrix} 5.0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & 6.0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & 5.0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & 6.0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & 5.333 & -1.333 & 0 & 0 & 0 & 0 \\ & & & & & 6.333 & 0 & 0 & 0 & 0 \\ & & & & & & 5.333 & -1.333 & 0 & 0 \\ & & & & & & & 6.333 & 0 & 0 \\ & & & & & & & & 6.02 & -.314 \\ & & & & & & & & & 6.02 \end{pmatrix} . \quad (22)$$

If we wish EM type estimation of variances we iterate on

$$\begin{aligned} \hat{\sigma}_e^2 &= (\mathbf{y}'\mathbf{y} - \mathbf{y}'\mathbf{X}\boldsymbol{\beta}^o - \mathbf{y}'\hat{\mathbf{a}}_p - \mathbf{y}'\hat{\mathbf{d}}_p)/[n - \text{rank}\ (\mathbf{X})], \\ \hat{\sigma}_a^2 &= (\hat{\mathbf{a}}'\mathbf{A}^{-1}\hat{\mathbf{a}} + tr\hat{\sigma}_e^2\mathbf{C}_{aa})/n, \end{aligned}$$

and

$$\hat{\sigma}_d^2 = (\hat{\mathbf{d}}'\mathbf{D}^{-1}\hat{\mathbf{d}} + tr\hat{\sigma}_e^2\mathbf{C}_{dd})/n,$$

for

$$\hat{\mathbf{a}}' = (\hat{\mathbf{a}}_m' \ \ \hat{\mathbf{a}}_p'),$$

$$\hat{\mathbf{d}}' = (\hat{\mathbf{d}}_m' \ \ \hat{\mathbf{d}}_p'),$$

and n = number of animals. A g-inverse of (29.19) is

$$\begin{pmatrix} \mathbf{C}_{xx} & \mathbf{C}_{xa} & \mathbf{C}_{xd} \\ \mathbf{C}_{xa}' & \mathbf{C}_{aa} & \mathbf{C}_{ad} \\ \mathbf{C}_{xd}' & \mathbf{C}_{ad}' & \mathbf{C}_{dd} \end{pmatrix}.$$

Remember that in these computations $Var(\mathbf{e}) = \mathbf{I}\sigma_e^2$ and the equations are set up with scaling, $Var(\mathbf{e}) = \mathbf{I}$, $Var(\mathbf{a}) = \mathbf{A}\sigma_a^2/\sigma_e^2$, $Var(\mathbf{d}) = \mathbf{D}\sigma_d^2/\sigma_e^2$.

4 A Reduced Set of Equations

When there are several genetic components in the model, a much more efficient computing strategy can be employed than that of Section 29.3. Let $\mathbf{m}$ be total genetic value of the members of a population, and this is

$$\mathbf{m} = \sum_i \mathbf{g}_i,$$

where $\mathbf{g}_i$ is the merit for a particular type of genetic component, additive for example. Then in a non-inbred population and ignoring linkage

$$Var(\mathbf{m}) = \sum_i Var(\mathbf{g}_i)$$

since

$$Cov(\mathbf{g}_i, \mathbf{g}'_j) = \mathbf{0}$$

for all $i \neq j$. Then a model is

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_m\mathbf{m} + \mathbf{e}. \tag{23}$$

We could, if we choose, add a term for other random components. Now mixed model equations for BLUE and BLUP are

$$\begin{pmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{Z}_m \\ \mathbf{Z}'_m\mathbf{R}^{-1}\mathbf{X} & \mathbf{Z}'_m\mathbf{R}^{-1}\mathbf{Z}_m + [Var(\mathbf{m})]^{-1} \end{pmatrix} \begin{pmatrix} \boldsymbol{\beta}^o \\ \hat{\mathbf{m}} \end{pmatrix} = \begin{pmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{Z}'_m\mathbf{R}^{-1}\mathbf{y} \end{pmatrix}. \tag{24}$$

If we are interested in BLUP of certain genetic components this is simply

$$\hat{\mathbf{g}}_i = Var(\mathbf{g}_i)[Var(\mathbf{m})]^{-1}\hat{\mathbf{m}}. \tag{25}$$

This method is illustrated by the example of Section 29.2. Except for scaling

$$Var(\mathbf{e}) = \mathbf{I},$$

$$Var(\mathbf{a}) = 2.25^{-1}\mathbf{A},$$

$$Var(\mathbf{d}) = 5^{-1}\mathbf{D}.$$

Then

$$Var(\mathbf{m}) = 2.25^{-1}\mathbf{A} + 5^{-1}\mathbf{D}$$

$$= \begin{pmatrix} .6444 & 0 & 0 & 0 & .2222 & .2222 & 0 & 0 & .1111 & .1111 \\ & .6444 & 0 & 0 & .2222 & .2222 & 0 & 0 & .1111 & .1111 \\ & & .6444 & 0 & 0 & 0 & .2222 & .2222 & .1111 & .1111 \\ & & & .6444 & 0 & 0 & .2222 & .2222 & .1111 & .1111 \\ & & & & .6444 & .2722 & 0 & 0 & .1111 & .2222 \\ & & & & & .6444 & 0 & 0 & .2222 & .1111 \\ & & & & & & .6444 & .2722 & .2222 & .1111 \\ & & & & & & & .6444 & .1111 & .2222 \\ & & & & & & & & .6444 & .1236 \\ & & & & & & & & & .6444 \end{pmatrix}. \tag{26}$$

Adding the inverse of this to the lower 10 × 10 block of the OLS equations of (29.27) we obtain the mixed model equations. The OLS equations including animals with missing records are

$$
\begin{pmatrix}
6 & 0 & 1 & 0 & 1 & 0 & 1 & 0 & 1 & 1 & 1 \\
 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & & & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & & & & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & & & & & 0 & 0 & 0 & 0 & 0 & 0 \\
 & & & & & & 1 & 0 & 0 & 0 & 0 \\
 & & & & & & & 0 & 0 & 0 & 0 \\
 & & & & & & & & 1 & 0 & 0 \\
 & & & & & & & & & 1 & 0 \\
 & & & & & & & & & & 1
\end{pmatrix}
\begin{pmatrix} \hat{\mu} \\ \hat{\mathbf{m}} \end{pmatrix}
=
\begin{pmatrix} 38 \\ 0 \\ 6 \\ 0 \\ 9 \\ 0 \\ 6 \\ 0 \\ 7 \\ 4 \\ 6 \end{pmatrix}. \qquad (27)
$$

The resulting solution is

$$\hat{\mu} = 6.400 \text{ as before, and}$$

$$\hat{\mathbf{m}} = [-.203,\ -.280,\ -.141,\ .933,\ -.259,\ -.402,\ .070,\ .319,\ -.837,\ -.131]'.$$

From $\hat{\mathbf{m}}$ and using the method of (29.25) we obtain the same solution to $\hat{\mathbf{a}}$ and $\hat{\mathbf{d}}$ as before.

To obtain REML estimates identical to those of Section 29.4 compute the same quantities except $\hat{\sigma}_e^2$ can be computed by

$$\hat{\sigma}_e^2 = (\mathbf{y}'\mathbf{y} - \mathbf{y}'\mathbf{X}\boldsymbol{\beta}^o - \mathbf{y}'\mathbf{Z}_m\hat{\mathbf{m}})/[n - \text{rank }(\mathbf{X})].$$

Then $\hat{\mathbf{a}}$ and $\hat{\mathbf{d}}$ are computed from $\hat{\mathbf{m}}$ as described in this section. With the scaling done

$$\mathbf{G} = \mathbf{A}\sigma_a^2/\sigma_e^2 + \mathbf{D}\sigma_d^2/\sigma_e^2,$$

$$\mathbf{C}_{aa} = (\sigma_a^2/\sigma_e^2)\mathbf{A} - (\sigma_a^2/\sigma_e^2)\mathbf{A}\mathbf{G}^{-1}(\mathbf{G} - \mathbf{C}_{mm})\mathbf{G}^{-1}\mathbf{A}(\sigma_a^2/\sigma_e^2),$$

$$\mathbf{C}_{dd} = (\sigma_d^2/\sigma_e^2)\mathbf{D} - (\sigma_d^2/\sigma_e^2)\mathbf{D}\mathbf{G}^{-1}(\mathbf{G} - \mathbf{C}_{mm})\mathbf{G}^{-1}\mathbf{D}(\sigma_d^2/\sigma_e^2),$$

where a g-inverse of the reduced coefficient matrix is

$$\begin{pmatrix} \mathbf{C}_{xx} & \mathbf{C}_{xm} \\ \mathbf{C}'_{xm} & \mathbf{C}_{mm} \end{pmatrix}.$$

In our example $\mathbf{C}_{aa}$ for both the extended and the reduced equations is

$$
\begin{pmatrix}
.4179 & -.0001 & .0042 & .0224 & .2057 & .1856 & .0112 & .0196 & .0942 & .1062 \\
 & .3651 & .0224 & .0571 & .1847 & .1802 & .0428 & .0590 & .1176 & .1264 \\
 & & .4179 & -.0001 & .0112 & .0196 & .2057 & .1856 & .1062 & .0942 \\
 & & & .3651 & .0428 & .0590 & .1847 & .1802 & .1264 & .1176 \\
 & & & & .4100 & .1862 & .0287 & .0365 & .1108 & .2084 \\
 & & & & & .3653 & .0365 & .0618 & .1953 & .1305 \\
 & & & & & & .4100 & .1862 & .2084 & .1108 \\
 & & & & & & & .3653 & .1305 & .1953 \\
 & & & & & & & & .3859 & .1304 \\
 & & & & & & & & & .3859
\end{pmatrix}.
$$

Similarly $\mathbf{C}_{dd}$ is

$$\begin{pmatrix} .2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & .1786 & 0 & .0034 & .0016 & .0064 & 0 & .0030 & .0045 & .0047 \\ & & .2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & .1786 & .0008 & .0030 & 0 & .0064 & .0047 & .0045 \\ & & & & .1986 & .0444 & 0 & .0007 & .0016 & .0011 \\ & & & & & .1778 & 0 & .0027 & .0062 & .0045 \\ & & & & & & .2 & 0 & 0 & 0 \\ & & & & & & & .1778 & .0047 & .0062 \\ & & & & & & & & .1778 & .0136 \\ & & & & & & & & & .1778 \end{pmatrix}.$$

$\mathbf{C}_{aa}$ and $\mathbf{C}_{dd}$ have rather large rounding errors.

5 Multiple or No Records

Next consider a model with repeated records and the traditional repeatability model. That is, all records have the same variance and all pairs of records on the same animal have the same covariance. Ordering the animals with no records first the model is

$$\mathbf{y} = [\mathbf{X}\ \ \mathbf{0}\ \ \mathbf{Z}\ \ \mathbf{0}\ \ \mathbf{Z}\ \ \mathbf{Z}](\boldsymbol{\beta} : \mathbf{a}_m : \mathbf{a}_p : \mathbf{d}_m : \mathbf{d}_p\ \ \mathbf{t})' + \mathbf{e}. \tag{28}$$

$\mathbf{y}$ is n x 1, $\mathbf{X}$ is n x p, the null matrices are n x n_m, $\mathbf{Z}$ is n x n_p. n is the number of records, n_m the number of animals with no record, and n_p the number of animals with 1 or more records. $\mathbf{a}_m$, $\mathbf{a}_p$ refer to $\mathbf{a}$ for animals with no records and with records respectively, and similarly for $\mathbf{d}_m$ and $\mathbf{d}_p$. $\mathbf{t}$ refers to permanent environmental effects for animals with records.

$$Var(\mathbf{a}) = \mathbf{A}\sigma_a^2,$$
$$Var(\mathbf{d}) = \mathbf{D}\sigma_d^2,$$
$$Var(\mathbf{t}) = \mathbf{I}\sigma_t^2,$$
$$Var(\mathbf{e}) = \mathbf{I}\sigma_e^2.$$

These 4 vectors are uncorrelated. The OLS equations are

$$\begin{pmatrix} \mathbf{X}'\mathbf{X} & \mathbf{0} & \mathbf{X}'\mathbf{Z} & \mathbf{0} & \mathbf{X}'\mathbf{Z} & \mathbf{X}'\mathbf{Z} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{Z}'\mathbf{X} & \mathbf{0} & \mathbf{Z}'\mathbf{Z} & \mathbf{0} & \mathbf{Z}'\mathbf{Z} & \mathbf{Z}'\mathbf{Z} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{Z}'\mathbf{X} & \mathbf{0} & \mathbf{Z}'\mathbf{Z} & \mathbf{0} & \mathbf{Z}'\mathbf{Z} & \mathbf{Z}'\mathbf{Z} \\ \mathbf{Z}'\mathbf{X} & \mathbf{0} & \mathbf{Z}'\mathbf{Z} & \mathbf{0} & \mathbf{Z}'\mathbf{Z} & \mathbf{Z}'\mathbf{Z} \end{pmatrix} \begin{pmatrix} \boldsymbol{\beta}^o \\ \hat{\mathbf{a}}_m \\ \hat{\mathbf{a}}_p \\ \hat{\mathbf{d}}_m \\ \hat{\mathbf{d}}_p \\ \hat{\mathbf{t}} \end{pmatrix} = \begin{pmatrix} \mathbf{X}'\mathbf{y} \\ \mathbf{0} \\ \mathbf{Z}'\mathbf{y} \\ \mathbf{0} \\ \mathbf{Z}'\mathbf{y} \\ \mathbf{Z}'\mathbf{y} \end{pmatrix} \tag{29}$$

The mixed model equations are formed by adding $\mathbf{A}^{-1}\sigma_e^2/\sigma_a^2$, $\mathbf{D}^{-1}\sigma_e^2/\sigma_d^2$, and $\mathbf{I}\sigma_e^2/\sigma_t^2$ to appropriate blocks in (29.29).

We illustrate with the same 10 animals as in the preceding section, but now there are multiple records as follows.

	Records		
Animals	1	2	3
1	X	X	X
2	6	5	4
3	X	X	X
4	9	8	X
5	X	X	X
6	6	5	6
7	X	X	X
8	7	3	X
9	4	5	X
10	6	X	X

X denotes no record. We assume that the first records have a common mean β_1, the second a common mean β_2, and the third a common mean β_3. It is assumed that $\sigma_e^2/\sigma_a^2 = 1.8$, $\sigma_e^2/\sigma_d^2 = 4$, $= \sigma_e^2/\sigma_t^2 = 4$. Then the mixed model coefficient matrix is in (29.30) ... (29.32). The right hand side vector is (38, 26, 10, 0, 15, 0, 17, 0, 17, 0, 10, 9, 6, 0, 15, 0, 17, 0, 17, 0, 10, 9, 6, 15, 17, 17, 10, 9, 6)'. The solution is

$$
\begin{aligned}
\boldsymbol{\beta}^{o'} &= (6.398,\ 5.226,\ 5.287), \\
\hat{\mathbf{a}}' &= (-.067,\ -.295,\ -.364,\ .726,\ -.201,\ -.228,\ .048,\ -.051, \\
&\quad -.355,\ -.166), \\
\hat{\mathbf{d}}' &= (0,\ -.103,\ 0,\ .491,\ .019,\ .077,\ -.048,\ -.190,\ -.241, \\
&\quad -.051), \\
\hat{\mathbf{t}}' &= (-.103,\ .491,\ .077,\ -.190,\ -.239,\ -.036).
\end{aligned}
$$

$\hat{\mathbf{t}}$ refers to the six animals with records. BLUP of the others is $\mathbf{0}$.

Upper left 13×13

$$
\begin{pmatrix}
6.0 & 0 & 0 & 0 & 1.0 & 0 & 1.0 & 0 & 1.0 & 0 & 1.0 & 1.0 & 1.0 \\
 & 5.0 & 0 & 0 & 1.0 & 0 & 1.0 & 0 & 1.0 & 0 & 1.0 & 1.0 & 0 \\
 & & 2.0 & 0 & 1.0 & 0 & 0 & 0 & 1.0 & 0 & 0 & 0 & 0 \\
 & & & 3.6 & 1.8 & 0 & 0 & -1.8 & -1.8 & 0 & 0 & 0 & 0 \\
 & & & & 6.6 & 0 & 0 & -1.8 & -1.8 & 0 & 0 & 0 & 0 \\
 & & & & & 3.6 & 1.8 & 0 & 0 & -1.8 & -1.8 & 0 & 0 \\
 & & & & & & 5.6 & 0 & 0 & -1.8 & -1.8 & 0 & 0 \\
 & & & & & & & 4.5 & 0 & 0 & .9 & 0 & -1.8 \\
 & & & & & & & & 7.5 & .9 & 0 & -1.8 & 0 \\
 & & & & & & & & & 4.5 & 0 & -1.8 & 0 \\
 & & & & & & & & & & 6.5 & 0 & -1.8 \\
 & & & & & & & & & & & 5.6 & 0 \\
 & & & & & & & & & & & & 4.6
\end{pmatrix} \tag{30}
$$

Upper right 13×16 and (lower left 16×13)'

$$
\begin{pmatrix}
0 & 1 & 0 & 1 & 0 & 1 & 0 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\
0 & 1 & 0 & 1 & 0 & 1 & 0 & 1 & 1 & 0 & 1 & 1 & 1 & 1 & 1 & 0 \\
0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 1 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 3 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 3 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 2 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 3 & 0 & 0 & 0 & 0 & 0 & 0 & 3 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 2 & 0 & 0 & 0 & 0 & 0 & 2 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 2 & 0 & 0 & 0 & 0 & 0 & 2 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 1
\end{pmatrix} \tag{31}
$$

Lower right 16 × 16

$$\left(\begin{array}{cccccccccccccccc}
4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & 7 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 3 & 0 & 0 & 0 & 0 & 0 \\
 & & 4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & & & 6 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 2 & 0 & 0 & 0 & 0 \\
 & & & & 4.267 & -1.067 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & & & & & 7.267 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & & & & & & 4.267 & -1.067 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & & & & & & & 6.267 & 0 & 0 & 0 & 0 & 0 & 2 & 0 & 0 \\
 & & & & & & & & 6.016 & -.251 & 0 & 0 & 0 & 0 & 2 & 0 \\
 & & & & & & & & & 5.016 & 0 & 0 & 0 & 0 & 0 & 1 \\
 & & & & & & & & & & 7 & 0 & 0 & 0 & 0 & 0 \\
 & & & & & & & & & & & 6 & 0 & 0 & 0 & 0 \\
 & & & & & & & & & & & & 7 & 0 & 0 & 0 \\
 & & & & & & & & & & & & & 6 & 0 & 0 \\
 & & & & & & & & & & & & & & 6 & 0 \\
 & & & & & & & & & & & & & & & 5
\end{array}\right) \qquad (32)$$

6 A Reduced Set of Equations for Multiple Records

As in Section 29.4 we can reduce the equations by now letting

$$\mathbf{m} = \sum_i \mathbf{g}_i + \mathbf{t},$$

where $\mathbf{g}_i$ have the same meaning as before, and $\mathbf{t}$ is permanent environmental effect with $Var(\mathbf{t}) = \mathbf{I}\sigma_t^2$. Then the mixed model equations are like those of (29.24) and from $\hat{\mathbf{m}}$ one can compute $\hat{\mathbf{g}}_i$ and $\hat{\mathbf{t}}$.

Using the same example as in Section 29.5 the OLS equations are

$$\left(\begin{array}{ccccccccccccc}
6 & 0 & 0 & 0 & 1 & 0 & 1 & 0 & 1 & 0 & 1 & 1 & 1 \\
 & 5 & 0 & 0 & 1 & 0 & 1 & 0 & 1 & 0 & 1 & 1 & 0 \\
 & & 2 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\
 & & & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & & & & 3 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & & & & & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & & & & & & 2 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & & & & & & & 0 & 0 & 0 & 0 & 0 & 0 \\
 & & & & & & & & 3 & 0 & 0 & 0 & 0 \\
 & & & & & & & & & 0 & 0 & 0 & 0 \\
 & & & & & & & & & & 2 & 0 & 0 \\
 & & & & & & & & & & & 2 & 0 \\
 & & & & & & & & & & & & 1
\end{array}\right)
\left(\begin{array}{c} \hat{\mu}_1 \\ \hat{\mu}_2 \\ \hat{\mu}_3 \\ \hat{\mathbf{m}} \end{array}\right)
=
\left(\begin{array}{c} 38 \\ 26 \\ 10 \\ 0 \\ 15 \\ 0 \\ 17 \\ 0 \\ 17 \\ 0 \\ 10 \\ 9 \\ 6 \end{array}\right).$$

Now with scaling $Var(\mathbf{e}) = \mathbf{I}$.

$$Var(\mathbf{m}) = 1.8^{-1}\mathbf{A} + .25\mathbf{D} + .25\mathbf{I}$$

$$= \frac{1}{576}\begin{pmatrix} 608 & 0 & 0 & 0 & 160 & 160 & 0 & 0 & 80 & 80 \\ & 608 & 0 & 0 & 160 & 160 & 0 & 0 & .80 & 80 \\ & & 608 & 0 & 0 & 0 & 160 & 160 & 80 & 80 \\ & & & 608 & 0 & 0 & 160 & 160 & 80 & 80 \\ & & & & 608 & 196 & 0 & 0 & 80 & 160 \\ & & & & & 608 & 0 & 0 & 160 & 80 \\ & & & & & & 608 & 196 & 160 & 80 \\ & & & & & & & 608 & 80 & 160 \\ & & & & & & & & 608 & 89 \\ & & & & & & & & & 608 \end{pmatrix}.$$

Adding the inverse of this to the lower 10 $\times$ 10 block of the OLS equations we obtain the mixed model equations. The solution is

$$(\hat{\mu}_1, \hat{\mu}_2, \hat{\mu}_3) = (6.398,\ 5.226,\ 5.287),$$

the same as before, and

$$\begin{aligned} \hat{\mathbf{m}} \ &= \ (-.067,\ -.500,\ -.364,\ 1.707,\ -.182,\ -.073,\ .001, \\ & \quad -.431,\ -.835,\ -.253)'. \end{aligned}$$

Then

$$\hat{\mathbf{a}} = Var(\mathbf{a})[Var(\mathbf{m})]^{-1}\hat{\mathbf{m}} = \text{same as before.}$$
$$\hat{\mathbf{d}} = Var(\mathbf{d})[Var(\mathbf{m})]^{-1}\hat{\mathbf{m}} = \text{same as before.}$$
$$\hat{\mathbf{t}} = Var(\mathbf{t})[Var(\mathbf{m})]^{-1}\hat{\mathbf{m}} = \text{same as before}$$

recognizing that $\hat{t}_i$ for an animal with no record is 0.

To compute EM type REML iterate on

$$\sigma_e^2 = [\mathbf{y}'\mathbf{y} - (\text{soln. vector})'\text{rhs}]/[n - \text{rank}(\mathbf{X})].$$

Compute $\mathbf{C}_{aa}$, $\mathbf{C}_{dd}$, $\mathbf{C}_{tt}$ as in Section 29.4. Now, however, $\mathbf{C}_{tt}$ will have dimension, 10, rather than 6 in order that the matrix of the quadratic in $\hat{\mathbf{t}}$ at each round of iteration will be $\mathbf{I}$. If we did not include missing t_i, a new matrix would need to be computed at each round of iteration.