Chapter 26
Animal Model, Multiple Traits

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1 No Missing Data

In this chapter we deal with the same model as in Chapter 22 except now there are 2 or more traits. First we shall discuss the simple situation in which every trait is observed on every animal. There are n animals and t traits. Therefore the record vector has nt elements, which we denote by

$$\mathbf{y}' = [\mathbf{y}_1' \;\; \mathbf{y}_2' \ldots \mathbf{y}_t'].$$

$\mathbf{y}_1'$ is the vector of n records on trait 1, etc. Let the model be

$$\begin{pmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \\ \vdots \\ \mathbf{y}_t \end{pmatrix} = \begin{pmatrix} \mathbf{X}_1 & 0 & \ldots & 0 \\ 0 & \mathbf{X}_2 & \ldots & 0 \\ \vdots & \vdots & & \vdots \\ 0 & 0 & \ldots & \mathbf{X}_t \end{pmatrix} \begin{pmatrix} \boldsymbol{\beta}_1 \\ \boldsymbol{\beta}_2 \\ \vdots \\ \boldsymbol{\beta}_t \end{pmatrix} + \begin{pmatrix} \mathbf{I} & 0 & \ldots & 0 \\ 0 & \mathbf{I} & \ldots & 0 \\ \vdots & \vdots & & \vdots \\ 0 & 0 & \ldots & \mathbf{I} \end{pmatrix} \begin{pmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \\ \vdots \\ \mathbf{a}_t \end{pmatrix} + \begin{pmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \\ \vdots \\ \mathbf{e}_t \end{pmatrix}. \quad (1)$$

Accordingly the model for records on the first trait is

$$\mathbf{y}_1 = \mathbf{X}_1\boldsymbol{\beta}_1 + \mathbf{a}_1 + \mathbf{e}_1, \text{ etc.} \quad (2)$$

Every $\mathbf{X}_i$ has n rows and p_i columns, the latter corresponding to $\boldsymbol{\beta}_i$ with p_i elements. Every $\mathbf{I}$ has order n x n, and every $\mathbf{e}_i$ has n elements.

$$Var \begin{pmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \\ \vdots \\ \mathbf{a}_t \end{pmatrix} = \begin{pmatrix} \mathbf{A}g_{11} & \mathbf{A}g_{12} & \ldots & \mathbf{A}g_{1t} \\ \mathbf{A}g_{12} & \mathbf{A}g_{22} & \ldots & \mathbf{A}g_{2t} \\ \vdots & \vdots & & \vdots \\ \mathbf{A}g_{1t} & \mathbf{A}g_{2t} & \ldots & \mathbf{A}g_{tt} \end{pmatrix} = \mathbf{G}. \quad (3)$$

g_{ij} represents the elements of the additive genetic variance-covariance matrix in a non-inbred population.

$$Var \begin{pmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \\ \vdots \\ \mathbf{e}_t \end{pmatrix} = \begin{pmatrix} \mathbf{I}r_{11} & \mathbf{I}r_{12} & \ldots & \mathbf{I}r_{1t} \\ \mathbf{I}r_{12} & \mathbf{I}r_{22} & \ldots & \mathbf{I}r_{2t} \\ \vdots & \vdots & & \vdots \\ \mathbf{I}r_{1t} & \mathbf{I}r_{2t} & \ldots & \mathbf{I}r_{tt} \end{pmatrix} = \mathbf{R}. \tag{4}$$

r_{ij} represents the elements of the environmental variance-covariance matrix. Then

$$\mathbf{G}^{-1} = \begin{pmatrix} \mathbf{A}^{-1}g^{11} & \ldots & \mathbf{A}^{-1}g^{1t} \\ \vdots & & \vdots \\ \mathbf{A}^{-1}g^{1t} & \ldots & \mathbf{A}^{-1}g^{tt} \end{pmatrix}. \tag{5}$$

g^{ij} are the elements of the inverse of the additive genetic variance covariance matrix.

$$\mathbf{R}^{-1} = \begin{pmatrix} \mathbf{I}r^{11} & \ldots & \mathbf{I}r^{1t} \\ \vdots & & \vdots \\ \mathbf{I}r^{1t} & \ldots & \mathbf{I}r^{tt} \end{pmatrix}. \tag{6}$$

r^{ij} are the elements of the inverse of the environmental variance-covariance matrix. Now the GLS equations regarding $\mathbf{a}$ fixed are

$$\begin{pmatrix} \mathbf{X'}_1\mathbf{X}_1r^{11} & \ldots & \mathbf{X'}_1\mathbf{X}_tr^{1t} & \mathbf{X'}_1r^{11} & \ldots & \mathbf{X'}_1r^{1t} \\ \vdots & & \vdots & \vdots & & \vdots \\ \mathbf{X'}_t\mathbf{X}_1r^{1t} & \ldots & \mathbf{X'}_t\mathbf{X}_tr^{tt} & \mathbf{X'}_tr^{1t} & \ldots & \mathbf{X'}_tr^{tt} \\ \mathbf{X}_1r^{11} & \ldots & \mathbf{X}_tr^{1t} & \mathbf{I}r^{11} & \ldots & \mathbf{I}r^{1t} \\ \vdots & & \vdots & \vdots & & \vdots \\ \mathbf{X}_1r^{1t} & \ldots & \mathbf{X}_tr^{tt} & \mathbf{I}r^{1t} & \ldots & \mathbf{I}r^{tt} \end{pmatrix} \begin{pmatrix} \boldsymbol{\beta}_1^o \\ \vdots \\ \boldsymbol{\beta}_t^o \\ \hat{\mathbf{a}}_1 \\ \vdots \\ \hat{\mathbf{a}}_t \end{pmatrix}$$
$$= \begin{pmatrix} \mathbf{X'}_1\mathbf{y}_1r^{11} & + & \ldots & + & \mathbf{X'}_1\mathbf{y}_tr^{1t} \\ \vdots & & & & \vdots \\ \mathbf{X'}_t\mathbf{y}_1r^{1t} & + & \ldots & + & \mathbf{X'}_t\mathbf{y}_tr^{tt} \\ \mathbf{y}_1r^{11} & + & \ldots & + & \mathbf{y}_tr^{1t} \\ \vdots & & & & \vdots \\ \mathbf{y}_1r^{1t} & + & \ldots & + & \mathbf{y}_tr^{tt} \end{pmatrix}. \tag{7}$$

The mixed model equations are formed by adding (26.5) to the lower t^2 blocks of (26.7).

If we wish to estimate the g_{ij} and r_{ij} by MIVQUE we take prior values of g_{ij} and r_{ij} for the mixed model equations and solve. We find that quadratics in $\hat{\mathbf{a}}$ and $\hat{\mathbf{e}}$ needed for MIVQUE are

$$\hat{\mathbf{a}}_i'\mathbf{A}^{-1}\hat{\mathbf{a}}_j \text{ for } i = l, \ldots, t;\ j = i, \ldots, t. \tag{8}$$

$$\hat{\mathbf{e}}_i'\hat{\mathbf{e}}_j \text{ for } i = l, \ldots, t;\ j = i, \ldots, t. \tag{9}$$

To obtain the expectations of (26.8) we first compute the variance-covariance matrix of the right hand sides of (26.7). This will consist of $t(t-1)/2$ matrices each of the same order as the matrix of (26.7) multiplied by an element of g_{ij}. It will also consist of the same number of matrices with the same order multiplied by an element of r_{ij}. The matrix for g_{kk} is

$$\begin{pmatrix} \mathbf{X'}_1\mathbf{AX}_1 r^{1k}r^{1k} & \ldots & \mathbf{X'}_1\mathbf{AX}_t r^{1k}r^{tk} & \mathbf{X'}_1\mathbf{A}r^{1k}r^{1k} & \ldots & \mathbf{X'}_1\mathbf{A}r^{1k}r^{tk} \\ \vdots & & \vdots & \vdots & & \vdots \\ \mathbf{X'}_t\mathbf{AX}_1 r^{tk}r^{1k} & \ldots & \mathbf{X'}_t\mathbf{AX}_t r^{tk}r^{tk} & \mathbf{X'}_t\mathbf{A}r^{tk}r^{1k} & \ldots & \mathbf{X'}_t\mathbf{A}r^{tk}r^{tk} \\ \mathbf{AX}_1 r^{1k}r^{1k} & \ldots & \mathbf{AX}_t r^{1k}r^{tk} & \mathbf{A}r^{1k}r^{1k} & \ldots & \mathbf{A}r^{1k}r^{tk} \\ \vdots & & \vdots & \vdots & & \vdots \\ \mathbf{AX}_1 r^{tk}r^{1k} & \ldots & \mathbf{AX}_t r^{tk}r^{tk} & \mathbf{A}r^{tk}r^{1k} & \ldots & \mathbf{A}r^{tk}r^{tk} \end{pmatrix} \tag{10}$$

The ij^{th} sub-block of the upper left set of $t \times t$ blocks is $\mathbf{X'}_i\mathbf{AX}_j r^{ik}r^{jk}$. The sub-block of the upper right set of $t \times t$ blocks is $\mathbf{X'}_i\mathbf{A}r^{ik}r^{jk}$. The sub-block of the lower right set of $t \times t$ blocks is $\mathbf{A}r^{ik}r^{jk}$.

The matrix for g_{km} is

$$\begin{pmatrix} \mathbf{P} & \mathbf{T} \\ \mathbf{T'} & \mathbf{S} \end{pmatrix}, \tag{11}$$

where

$$\mathbf{P} = \begin{pmatrix} 2\mathbf{X'}_1\mathbf{AX}_1 r^{1k}r^{1m} & \ldots & \mathbf{X'}_1\mathbf{AX}_t(r^{1k}r^{tm} + r^{1m}r^{tk}) \\ \vdots & & \vdots \\ \mathbf{X'}_t\mathbf{AX}_1(r^{1k}r^{tm} + r^{1m}r^{tk}) & \ldots & 2\mathbf{X'}_t\mathbf{AX}_t r^{tk}r^{tm} \end{pmatrix},$$

$$\mathbf{T} = \begin{pmatrix} 2\mathbf{X'}_1\mathbf{A}r^{1k}r^{1m} & \ldots & \mathbf{X'}_1\mathbf{A}(r^{1k}r^{tm} + r^{1m}r^{tk}) \\ \vdots & & \vdots \\ \mathbf{X'}_t\mathbf{A}(r^{1k}r^{tm} + r^{1m}r^{tk}) & \ldots & 2\mathbf{X'}_t\mathbf{A}r^{tk}r^{tm} \end{pmatrix},$$

and

$$\mathbf{S} = \begin{pmatrix} 2\mathbf{A}r^{1k}r^{1m} & \ldots & \mathbf{A}(r^{1k}r^{tm} + r^{1m}r^{tk}) \\ \vdots & & \vdots \\ \mathbf{A}(r^{1k}r^{tm} + r^{1m}r^{tk}) & \ldots & 2\mathbf{A}r^{tk}r^{tm} \end{pmatrix}.$$

The ij^{th} sub-block of the upper left set of $t \times t$ blocks is

$$\mathbf{X'}_i\mathbf{AX}_j(r^{ik}r^{jm} + r^{im}r^{jk}). \tag{12}$$

The ij^{th} sub-block of the upper right set is

$$\mathbf{X'}_i\mathbf{A}(r^{ik}r^{jm} + r^{im}r^{jk}). \tag{13}$$

The ij^{th} sub-block of the lower right set is

$$\mathbf{A}(r^{ik}r^{jm} + r^{im}r^{jk}). \tag{14}$$

The matrix for r_{kk} is the same as (26.10) except that $\mathbf{I}$ replaces $\mathbf{A}$. Thus the 3 types of sub-blocks are $\mathbf{X'}_i\mathbf{X}_j r^{ik}r^{jk}$, $\mathbf{X'}_i r^{ik}r^{jk}$, and $\mathbf{I}r^{ik}r^{jk}$. The matrix for r_{km} is the same as (26.11) except that $\mathbf{I}$ replaces $\mathbf{A}$. Thus the 3 types of blocks are $\mathbf{X'}_i\mathbf{X}_j(r^{ik}r^{jm} + r^{im}r^{jk})$, $\mathbf{X'}_i(r^{ik}r^{jm} + r^{im}r^{jk})$, and $\mathbf{I}(r^{ik}r^{jm} + r^{im}r^{jk})$.

Now define the $p+1, \ \ldots, \ p+n$ rows of a g-inverse of mixed model coefficient matrix as $\mathbf{C}_1$, the next n rows as $\mathbf{C}_2$, etc., with the last n rows being $\mathbf{C}_t$. Then

$$Var(\hat{\mathbf{a}}_i) = \mathbf{C}_i[Var(\mathbf{r})]\mathbf{C}'_i, \tag{15}$$

where $Var(\mathbf{r})$ = variance of right hand sides expressed as matrices multiplied by the g_{ij} and r_{ij} as described above.

$$Cov(\hat{\mathbf{a}}_i, \hat{\mathbf{a}}'_j) = \mathbf{C}_i[Var(\mathbf{r})]\mathbf{C}'_j. \tag{16}$$

Then

$$E(\hat{\mathbf{a}}_i\mathbf{A}^{-1}\hat{\mathbf{a}}'_i) = tr\mathbf{A}^{-1} \ Var(\hat{\mathbf{a}}_i). \tag{17}$$

$$E(\hat{\mathbf{a}}_i\mathbf{A}^{-1}\hat{\mathbf{a}}'_j) = tr\mathbf{A}^{-1} \ Cov(\hat{\mathbf{a}}_i, \hat{\mathbf{a}}'_j). \tag{18}$$

To find the quadratics of (26.9) and their expectations we first compute

$$\mathbf{I} - \mathbf{WCW'}\tilde{\mathbf{R}}^{-1}, \tag{19}$$

where $\mathbf{W} = (\mathbf{X} \ \ \mathbf{Z})$ and $\mathbf{C}$ = g-inverse of mixed model coefficient matrix. Then

$$\hat{\mathbf{e}} = (\mathbf{I} - \mathbf{WCW'}\tilde{\mathbf{R}}^{-1})\mathbf{y}. \tag{20}$$

Let the first n rows of (26.19) be denoted $\mathbf{B}_1$, the next n rows $\mathbf{B}_2$, etc. Also let

$$\mathbf{B}_i \equiv (\mathbf{B}_{i1} \ \ \mathbf{B}_{i2} \ \ldots \ \mathbf{B}_{it}). \tag{21}$$

Each $\mathbf{B}_{ij}$ has dimension $n \times n$ and is symmetric. Also $\mathbf{I} - \mathbf{WCW'}\tilde{\mathbf{R}}^{-1}$ is symmetric and as a consequence $\mathbf{B}_{ij} = \mathbf{B}_{ji}$. Use can be made of these facts to reduce computing labor. Now

$$\begin{aligned} \hat{\mathbf{e}}_i &= \mathbf{B}_i\mathbf{y} \ (i = 1, \ \ldots, \ t). & (22)\\ Var(\hat{\mathbf{e}}_i) &= \mathbf{B}_i[Var(\mathbf{y})]\mathbf{B}'_i. & (23)\\ Cov(\hat{\mathbf{e}}_i, \hat{\mathbf{e}}_j) &= \mathbf{B}_i[Var(\mathbf{y})]\mathbf{B}'_j. & (24) \end{aligned}$$

By virtue of the form of $Var(\mathbf{y})$,

$$\begin{aligned} Var(\hat{\mathbf{e}}_i) &= \sum_{k=1}^{t}\mathbf{B}^2_{ik}r_{kk} + \sum_{k=1}^{t-1}\sum_{m=k+1}^{t}2\mathbf{B}_{ik}\mathbf{B}_{im}r_{km} \\ &+ \sum_{k=1}^{t}\mathbf{B}_{ik}\mathbf{A}\mathbf{B}_{ik}g_{kk} + \sum_{k=1}^{t-1}\sum_{m=k+1}^{t}2\mathbf{B}_{ik}\mathbf{A}\mathbf{B}_{im}g_{km}. \end{aligned} \tag{25}$$

$$
\begin{aligned}
Cov(\hat{\mathbf{e}}_i, \hat{\mathbf{e}}_j) &= \sum_{k=1}^{t} \mathbf{B}_{ik}\mathbf{B}_{jk} r_{kk} \\
&+ \sum_{k=1}^{t-1} \sum_{m=k+1}^{t} (\mathbf{B}_{ik}\mathbf{B}_{jm}\mathbf{B}_{im}\mathbf{B}_{jk}) r_{km} \\
&+ \sum_{k=1}^{t} \mathbf{B}_{ik}\mathbf{A}\mathbf{B}_{jk} g_{kk} \\
&+ \sum_{k=1}^{t-1} \sum_{m=k+1}^{t} (\mathbf{B}_{ik}\mathbf{A}\mathbf{B}_{jm} + \mathbf{B}_{im}\mathbf{A}\mathbf{B}_{jk}) g_{km}. \qquad (26) \\
E(\hat{\mathbf{e}}_i'\hat{\mathbf{e}}_i) &= tr Var(\hat{\mathbf{e}}_i). \qquad (27) \\
E(\hat{\mathbf{e}}_i'\hat{\mathbf{e}}_j) &= tr Cov(\hat{\mathbf{e}}_i, \hat{\mathbf{e}}_j'). \qquad (28)
\end{aligned}
$$

Note that only the diagonals of the matrices of (26.25) and (26.26) are needed.

2 Missing Data

When data are missing on some traits of some of the animals, the computations are more difficult. An attempt is made in this section to present algorithms that are efficient for computing, including strategies for minimizing data storage requirements. Henderson and Quaas (1976) discuss BLUP techniques for this situation.

The computations for the missing data problem are more easily described and carried out if we order the records, traits within animals. It also is convenient to include missing data as a dummy value = 0. Then $\mathbf{y}$ has nt elements as follows:

$$\mathbf{y}' = (\mathbf{y}_1'\mathbf{y}_2' \ \ldots \ \mathbf{y}_n'),$$

where $\mathbf{y}_i$ is the vector of records on the t traits for the i^{th} animal. With no missing data the model for the nt records is

$$\begin{pmatrix} y_{11} \\ y_{12} \\ \vdots \\ y_{1t} \\ y_{21} \\ y_{22} \\ \vdots \\ y_{2t} \\ \vdots \\ y_{n1} \\ y_{n2} \\ \vdots \\ y_{nt} \end{pmatrix} = \begin{pmatrix} \mathbf{x}'_{11} & 0 & \ldots & 0 \\ 0 & \mathbf{x}'_{12} & \ldots & 0 \\ \vdots & \vdots & & \vdots \\ 0 & 0 & \ldots & \mathbf{x}'_{1t} \\ \mathbf{x}'_{21} & 0 & \ldots & 0 \\ 0 & \mathbf{x}'_{22} & \ldots & 0 \\ \vdots & \vdots & & \vdots \\ 0 & 0 & \ldots & \mathbf{x}'_{2t} \\ \vdots & \vdots & & \vdots \\ \mathbf{x}'_{n1} & 0 & \ldots & 0 \\ 0 & \mathbf{x}'_{n2} & \ldots & 0 \\ \vdots & \vdots & & \vdots \\ 0 & 0 & \ldots & \mathbf{x}'_{nt} \end{pmatrix} \begin{pmatrix} \boldsymbol{\beta}_1 \\ \boldsymbol{\beta}_2 \\ \vdots \\ \boldsymbol{\beta}_t \end{pmatrix} + \begin{pmatrix} a_{11} \\ a_{12} \\ \vdots \\ a_{1t} \\ a_{21} \\ a_{22} \\ \vdots \\ a_{2t} \\ \vdots \\ a_{n1} \\ a_{n2} \\ \vdots \\ a_{nt} \end{pmatrix} + \begin{pmatrix} e_{11} \\ e_{12} \\ \vdots \\ e_{1t} \\ e_{21} \\ e_{22} \\ \vdots \\ e_{2t} \\ \vdots \\ e_{n1} \\ e_{n2} \\ \vdots \\ e_{nt} \end{pmatrix}.$$

$\mathbf{x}'_{ij}$ is a row vector relating the record on the j^{th} trait of the i^{th} animal to $\boldsymbol{\beta}_j$, the fixed effects for the j^{th} trait. $\boldsymbol{\beta}_j$ has p_j elements and $\sum_j p_j = p$. When a record is missing, it is set to 0 and so are the elements of the model for that record. Thus, whether data are missing or not, the incidence matrix has dimension, nt by $(p + nt)$. Now $\mathbf{R}$ has block diagonal form as follows.

$$\mathbf{R} = \begin{pmatrix} \mathbf{R}_1 & 0 & \ldots & 0 \\ 0 & \mathbf{R}_2 & \ldots & 0 \\ \vdots & \vdots & & \vdots \\ 0 & 0 & \ldots & \mathbf{R}_n \end{pmatrix}. \tag{29}$$

For an animal with no missing data, $\mathbf{R}_i$ is the $t \times t$ environmental covariance matrix. For an animal with missing data the rows (and columns) of $\mathbf{R}_i$ pertaining to missing data are set to zero. Then in place of $\mathbf{R}^{-1}$ ordinarily used in the mixed model equations, we use $\mathbf{R}^-$ which is

$$\begin{pmatrix} \mathbf{R}_1^- & & & \mathbf{0} \\ & \mathbf{R}_2^- & & \\ & & \ddots & \\ \mathbf{0} & & & \mathbf{R}_n^- \end{pmatrix}. \tag{30}$$

$\mathbf{R}_1^-$ is the zeroed type of g-inverse described in Section 3.3. It should be noted that $\mathbf{R}_i$ is the same for every animal that has the same missing data. There are at most $t^2 - 1$ such unique matrices, and in the case of sequential culling only t such matrices corresponding to trait 1 only, traits 1 and 2 only, ..., all traits. Thus we do not need to store $\mathbf{R}$ and $\mathbf{R}^-$ but only the unique types of $\mathbf{R}_i^-$.

$Var(\mathbf{a})$ has a simple form, which is

$$Var(\mathbf{a}) = \begin{pmatrix} a_{11}\mathbf{G}_0 & a_{12}\mathbf{G}_0 & \ldots & a_{1n}\mathbf{G}_0 \\ a_{12}\mathbf{G}_0 & a_{22}\mathbf{G}_0 & \ldots & a_{2n}\mathbf{G}_0 \\ \vdots & \vdots & & \vdots \\ a_{1n}\mathbf{G}_0 & a_{2n}\mathbf{G}_0 & \ldots & a_{nn}\mathbf{G}_0 \end{pmatrix}, \quad (31)$$

where $\mathbf{G}_0$ is the $t \times t$ covariance matrix of additive effects in an unselected non-inbred population. Then

$$[Var(\mathbf{a})]^{-1} = \begin{pmatrix} a^{11}\mathbf{G}_0^{-1} & a^{12}\mathbf{G}_0^{-1} & \ldots & a^{1n}\mathbf{G}_0^{-1} \\ a^{12}\mathbf{G}_0^{-1} & a^{22}\mathbf{G}_0^{-1} & \ldots & a^{2n}\mathbf{G}_0^{-1} \\ \vdots & \vdots & & \vdots \\ a^{1n}\mathbf{G}_0^{-1} & a^{2n}\mathbf{G}_0^{-1} & \ldots & a^{nn}\mathbf{G}_0^{-1} \end{pmatrix}. \quad (32)$$

a^{ij} are the elements of the inverse of $\mathbf{A}$. Note that all nt of the a_{ij} are included in the mixed model equations even though there are missing data.

We illustrate prediction by the following example that includes 4 animals and 3 traits with the $\boldsymbol{\beta}_j$ vector having 2, 1, 2 elements respectively.

	Trait		
Animal	1	2	3
1	5	3	6
2	2	5	7
3	-	3	4
4	2	-	-

$$\mathbf{X} \text{ for } \boldsymbol{\beta}_1 = \begin{pmatrix} 1 & 2 \\ 1 & 3 \\ 1 & 4 \end{pmatrix},$$

$$\text{for } \boldsymbol{\beta}_2 = \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix},$$

$$\text{and for } \boldsymbol{\beta}_3 = \begin{pmatrix} 1 & 3 \\ 1 & 4 \\ 1 & 2 \end{pmatrix}.$$

Then, with missing records included, the incidence matrix is

$$\begin{pmatrix}
1 & 2 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 1 & 3 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
1 & 3 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 1 & 4 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 1 & 2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\
1 & 4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0
\end{pmatrix}. \tag{33}$$

We assume that the environmental covariance matrix is

$$\begin{pmatrix} 5 & 3 & 1 \\ & 6 & 4 \\ & & 7 \end{pmatrix}.$$

Then $\mathbf{R}^-$ for animals 1 and 2 is

$$\begin{pmatrix} .3059 & -.2000 & .0706 \\ & .4000 & -.2000 \\ & & .2471 \end{pmatrix},$$

$\mathbf{R}^-$ for animal 3 is

$$\begin{pmatrix} 0 & 0 & 0 \\ & .2692 & -.1538 \\ & & .2308 \end{pmatrix},$$

and for animal 4 is

$$\begin{pmatrix} .2 & 0 & 0 \\ & 0 & 0 \\ & & 0 \end{pmatrix}.$$

Suppose that

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

and

$$\mathbf{G}_0 = \begin{pmatrix} 2 & 1 & 1 \\ & 3 & 2 \\ & & 4 \end{pmatrix}.$$

$Var(\hat{\mathbf{a}})$ is

$$\begin{pmatrix}
2.0 & 1.0 & 1.0 & 0 & 0 & 0 & 1.0 & .5 & .5 & 0 & 0 & 0 \\
 & 3.0 & 2.0 & 0 & 0 & 0 & .5 & 1.5 & 1.0 & 0 & 0 & 0 \\
 & & 4.0 & 0 & 0 & 0 & .5 & 1.0 & 2.0 & 0 & 0 & 0 \\
 & & & 2.0 & 1.0 & 1.0 & 1.0 & .5 & .5 & 1.0 & .5 & .5 \\
 & & & & 3.0 & 2.0 & .5 & 1.5 & 1.0 & .5 & 1.5 & 1.0 \\
 & & & & & 4.0 & .5 & 1.0 & 2.0 & .5 & 1.0 & 2.0 \\
 & & & & & & 2.0 & 1.0 & 1.0 & .5 & .25 & .25 \\
 & & & & & & & 3.0 & 2.0 & .25 & .75 & .5 \\
 & & & & & & & & 4.0 & .25 & .5 & 1.0 \\
 & & & & & & & & & 2.0 & 1.0 & 1.0 \\
 & & & & & & & & & & 3.0 & 2.0 \\
 & & & & & & & & & & & 4.0
\end{pmatrix}. \quad (34)$$

Using the incidence matrix, $\mathbf{R}^{-}$, $\mathbf{G}^{-1}$, and $\mathbf{y}$ we get the coefficient matrix of mixed model equations in (26.35) ... (26.37). The right hand side vector is (1.8588, 4.6235, -.6077, 2.5674, 8.1113, 1.3529, -1.0000, 1.2353, .1059, .2000, .8706, 0, .1923, .4615, .4000, 0, 0)$'$. The solution vector is (8.2451, -1.7723, 3.9145, 3.4054, .8066, .1301, -.4723, .0154, -.2817, .3965, -.0911, -.1459, -.2132, -.2480, .0865, .3119, .0681)'.

Upper left 8 x 8 (times 1000)

$$\begin{pmatrix}
812 & 2329 & -400 & 141 & 494 & 306 & -200 & 71 \\
 & 7176 & -1000 & 353 & 1271 & 612 & -400 & 141 \\
 & & 1069 & -554 & -1708 & -200 & 400 & -200 \\
 & & & 725 & 2191 & 71 & -200 & 247 \\
 & & & & 7100 & 212 & -600 & 741 \\
 & & & & & 1229 & -431 & -045 \\
 & & & & & & 1208 & -546 \\
 & & & & & & & 824
\end{pmatrix}. \quad (35)$$

Upper right 8 x 9 and (lower left 9 $\times$ 8)' (times 1000)

$$\begin{pmatrix}
306 & -200 & 71 & 0 & 0 & 0 & 200 & 0 & 0 \\
918 & -600 & 212 & 0 & 0 & 0 & 800 & 0 & 0 \\
-200 & 400 & -200 & 0 & 269 & -154 & 0 & 0 & 0 \\
71 & -200 & 247 & 0 & -154 & 231 & 0 & 0 & 0 \\
282 & -800 & 988 & 0 & -308 & 462 & 0 & 0 & 0 \\
308 & -77 & -38 & -615 & 154 & 77 & 0 & 0 & 0 \\
-77 & 269 & -115 & 154 & -538 & 231 & 0 & 0 & 0 \\
-38 & -115 & 192 & 77 & 231 & -385 & 0 & 0 & 0
\end{pmatrix}. \quad (36)$$

Lower right 9 × 9 (times 1000)

$$\begin{pmatrix} 1434 & -482 & -70 & -615 & 154 & 77 & -410 & 103 & 51 \\ & 1387 & -623 & 154 & -538 & 231 & 103 & -359 & 154 \\ & & 952 & 77 & 231 & -385 & 51 & 154 & -256 \\ & & & 1231 & -308 & -154 & 0 & 0 & 0 \\ & & & & 1346 & -615 & 0 & 0 & 0 \\ & & & & & 1000 & 0 & 0 & 0 \\ & & & & & & 1020 & -205 & -103 \\ & & & & & & & 718 & -308 \\ & & & & & & & & 513 \end{pmatrix}. \tag{37}$$

3 EM Algorithm

In spite of its possible slow convergence I tend to favor the EM algorithm for REML to estimate variances and covariances. The reason for this preference is its simplicity as compared to iterated MIVQUE and, above all, because the solution remains in the parameter space at each round of iteration.

If the data were stored animals in traits and $\hat{\mathbf{a}}_i$ = BLUP for the n breeding values on the i^{th} trait, g_{ij} would be estimated by iterating on

$$\hat{g}_{ij} = (\hat{\mathbf{a}}_i \mathbf{A}^{-1} \hat{\mathbf{a}}_j + tr\mathbf{A}^{-1}\mathbf{C}_{ij})/n, \tag{38}$$

where $\mathbf{C}_{ij}$ is the submatrix pertaining to $Cov(\hat{a}_i - a_i,\ \hat{a}'_j - a'_j)$ in a g-inverse of the mixed model coefficient matrix. These same computations can be effected from the solution with ordering traits in animals. The following FORTRAN routine accomplishes this.

```
      REAL *8  A( ), C( ), U( ), S
      INTEGER T
      .
      .
      .
      NT=N*T
      DO 7 I=1, T
      DO 7 J=I, T
      S=0.  DO
      DO 6 K=1, N
      DO 6 L=1, N
6     S=S+A(IHMSSF(K,L,N))*U(T*K-T+I)*U(T*L-T+J)
7     Store S
      .
      .
      .
      DO 9 I=1, T
      DO 9 J=I, T
      S=0. DO
      DO 8 K=1, N
      DO 8 L=1, N
8     S=S+A(IHMSSF(K,L,N))*C(IHMSSF(T*K-T+I,T*L-T+J,NT))
9     Store S
```

A is a one dimensional array with N(N+1)/2 elements containing $\mathbf{A}^{-1}$. C is a one dimensional array with NT(NT+1)/2 elements containing the lower $(\mathrm{NT})^2$ submatrix of a g-inverse of the coefficient matrix. This also is half-stored. U is the solution vector for $\mathbf{a}'$. IHMSSF is a half-stored matrix subscripting function. The $t(t+1)/2$ values of S in statement 7 are the values of $\hat{\mathbf{a}}_i'\mathbf{A}^{-1}\hat{\mathbf{a}}_i$. The values of S in statement 9 are the values of $tr\mathbf{A}^{-1}\mathbf{C}_{ij}$.

In our example these are the following for the first round. (.1750, -.1141, .0916, .4589, .0475, .1141), for $\hat{\mathbf{a}}_i'\mathbf{A}^{-1}\mathbf{a}_j$, and (7.4733, 3.5484, 3.4788, 10.5101, 7.0264, 14.4243) for $tr\mathbf{A}^{-1}\mathbf{C}_{ij}$. This gives us as the first estimate of $\mathbf{G}_0$ the following,

$$\begin{pmatrix} 1.912 & .859 & .893 \\ & 2.742 & 1.768 \\ & & 3.635 \end{pmatrix}.$$

Note that the matrix of the quadratics in $\hat{\mathbf{a}}$ remain the same for all rounds of iteration, that is, $\mathbf{A}^{-1}$.

In constrast, the quadratics in $\hat{\mathbf{e}}$ change with each round of iteration. However, they have a simple form since they are all of the type,

$$\sum_{i=1}^{n} \hat{\mathbf{e}}_i' \mathbf{Q}_i \hat{\mathbf{e}}_i,$$

where $\hat{\mathbf{e}}_i$ is the vector of BLUP of errors for the t traits in the i^{th} animal. The $\hat{\mathbf{e}}$ are computed as follows

$$\hat{e}_{ij} = y_{ij} - \mathbf{x}_{ij}' \boldsymbol{\beta}_j^o - \hat{a}_{ij} \tag{39}$$

when y_{ij} is observed. $\hat{e}_{ij}$ is set to 0 for $y_{ij} = 0$. This is not BLUP, but suffices for subsequent computations. At each round we iterate on

$$tr\mathbf{Q}_{ij}\mathbf{R} = (\hat{\mathbf{e}}'\mathbf{Q}_{ij}\hat{\mathbf{e}} + tr\mathbf{Q}_{ij}\mathbf{WCW}') \ i = 1, \ \ldots, \ t_{ij}, \ j = i, \ \ldots, \ t. \tag{40}$$

This gives at each round a set of equations of the form

$$\mathbf{T}\hat{\mathbf{r}} = \mathbf{q}, \tag{41}$$

where $\mathbf{T}$ is a symmetric $t \times t$ matrix, $\mathbf{r} = (r_{11} \ r_{12} \ \ldots \ r_{tt})'$, and $\mathbf{q}$ is a $t \times 1$ vector of numbers. Advantage can be taken of the symmetry of $\mathbf{T}$, so that only $t(t+1)/2$ coefficients need be computed rather than t^2.

Advantage can be taken of the block diagonal form of all $\mathbf{Q}_{ij}$. Each of them has the following form

$$\mathbf{Q}_{ij} = \begin{pmatrix} \mathbf{B}_{1ij} & & & \mathbf{0} \\ & \mathbf{B}_{2ij} & & \\ & & \ddots & \\ \mathbf{0} & & & \mathbf{B}_{nij} \end{pmatrix}. \tag{42}$$

There are at most $t^2 - 1$ unique $\mathbf{B}_{kij}$ for any $\mathbf{Q}_{ij}$, these corresponding to the same number of unique $\mathbf{R}_k^-$. The $\mathbf{B}$ can be computed easily as follows. Let

$$\mathbf{R}_k^- = \begin{pmatrix} f_{11} & f_{12} & \ldots & f_{1t} \\ f_{12} & f_{22} & \ldots & f_{2t} \\ \vdots & \vdots & & \vdots \\ f_{1t} & f_{2t} & \ldots & f_{tt} \end{pmatrix} \equiv (\mathbf{f}_1 \ \mathbf{f}_2 \ \ldots \ \mathbf{f}_t).$$

Then

$$\mathbf{B}_{kii} = \mathbf{f}_i \mathbf{f}_i' \tag{43}$$

$$\mathbf{B}_{kij} = (\mathbf{f}_i \mathbf{f}_j') + (\mathbf{f}_i \mathbf{f}_j')' \text{ for } i \neq j. \tag{44}$$

In computing $tr\mathbf{Q}_{ij}\mathbf{R}$ remember that $\mathbf{Q}$ and $\mathbf{R}$ have the same block diagonal form. This computation is very easy for each of the n products. Let

$$\mathbf{B}_{kij} = \begin{pmatrix} b_{11} & b_{12} & \ldots & b_{1t} \\ b_{12} & b_{22} & \ldots & b_{2t} \\ \vdots & \vdots & & \vdots \\ b_{1t} & b_{2t} & \ldots & b_{tt} \end{pmatrix}.$$

Then the coefficient of r_{ii} contributed by the k^{th} animal in the trace is b_{ii}. The coefficient of r_{ij} is $2b_{ij}$.

Finally note that we need only the n blocks of order $t \times t$ down the diagonals of $\mathbf{WCW}'$ for $tr\mathbf{Q}_{ij}\mathbf{WCW}'$. Partition $\mathbf{C}$ as

$$\mathbf{C} = \begin{pmatrix} \mathbf{C}_{xx} & \mathbf{C}_{x1} & \ldots & \mathbf{C}_{xn} \\ \mathbf{C}'_{x1} & \mathbf{C}_{11} & \ldots & \mathbf{C}_{1n} \\ \vdots & \vdots & & \vdots \\ \mathbf{C}'_{xn} & \mathbf{C}'_{1n} & \ldots & \mathbf{C}_{nn} \end{pmatrix}.$$

Then the block of $\mathbf{WCW}'$ for the i^{th} animal is

$$\mathbf{X}_i\mathbf{C}_{xx}\mathbf{X}'_i + \mathbf{X}_i\mathbf{C}_{xi} + (\mathbf{X}_i\mathbf{C}_{xi})' + \mathbf{C}_{ii} \tag{45}$$

and then zeroed for missing rows and columns, although this is not really necessary since the $\mathbf{Q}_{kij}$ are correspondingly zeroed. $\mathbf{X}_i$ is the submatrix of $\mathbf{X}$ pertaining to the i^{th} animal. This submatrix has order $t \times p$.

We illustrate some of these computations for $\hat{\mathbf{r}}$. First, consider computation of $\mathbf{Q}_{ij}$. Let us look at $\mathbf{B}_{211}$, that is, the block for the second animal in $\mathbf{Q}_{11}$.

$$\mathbf{R}_2^- = \begin{pmatrix} .3059 & -.2000 & .0706 \\ -.2000 & .4000 & -.2000 \\ .0706 & -.2000 & .2471 \end{pmatrix}.$$

Then

$$\mathbf{B}_{211} = \begin{pmatrix} .3059 \\ -.2000 \\ .0706 \end{pmatrix} (.3059 \quad -.2000 \quad .0706) = \begin{pmatrix} .0936 & -.0612 & .0216 \\ & .0400 & -.0141 \\ & & .0050 \end{pmatrix}.$$

Look at $\mathbf{B}_{323}$, that is, the block for the third animal in $\mathbf{Q}_{23}$.

$$\mathbf{R}_3^- = \begin{pmatrix} 0 & 0 & 0 \\ 0 & .2692 & -.1538 \\ 0 & -.1538 & .2308 \end{pmatrix}.$$

Then

$$\begin{aligned} \mathbf{B}_{323} &= \begin{pmatrix} 0 \\ .2692 \\ -.1538 \end{pmatrix} (0 \quad -.1538 \quad .2308) + \text{ transpose of this product} \\ &= \begin{pmatrix} 0 & 0 & 0 \\ 0 & -.0414 & .0621 \\ 0 & .0237 & -.03500 \end{pmatrix} + (\ )' \\ &= \begin{pmatrix} 0 & 0 & 0 \\ 0 & -.0828 & .0858 \\ 0 & .0858 & -.0710 \end{pmatrix}. \end{aligned}$$

Next we compute $tr\mathbf{Q}_{ij}\mathbf{R}$. Consider the contribution of the first animal to $tr\mathbf{Q}_{12}\mathbf{R}$.

$$\mathbf{B}_{112} = \begin{pmatrix} -.1224 & .1624 & -.0753 \\ & -.1600 & .0682 \\ & & -.0282 \end{pmatrix}.$$

Then this animal contributes

$$-.1224\, r_{11} + .2(.1624)\, r_{12} - 2(.0753)\, r_{13} - .1600\, r_{22} + 2(.0682)\, r_{23} - .0282\, r_{33}.$$

Finally we illustrate computing a block of $\mathbf{WCW}'$ by (26.45). We use the third animal.

$$\mathbf{X}_3 = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 2 \end{pmatrix}.$$

$$\mathbf{C}_{xx} = \begin{pmatrix} 29.4578 & -9.2266 & 3.0591 & 2.7324 & -.3894 \\ & 3.1506 & -.6444 & -.5254 & .0750 \\ & & 3.5851 & 2.3081 & .0305 \\ & & & 30.8055 & -8.5380 \\ & & & & 2.7720 \end{pmatrix}.$$

$$\mathbf{C}_{x3} = \begin{pmatrix} -1.7046 & -1.2370 & -1.0037 \\ .2759 & .2264 & .1692 \\ -.6174 & -1.9083 & -1.2645 \\ -.8627 & -1.2434 & -4.7111 \\ .0755 & -.0107 & .7006 \end{pmatrix}.$$

$$\mathbf{C}_{33} = \begin{pmatrix} 1.9642 & .9196 & .9374 \\ & 2.7786 & 1.8497 \\ & & 3.8518 \end{pmatrix}.$$

Then the computations of (26.45) give

$$\begin{pmatrix} 1.9642 & .3022 & .2257 \\ & 2.5471 & 1.6895 \\ & & 4.9735 \end{pmatrix}.$$

Since the first trait was missing on animal 3, the block of $\mathbf{WCW}'$ becomes

$$\begin{pmatrix} 0 & 0 & 0 \\ & 2.5471 & 1.6895 \\ & & 4.9735 \end{pmatrix}.$$

Combining these results, $\hat{\mathbf{r}}$ for the first round is the solution to

$$\begin{pmatrix} .227128 & -.244706 & .086367 & .080000 & -.056471 & .009965 \\ & .649412 & -.301176 & -.320000 & .272941 & -.056471 \\ & & .322215 & .160000 & -.254118 & .069758 \\ & & & .392485 & -.402840 & .103669 \\ & & & & .726892 & -.268653 \\ & & & & & .175331 \end{pmatrix} \hat{\mathbf{r}}$$

$$
\begin{aligned}
= \quad & (.137802,\ -.263298,\ .084767,\ .161811, -.101820,\ .029331)' \\
& + (.613393,\ -.656211,\ .263861,\ .713786,\ -.895139,\ .571375)'.
\end{aligned}
$$

This gives the solution

$$
\hat{\mathbf{R}} = \begin{pmatrix} 3.727 & 1.295 & .311 \\ & 3.419 & 2.270 \\ & & 4.965 \end{pmatrix} .
$$