ANIMAL BREEDING NOTES

CHAPTER 19M

DIRECT MATERNAL MULTIBREED ANIMAL MODEL

Direct Maternal Multibreed Animal Model (DMMAM)

Objective: to predict direct and maternal additive genetic effects (DMAMBV), direct and maternal nonadditive genetic effects (DMNMBV), and direct and maternal total genetic effects (DMTMBV) for animals based on their own records and records of their relatives in a multibreed population.

Assumptions

1) Animals belong to a multibreed population, i.e., a population composed of purebred and crossbred animals that interbreed;

2) Animals may have 1 or more records;

3) Records are influenced by direct and maternal effects;

4) Nonadditive genetic effects are explained in terms of intrabreed and interbreed interaction effects at 1 or more loci that are modeled as independent regression effects;

5) Multibreed additive genetic variances and covariances among records are linear combinations of intrabreed and interbreed additive genetic variances and covariances;

6) Multibreed nonadditive genetic variances and covariances among records are linear combinations of intrabreed and interbreed nonadditive genetic variances and covariances;

7) Multibreed environmental variances and covariances among records are linear combinations of intrabreed and interbreed environmental variances and covariances; and

8) There is either no selection in the population, or:
   a. if selection occurred based on records, selection was within fixed effects, and
b. if selection occurred based on DMAMBV, the relationship matrix was complete.

The **DMMAM** is:

\[
y = Xb + Z_\text{a} g_\text{a} + Z_\text{n} g_\text{n} + Z_\text{a} a_\text{a} + Z_\text{n} a_\text{n} + e
\]

\[
E[y] = Xb + Z_\text{a} g_\text{a} + Z_\text{n} g_\text{n}
\]

\[
\begin{bmatrix}
a_\text{a} \\
a_\text{n} \\
e
\end{bmatrix} = 
\begin{bmatrix}
G_\text{a} & 0 & 0 \\
0 & G_\text{n} & 0 \\
0 & 0 & R
\end{bmatrix}
\]

\[
\text{var}(y) = Z_\text{a}G_\text{a}Z_\text{a} + Z_\text{n}G_\text{n}Z_\text{n} + R,
\]

where

- **y** = vector of animal records,
- **b** = vector of unknown fixed effects (e.g., contemporary groups, sex of calf, age of dam),
- **g_\text{a}** = vector of unknown **direct and maternal** additive group genetic effects (e.g., breed, breed \times year of birth),
- **g_\text{n}** = vector of unknown **direct and maternal** nonadditive group genetic effects (e.g., heterosis at 1 locus, heterosis at 2 loci),
- **a_\text{a}** = vector of unknown random **direct and maternal** additive genetic effects (**DMAMBV**),
- **a_\text{n}** = vector of unknown random **direct and maternal** nonadditive genetic effects (**DMNMBV**),
- **e** = vector of unknown random residual effects,
- **X** = known incidence matrix relating records to fixed effects in vector **b**,
- **Z_\text{a}** = known incidence matrix relating records to elements of vector **a_\text{a}**,
- **Z_\text{n}** = known incidence matrix relating records to elements of vector **a_\text{n}**,
additive genetic groups in vector $g_a$.

$$Q_n = \text{known incidence matrix relating random direct and maternal nonadditive genetic effects to nonadditive genetic groups in vector } g_n,$$

$$G_a = \{G_{ij}\}, \text{ where } G_{ij} = \text{matrix of multibreed direct and maternal additive genetic covariances between animals } i \text{ and } j,$$

$$G_n = \text{diag}\{A_m^*V_{0nm}, m = 1, \ldots, N_m\}, \text{ where } A_m \text{ is the matrix of probabilities that pairs of animals received the same alleles at } m \text{ loci, and } V_{0nm} \text{ is the matrix of direct and maternal variances and covariances due to interaction effects among alleles at } m \text{ loci. If } m = 1, \text{ then } G_n = A^*V_{0n1}, \text{ where } A = \text{matrix of additive relationships and } V_{0n1} = \text{matrix of direct and maternal variances and covariances due to intralocus interaction effects (intrabreed and interbreed). Further, if only interbreed intralocus effects are included in the model, then } V_{0n1} = \text{matrix of direct and maternal variances and covariances due to intralocus interbreed interaction effects = variance of random direct and maternal heterosis effects,}$$

$$R = \text{diag}\{\sigma_{ei}^2\}, \text{ where } \sigma_{ei}^2 = \text{multibreed residual variance for animal } i. \text{ Multibreed residual variances are allowed to vary among animals of different breed composition due to environmental and nonadditive genetic effects not included in the multibreed model. If animals of all breed compositions are assumed to be similarly affected by environmental effects, and residual nonadditive genetic effects are assumed to be equal across breed compositions, then } R = I^*\sigma_e^2, \text{ where } \sigma_e^2 = \text{residual variance common to all animals in a multibreed population.}$$

The mixed model equations (MME) for the DMMAM are:
Example 1 of the DMMAM for a Non-inbred Multibreed Population

<table>
<thead>
<tr>
<th>Animal</th>
<th>Breed Composn</th>
<th>Sex</th>
<th>Weaning weight (kg)</th>
<th>Sire</th>
<th>Breed Composn</th>
<th>Dam</th>
<th>Breed Composn</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>A</td>
<td>M</td>
<td>289</td>
<td>0</td>
<td>A</td>
<td>0</td>
<td>A</td>
</tr>
<tr>
<td>2</td>
<td>B</td>
<td>F</td>
<td>245</td>
<td>0</td>
<td>B</td>
<td>0</td>
<td>B</td>
</tr>
<tr>
<td>3</td>
<td>½ A ½ B</td>
<td>F</td>
<td>256</td>
<td>0</td>
<td>A</td>
<td>2</td>
<td>B</td>
</tr>
<tr>
<td>4</td>
<td>½ A ½ B</td>
<td>F</td>
<td>261</td>
<td>1</td>
<td>A</td>
<td>0</td>
<td>B</td>
</tr>
<tr>
<td>5</td>
<td>½ A ½ B</td>
<td>M</td>
<td>292</td>
<td>1</td>
<td>A</td>
<td>2</td>
<td>B</td>
</tr>
<tr>
<td>6</td>
<td>¾ A ¾ B</td>
<td>M</td>
<td>286</td>
<td>1</td>
<td>A</td>
<td>3</td>
<td>½ A ½ B</td>
</tr>
</tbody>
</table>

Assumptions for the Example

1) Matrices of direct and maternal additive genetic variances and covariances:

Intrabreed direct-maternal additive genetic covariance matrix for breed A:

\[
V_{aAA} = \begin{bmatrix} 36 & 8 \\ 8 & 24 \end{bmatrix} \text{ kg}^2
\]

Intrabreed direct-maternal additive genetic covariance matrix for breed B:

\[
V_{aBB} = \begin{bmatrix} 9 & 2 \\ 2 & 4 \end{bmatrix} \text{ kg}^2
\]

Interbreed direct-maternal additive genetic covariance matrix for combination of breeds AB:

\[
V_{aAB} = \frac{1}{2} V_{aAA} + \frac{1}{2} V_{aBB} - \frac{1}{2} \text{ Cov}(A, B)
\]
2) Matrices of direct and maternal nonadditive genetic variances and covariances due to sire × breed group of dam interaction effects = nonadditive genetic variances due to dam × breed group of sire interaction effects. Variation from nonadditive effects due to sire × dam intra and interbreed interaction effects are assumed to be part of the residual variance.

Intrabreed direct-maternal nonadditive genetic covariance matrix for breed A:

\[
V_{nAA} = \begin{bmatrix} 4 & 1 \\ 1 & 2 \end{bmatrix} \text{kg}^2
\]

Intrabreed direct-maternal nonadditive genetic covariance matrix for breed B:

\[
V_{nBB} = \begin{bmatrix} 9 & 2 \\ 2 & 4 \end{bmatrix} \text{kg}^2
\]

Interbreed direct-maternal additive genetic covariance matrix for combination of breeds AB:

\[
V_{nAB} = \begin{bmatrix} 16 & 6 \\ 6 & 12 \end{bmatrix} \text{kg}^2
\]

Simplifying assumption: only intralocus interbreed sire × breed group of dam and dam × breed group of sire interaction effects (i.e., sire and dam random heterosis effects) are important. Intralocus intrabreed AA and BB nonadditive effects and interactions among alleles at 2 or more loci due to sire × breed group of dam and dam × breed group of sire interactions are assumed to be contained in the residual. Thus, only intralocus interbreed interactions will be fitted in the model for the example. Consequently, only

\[
V_{nAB} = \begin{bmatrix} 16 & 6 \\ 6 & 12 \end{bmatrix} \text{kg}^2
\]

will be needed.
3) Environmental variances:

Environmental variance for breed A = \( \sigma_{eAA}^2 = 49 \text{ kg}^2 \)

Environmental variance for breed B = \( \sigma_{eBB}^2 = 16 \text{ kg}^2 \)

Environmental variance for combination of breeds AB = \( \sigma_{eAB}^2 = 25 \text{ kg}^2 \)

4) Environmental covariances among records of different animals are zero.

Direct Maternal Multibreed Animal Model for the Example

\[
\text{Wean wt} = \text{overall mean} + \text{direct breed regression} + \text{maternal breed regression} \\
+ \text{direct heterosis regression} + \text{maternal heterosis regression} + \text{sex} \\
+ \text{animal direct additive genetic} + \text{animal maternal additive genetic} \\
+ \text{animal direct nonadditive genetic regression} \\
+ \text{animal maternal nonadditive genetic regression} \\
+ \text{residual}
\]

\[
E [\text{Wean wt}] = \text{overall mean} + \text{direct breed regression} + \text{maternal breed regression} \\
+ \text{direct heterosis regression} + \text{maternal heterosis regression} + \text{sex}
\]

\[
\text{Var (Wean wt)} = \text{var (animal direct additive genetic} + \text{animal maternal additive genetic}) \\
+ \text{var (animal direct nonadditive genetic regression} + \text{animal maternal} \\
\text{nonadditive genetic regression}) + \text{var (residual)}
\]

\[
\text{cov(Wean wt}_i, \text{Wean wt}_{i'}) = \text{cov (animal direct add gen}_i, \text{animal direct add gen}_{i'}) \\
+ \text{cov (animal direct add gen}_i, \text{animal maternal add gen}_{i'}) \\
+ \text{cov (animal maternal add gen}_i, \text{animal direct add gen}_{i'}) \\
+ \text{cov (animal maternal add gen}_i, \text{animal maternal add gen}_{i'}) \\
+ \text{cov (animal direct nonadd gen}_i, \text{animal direct nonadd gen}_{i'})
\]
The vectors and matrices of the DMMAM model are:

\[
\begin{bmatrix}
269 \\
245 \\
256 \\
261 \\
292 \\
286
\end{bmatrix} = \begin{bmatrix} 1 & 1 & 1 & 0 & 0 & 0 & 0 & 1 & 0 \\
1 & 0 & 0 & 1 & 1 & 0 & 0 & 0 & 1 \\
1 & 1/2 & 0 & 1/2 & 1 & 1 & 0 & 0 & 1 \\
1 & 1/2 & 0 & 1/2 & 1 & 1 & 0 & 0 & 1 \\
1 & 1/2 & 0 & 1/2 & 1 & 1 & 0 & 1 & 0 \\
1 & 3/4 & 1/2 & 1/4 & 1/2 & 1/2 & 1 & 1 & 0 \\
\end{bmatrix} + \begin{bmatrix}
\text{mean} \\
\text{breed}_A \text{d} \\
\text{breed}_A \text{m} \\
\text{breed}_B \text{d} \\
\text{breed}_B \text{m} \\
\text{heterosis}_{ABd} \\
\text{heterosis}_{ABm} \\
\text{sex}_M \\
\text{sex}_F
\end{bmatrix}
\]
Matrices of Direct and Maternal Multibreed Additive Genetic Variances and Covariances

Matrices of multibreed direct and maternal additive genetic variances and covariances are computed by conditioning them on breed of origin of alleles using the expression:

\[
V_{at} = E[\text{var}(t | b)] + \text{var}(E[t | b])
\]

\[
V_{at} = \sum_{b=1}^{n_b} p_b^x (V_{at})_b + \sum_{b=1}^{n_b-1} \sum_{b'>b} (p_b^x p_{b'}^d + p_{b'}^x p_b^d) (V_{at})_{bb'}
\]

where \(a = \) additive genetic, \(t = 2 \times 1\) vector of direct and maternal effects for trait \(t\), superscripts \(i\) = individual, \(s = \) sire, and \(d = \) dam, subscripts \(b\) and \(b'\) represent two breeds, and

\[
\begin{align*}
n_b & = \text{number of breeds}, \\
p_b^x & = \text{expected fraction of breed } b \text{ in animal } x, \ x = i, s, d, \\
(V_{at})_b & = \text{matrix of direct and maternal additive intrabreed genetic variances and covariances for trait } t \text{ in breed } b, \\
(V_{at})_{bb'} & = \text{matrix of direct and maternal additive interbreed genetic variances and covariances for trait } t \text{ in pair of breeds } b \text{ and } b'.
\end{align*}
\]
The matrices of direct and maternal multibreed additive genetic variances and covariances for the 6 animals in the example are:

<table>
<thead>
<tr>
<th>Animal</th>
<th>Number</th>
<th>Breed Group</th>
<th>Direct-Maternal Multibreed Additive Genetic Covariance Matrix</th>
</tr>
</thead>
</table>
| Parents | 1      | A           | \[
\begin{bmatrix}
36 & 8 \\
8 & 24
\end{bmatrix}
\] |
|         | 2      | B           | \[
\begin{bmatrix}
9 & 2 \\
2 & 4
\end{bmatrix}
\] |
|         | 3      | \(\frac{1}{2}A\) \(\frac{1}{2}B\) | \(\frac{1}{2} \begin{bmatrix}
36 & 8 \\
8 & 24
\end{bmatrix} + \frac{1}{2} \begin{bmatrix}
9 & 2 \\
2 & 4
\end{bmatrix} = \begin{bmatrix}
22.5 & 5 \\
5 & 14
\end{bmatrix}\) |
| Non-parents | 4 | \(\frac{1}{2}A\) \(\frac{1}{2}B\) | \(\frac{1}{2} \begin{bmatrix}
36 & 8 \\
8 & 24
\end{bmatrix} + \frac{1}{2} \begin{bmatrix}
9 & 2 \\
2 & 4
\end{bmatrix} = \begin{bmatrix}
22.5 & 5 \\
5 & 14
\end{bmatrix}\) |
|         | 5      | \(\frac{1}{2}A\) \(\frac{1}{2}B\) | \(\frac{1}{2} \begin{bmatrix}
36 & 8 \\
8 & 24
\end{bmatrix} + \frac{1}{2} \begin{bmatrix}
9 & 2 \\
2 & 4
\end{bmatrix} = \begin{bmatrix}
22.5 & 5 \\
5 & 14
\end{bmatrix}\) |
|         | 6      | \(\frac{3}{4}A\) \(\frac{1}{4}B\) | \(\frac{3}{4} \begin{bmatrix}
36 & 8 \\
8 & 24
\end{bmatrix} + \frac{1}{4} \begin{bmatrix}
9 & 2 \\
2 & 4
\end{bmatrix} + [(1)(0) + (\frac{1}{2})(\frac{1}{2})] \begin{bmatrix}
4 & 1 \\
1 & 3
\end{bmatrix} = \begin{bmatrix}
30.25 & 6.75 \\
6.75 & 19.75
\end{bmatrix}\) |

Inverse of the Multibreed Additive Genetic Covariance Matrix for Direct and Maternal Effects

The equation for the inverse of the covariance matrix of direct and maternal multibreed additive genetic effects, \(G^{-1}\), can be written as follows:

\[
G^{-1} = \{g_{ij}\} = \{\sum_{k=1}^{K} t_{ik} \ast d_{ak}^{-1} \ast t_{kj}\}
\]

where \(K\) is the number of animals in the pedigree, \(t_{ik}\) are elements of \(T^* = (I - \frac{1}{2}P^*)\), \(d_{ak}^{-1}\) are 2 × 2 direct-maternal submatrices of block-diagonal matrix \(D_{a}^{-1}\), and \(t_{kj}\) are elements of \(T = (I - \frac{1}{2}P)\).
and

\[ I = \text{identity matrix}, \]

\[ P = \text{matrix that relates animals to their sires and dams; each row of } P \text{ contains up to 2 nonzero elements: a 1 for the sire and a 1 for the dam of an animal,} \]

\[ D_{a}^{-1} = \text{inverse of block-diagonal matrix of residual direct and maternal additive genetic variances and covariances. Because } D_{a}^{-1} \text{ is block-diagonal, its inverse is equal to the inverse of its diagonal submatrices, i.e., } D_{a}^{-1} = \{ d_{ii}^{-1} \}. \]

The $2 \times 2$ direct-maternal submatrices of block-diagonal matrix $D_{a}^{-1}$ are computed using the expression:

\[ d_{aii}^{-1} = \left[ (V_{ai})_{i} - \frac{1}{4} \delta_{s} (V_{ai})_{s} + \sum_{c=1}^{n} F_{cs} (V_{ai})_{cs} \right] - \frac{1}{4} \delta_{d} (V_{ai})_{d} + \sum_{c=1}^{n} F_{cd} (V_{ai})_{cd} \]

where $F_{cs}$ and $F_{cd}$ are the coefficients of inbreeding of common ancestors of the sire and the dam of animal $i$, and $\delta_{s} = 1$ if the sire is known, else $\delta_{s} = 0$, and $\delta_{d} = 1$ if the dam is known, else $\delta_{d} = 0$.

In non-inbred multibreed populations, the $F_{cs}$ and $F_{cd}$ are equal to zero. Thus, the expression for $d_{aii}^{-1}$ simplifies to:

\[ d_{aii}^{-1} = \left[ (V_{ai})_{i} - \frac{1}{4} \delta_{s} (V_{ai})_{s} - \frac{1}{4} \delta_{d} (V_{ai})_{d} \right]^{-1} \]

The $d_{aii}^{-1}$ for the six animals in the example, computed using the formula for a non-inbred multibreed population, are:
The lower-triangular matrix $P$ is:

$$P = \begin{bmatrix}
0 & 0 & 0 & 0 & 1 & 1 & 1 \\
0 & 0 & 0 & 0 & 1 & 1 & 0 \\
0 & 1 & 0 & 0 & 1 & 0 & 1 \\
- & - & - & - & - & - & - \\
1 & 0 & 0 & 0 & 1 & 0 & 0 \\
1 & 1 & 0 & 0 & 0 & 1 & 0 \\
1 & 0 & 1 & 0 & 0 & 0 & 0
\end{bmatrix}$$
The inverse of the block-diagonal matrix $D_a$ is:

$$D_a^{-1} = \begin{bmatrix} d_{a11}^{-1} & & & & \\ & d_{a22}^{-1} & & & \\ & & d_{a33}^{-1} & & \\ & & & d_{a44}^{-1} & \\ & & & & d_{a55}^{-1} \\ & & & & & d_{a66}^{-1} \end{bmatrix}$$

where

$$d_{a11}^{-1} = \begin{bmatrix} 36 & 8 \\ 8 & 24 \end{bmatrix}^{-1}$$
$$d_{a22}^{-1} = \begin{bmatrix} 9 & 2 \\ 2 & 4 \end{bmatrix}^{-1}$$
$$d_{a33}^{-1} = \begin{bmatrix} 20.25 & 4.5 \\ 4.5 & 13 \end{bmatrix}^{-1}$$
$$d_{a44}^{-1} = \begin{bmatrix} 13.5 & 3 \\ 3 & 8 \end{bmatrix}^{-1}$$
$$d_{a55}^{-1} = \begin{bmatrix} 11.25 & 2.5 \\ 2.5 & 12.75 \end{bmatrix}^{-1}$$
$$d_{a66}^{-1} = \begin{bmatrix} 15.625 & 3.5 \\ 3.5 & 10.25 \end{bmatrix}^{-1}$$

The inverse of the multibreed additive genetic covariance matrix for direct and maternal effects, is:

$$G_a^{-1} = \begin{bmatrix} g_a^{11} & g_a^{12} & g_a^{13} & g_a^{14} & g_a^{15} & g_a^{16} \\ g_a^{12} & g_a^{22} & g_a^{23} & 0 & 0 & g_a^{25} \\ g_a^{13} & g_a^{23} & g_a^{33} & 0 & 0 & g_a^{36} \\ - & - & - & - & - & - \\ g_a^{14} & 0 & 0 & g_a^{44} & 0 & 0 \\ g_a^{15} & g_a^{25} & 0 & 0 & g_a^{55} & 0 \\ g_a^{16} & 0 & g_a^{36} & 0 & 0 & g_a^{66} \end{bmatrix}$$

$$\downarrow$$

parents nonparents
The rules used to compute the elements of $G_a^{-1}$ are:

1) Add $d_{a_{ii}}^{-1}$ to $i \times i$,

2) Add $-\frac{1}{2} d_{a_{ii}}^{-1}$ to $i \times s$ and $s \times i$ if the sire of animal $i$ is identified,

3) Add $-\frac{1}{2} d_{a_{ii}}^{-1}$ to $i \times d$ and $d \times i$ if the dam of animal $i$ is identified, and

4) Add $\frac{1}{4} d_{a_{ii}}^{-1}$ to $s \times s$, $s \times d$, $d \times s$, and $d \times d$ if the sire and dam of animal $i$ are identified.

Notice that the rules to compute $G_a^{-1}$ for direct and maternal effects are the same as those for single traits, except that the $d_{a_{ii}}^{-1}$ are $2 \times 2$ submatrices of direct and maternal variances and covariances instead of scalars. Because direct and maternal effects are treated as distinct traits, the rules to compute $G_a^{-1}$ for direct and maternal effects are in effect rules to obtain $G_a^{-1}$ for multiple traits.

Thus,

\[
\begin{align*}
    g_{a11} &= \left[\begin{array}{cc} 36 & 8 \\ 8 & 24 \end{array}\right]^{-1} + \frac{1}{4} \left[\begin{array}{cc} 13.5 & 3 \\ 3 & 8 \end{array}\right]^{-1} + \frac{1}{4} \left[\begin{array}{cc} 11.25 & 2.5 \\ 2.5 & 12.75 \end{array}\right]^{-1} + \frac{1}{4} \left[\begin{array}{cc} 15.625 & 3.5 \\ 3.5 & 10.25 \end{array}\right]^{-1} \\
    g_{a12} &= \frac{1}{4} \left[\begin{array}{cc} 11.25 & 2.5 \\ 2.5 & 12.75 \end{array}\right]^{-1} \\
    g_{a13} &= \frac{1}{4} \left[\begin{array}{cc} 15.625 & 3.5 \\ 3.5 & 10.25 \end{array}\right]^{-1} \\
    g_{a14} &= -\frac{1}{2} \left[\begin{array}{cc} 13.5 & 3 \\ 3 & 8 \end{array}\right]^{-1} \\
    g_{a15} &= -\frac{1}{2} \left[\begin{array}{cc} 11.25 & 2.5 \\ 2.5 & 12.75 \end{array}\right]^{-1} \\
    g_{a16} &= -\frac{1}{2} \left[\begin{array}{cc} 15.625 & 3.5 \\ 3.5 & 10.25 \end{array}\right]^{-1} \\
    g_{a22} &= \left[\begin{array}{cc} 9 & 2 \\ 2 & 4 \end{array}\right]^{-1} + \frac{1}{4} \left[\begin{array}{cc} 20.25 & 4.5 \\ 4.5 & 13 \end{array}\right]^{-1} + \frac{1}{4} \left[\begin{array}{cc} 11.25 & 2.5 \\ 2.5 & 12.75 \end{array}\right]^{-1} \\
    g_{a23} &= -\frac{1}{2} \left[\begin{array}{cc} 20.25 & 4.5 \\ 4.5 & 13 \end{array}\right]^{-1}
\end{align*}
\]
\[ g_{a}^{25} = -\frac{1}{2} \begin{bmatrix} 11.25 & 2.5 \\ 2.5 & 12.75 \end{bmatrix}^{-1} \]

\[ g_{a}^{33} = \begin{bmatrix} 20.25 & 4.5 \\ 4.5 & 13 \end{bmatrix}^{-1} + \frac{1}{4} \begin{bmatrix} 11.25 & 2.5 \\ 2.5 & 12.75 \end{bmatrix}^{-1} \]

\[ g_{a}^{36} = -\frac{1}{2} \begin{bmatrix} 15.625 & 3.5 \\ 3.5 & 10.25 \end{bmatrix}^{-1} \]

\[ g_{a}^{44} = \begin{bmatrix} 13.5 & 3 \\ 3 & 8 \end{bmatrix}^{-1} \]

\[ g_{a}^{55} = \begin{bmatrix} 11.25 & 2.5 \\ 2.5 & 12.75 \end{bmatrix}^{-1} \]

\[ g_{a}^{66} = \begin{bmatrix} 15.625 & 3.5 \\ 3.5 & 10.25 \end{bmatrix}^{-1} \]

The inverse of the direct and maternal multibreed additive genetic covariance matrix is obtained by substituting submatrices \( \{g_{a}^{ij}\}, i, j = 1, \ldots, 6, \) in matrix \( G_{a}^{-1}. \)

**Matrices of Direct and Maternal Multibreed Nonadditive Genetic Variances and Covariances**

Matrices of direct and maternal multibreed nonadditive genetic variances and covariances in a regression model that accounts for sire × breed group of dam and dam × breed group of sire interaction effects are equal to the intrabreed and interbreed matrices of direct and maternal interaction variances and covariances at 1 or more loci. Nonadditive genetic regression effects are independent of each other. For example, if 2 nonadditive genetic effects (e.g., intrabreed AA and interbreed AB) were fitted in a model, the matrix of direct and maternal multibreed nonadditive genetic variances and covariances would be block-diagonal with 2 blocks, i.e., \( G_{n} = \text{diag}\{G_{nAA}, G_{nAB}\}. \) However, only a single random nonadditive genetic effect: intralocus interbreed interaction will be fitted here. Under this assumption, \( G_{n} = G_{nAB}, \) and the only nonadditive genetic matrix of direct and maternal variances and covariances needed for the example is the
direct-maternal covariance matrix of intralocus interbreed interaction effects, i.e., \( V_{nAB} = \begin{bmatrix} 16 & 6 \\ 6 & 12 \end{bmatrix} \) kg\(^2\).

The direct-maternal multibreed nonadditive genetic covariance matrices for the 6 animals in the example is:

<table>
<thead>
<tr>
<th>Animal</th>
<th>Number</th>
<th>Breed Group</th>
<th>Direct-Maternal Multibreed Nonadditive Genetic Covariance Matrix</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parents</td>
<td>1</td>
<td>A</td>
<td>[16 \ 6 \ 6 \ 12]</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>B</td>
<td>[16 \ 6 \ 6 \ 12]</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>(\frac{1}{2}A \frac{1}{2}B)</td>
<td>[16 \ 6 \ 6 \ 12]</td>
</tr>
<tr>
<td>Non-parents</td>
<td>4</td>
<td>(\frac{1}{2}A \frac{1}{2}B)</td>
<td>[16 \ 6 \ 6 \ 12]</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>(\frac{1}{2}A \frac{1}{2}B)</td>
<td>[16 \ 6 \ 6 \ 12]</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>(\frac{3}{4}A \frac{1}{4}B)</td>
<td>[16 \ 6 \ 6 \ 12]</td>
</tr>
</tbody>
</table>

**Inverse of the Direct-Maternal Multibreed Nonadditive Genetic Covariance Matrix**

Direct-maternal covariance matrices among sire \(\times\) breed group of dam and dam \(\times\) breed group of sire interaction effects are assumed to be caused by similarities among sires and(or) dams due to common ancestry. Thus, the equation for the inverse of the covariance matrix of direct and maternal multibreed nonadditive genetic effects due to intralocus interbreed sire \(\times\) breed group of dam interaction and dam \(\times\) breed group of sire interaction effects, \(G_n^{-1}\), is:

\[ G_n^{-1} = \{g_{n}^{ij}\} \]
\[
\sum_{k=1}^{K} t_{ik} \cdot d_{nk}^{-1} \cdot t_{kj}
\]

where \( K \) is the number of animals in the pedigree, \( t_{ik} \) are elements of \( T' = (I - \frac{1}{2} P') \), \( d_{nk}^{-1} \) are 2 × 2 direct-maternal submatrices of block-diagonal matrix \( D_n^{-1} \), and \( t_{kj} \) are elements of \( T = (I - \frac{1}{2} P) \), and

\[
I = \text{identity matrix},
\]
\[
P = \text{matrix that relates animals to their sires and dams; each row of } P \text{ contains up to 2 nonzero elements: a 1 for the sire and a 1 for the dam of an animal},
\]
\[
D_n^{-1} = \text{inverse of block-diagonal matrix of residual direct and maternal nonadditive genetic variances and covariances, where } D_n^{-1} = \{ d_{nii}^{-1} \}.
\]

The 2 × 2 direct-maternal submatrices of block-diagonal matrix \( D_n^{-1} \) are computed using the expression:

\[
d_{nii}^{-1} = \left[ (1 - \frac{1}{4}\delta_s (1 + F_s) - \frac{1}{4}\delta_d (1 + F_d)) \cdot V_{nAB} \right]^{-1} = \left[ (1 - \frac{1}{4}\delta_s (1 + F_s) - \frac{1}{4}\delta_d (1 + F_d)) \right]^{-1} \cdot V_{nAB}^{-1}
\]

because \( V_{nAB} \) is the same for all sire × breed group of dam combinations, and \( F_s \) and \( F_d \) are the coefficients of inbreeding of the sire and the dam of animal \( i \), and \( \delta_s = 1 \) if the sire is known, else \( \delta_s = 0 \), and \( \delta_d = 1 \) if the dam is known, else \( \delta_d = 0 \).

In non-inbred multibreed populations, the \( F_s \) and \( F_d \) are equal to zero. Thus, the expression for \( d_{nii}^{-1} \) simplifies to:

\[
d_{nii}^{-1} = \left[ (1 - \frac{1}{4}\delta_s - \frac{1}{4}\delta_d) \cdot V_{nAB} \right]^{-1} = \left[ (1 - \frac{1}{4}\delta_s - \frac{1}{4}\delta_d) \right]^{-1} \cdot V_{nAB}^{-1}
\]

The diagonal elements of the \( D_n^{-1} \) matrix are:
<table>
<thead>
<tr>
<th>Animal</th>
<th>Number</th>
<th>Breed Group</th>
<th>((d_{nii})^{-1} \cdot V_{nAB}^{-1})</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parents</td>
<td>1</td>
<td>A</td>
<td>([16 \quad 6]^{-1} = [16 \quad 6]^{-1})</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>B</td>
<td>([16 \quad 6]^{-1} = [16 \quad 6]^{-1})</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>(\frac{1}{2} \ A \frac{1}{2} B)</td>
<td>([16 \quad 6]^{-1} = [12 \quad 4.5]^{-1})</td>
</tr>
<tr>
<td>Non-parents</td>
<td>4</td>
<td>(\frac{1}{2} \ A \frac{1}{2} B)</td>
<td>([16 \quad 6]^{-1} = [12 \quad 4.5]^{-1})</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>(\frac{1}{2} \ A \frac{1}{2} B)</td>
<td>([16 \quad 6]^{-1} = [8 \quad 3]^{-1})</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>(\frac{3}{4} \ A \frac{1}{4} B)</td>
<td>([16 \quad 6]^{-1} = [8 \quad 3]^{-1})</td>
</tr>
</tbody>
</table>

The \(P\) matrix is:

\[
P = \begin{bmatrix}
0 & | & 0 & | & 0 & | & 0 & | & 0 & | & 0 & | & 0 & | & 0 & | & 0 \\
0 & & 0 & & 0 & & 1 & & 0 & & 1 & & 0 & & 0 & & 1 & & 0 & & 1 & & 0 & & 1 & & 0 & & 0 & & 0 & & 0
\end{bmatrix}
\]

The inverse of the block-diagonal matrix \(D_n\) is:

\[
D_n^{-1} = \{d_{nii}^{-1}\}
\]

where

\[
d_{n11}^{-1} = \begin{bmatrix} 16 & 6 \end{bmatrix}^{-1}
\]
\[
\begin{align*}
d_{n22}^{-1} &= \begin{bmatrix} 16 & 6 \\ 6 & 12 \end{bmatrix}^{-1} \\
&= \begin{bmatrix} 0.4 & -0.2 \\ -0.2 & 0.4 \end{bmatrix} \\
d_{n33}^{-1} &= \begin{bmatrix} 12 & 4.5 \\ 4.5 & 9 \end{bmatrix}^{-1} \\
&= \begin{bmatrix} 0.4 & -0.2 \\ -0.2 & 0.4 \end{bmatrix} \\
d_{n44}^{-1} &= \begin{bmatrix} 12 & 4.5 \\ 4.5 & 9 \end{bmatrix}^{-1} \\
&= \begin{bmatrix} 0.4 & -0.2 \\ -0.2 & 0.4 \end{bmatrix} \\
d_{n55}^{-1} &= \begin{bmatrix} 8 & 3 \\ 3 & 6 \end{bmatrix}^{-1} \\
&= \begin{bmatrix} 0.5 & -0.1 \\ -0.1 & 0.5 \end{bmatrix} \\
d_{n66}^{-1} &= \begin{bmatrix} 8 & 3 \\ 3 & 6 \end{bmatrix}^{-1} \\
&= \begin{bmatrix} 0.5 & -0.1 \\ -0.1 & 0.5 \end{bmatrix}
\end{align*}
\]

The inverse of the direct-maternal multibreed nonadditive genetic covariance matrix is:
\[
G_n^{-1} = (D_n^{-1} - \frac{1}{2} D_n^{-1} P - \frac{1}{2} P' D_n^{-1} + \frac{1}{4} P' D_n^{-1} P) \ast V_{nAB}^{-1}
\]

\[
G_n^{-1} = \begin{bmatrix}
g_n^{11} & g_n^{12} & g_n^{13} & g_n^{14} & g_n^{15} & g_n^{16}
g_n^{12} & g_n^{22} & g_n^{23} & 0 & g_n^{25} & 0 
g_n^{13} & g_n^{23} & g_n^{33} & 0 & 0 & g_n^{36} 
g_n^{14} & 0 & 0 & g_n^{44} & 0 & 0 
g_n^{15} & g_n^{25} & 0 & 0 & g_n^{55} & 0 
g_n^{16} & 0 & g_n^{36} & 0 & 0 & g_n^{66}
\end{bmatrix}
\]

The rules used to compute the elements of matrix $G_n^{-1}$ for direct and maternal interbreed intralocus interaction effects are:

1) Add $d_{nn}^{-1}$ to $i \times i$,  
2) Add $-\frac{1}{2} d_{nn}^{-1}$ to $i \times s$ and $s \times i$ if the sire of animal $i$ is identified, 
3) Add $-\frac{1}{2} d_{nn}^{-1}$ to $i \times d$ and $d \times i$ if the dam of animal $i$ is identified, and 
4) Add $\frac{1}{4} d_{nn}^{-1}$ to $s \times s$, $s \times d$, $d \times s$, and $d \times d$ if the sire and dam of animal $i$ are identified.
where the $d_{nii}$ are 2 × 2 submatrices of direct and maternal interbreed nonadditive genetic variances and covariances.

Thus,

\[
g_{n11} = \begin{bmatrix} 16 & 6 \\ 6 & 12 \end{bmatrix}^{-1} + \frac{1}{4} \begin{bmatrix} 12 & 4.5 \\ 4.5 & 9 \end{bmatrix}^{-1} + \frac{1}{4} \begin{bmatrix} 8 & 3 \\ 3 & 6 \end{bmatrix}^{-1} + \frac{1}{4} \begin{bmatrix} 8 & 3 \\ 3 & 6 \end{bmatrix}^{-1}
\]

\[
g_{n12} = \frac{1}{4} \begin{bmatrix} 8 & 3 \\ 3 & 6 \end{bmatrix}^{-1}
\]

\[
g_{n13} = \frac{1}{4} \begin{bmatrix} 8 & 3 \\ 3 & 6 \end{bmatrix}^{-1}
\]

\[
g_{n14} = -\frac{1}{2} \begin{bmatrix} 12 & 4.5 \\ 4.5 & 9 \end{bmatrix}^{-1}
\]

\[
g_{n15} = -\frac{1}{2} \begin{bmatrix} 8 & 3 \\ 3 & 6 \end{bmatrix}^{-1}
\]

\[
g_{n16} = -\frac{1}{2} \begin{bmatrix} 8 & 3 \\ 3 & 6 \end{bmatrix}^{-1}
\]

\[
g_{n22} = \begin{bmatrix} 16 & 6 \\ 6 & 12 \end{bmatrix}^{-1} + \frac{1}{4} \begin{bmatrix} 12 & 4.5 \\ 4.5 & 9 \end{bmatrix}^{-1} + \frac{1}{4} \begin{bmatrix} 8 & 3 \\ 3 & 6 \end{bmatrix}^{-1}
\]

\[
g_{n23} = -\frac{1}{2} \begin{bmatrix} 12 & 4.5 \\ 4.5 & 9 \end{bmatrix}^{-1}
\]

\[
g_{n25} = -\frac{1}{2} \begin{bmatrix} 8 & 3 \\ 3 & 6 \end{bmatrix}^{-1}
\]

\[
g_{n33} = \begin{bmatrix} 12 & 4.5 \\ 4.5 & 9 \end{bmatrix}^{-1} + \frac{1}{4} \begin{bmatrix} 8 & 3 \\ 3 & 6 \end{bmatrix}^{-1}
\]

\[
g_{n36} = -\frac{1}{2} \begin{bmatrix} 8 & 3 \\ 3 & 6 \end{bmatrix}^{-1}
\]

\[
g_{n44} = \begin{bmatrix} 12 & 4.5 \\ 4.5 & 9 \end{bmatrix}^{-1}
\]

\[
g_{n55} = \begin{bmatrix} 8 & 3 \\ 3 & 6 \end{bmatrix}^{-1}
\]
The inverse of the direct and maternal multibreed nonadditive genetic covariance matrix is obtained by substituting submatrices \( \{g_{ij}^{n}\} \), \( i, j = 1, \ldots, 6 \), in matrix \( G_n^{-1} \).

**Multibreed Environmental Variances**

Multibreed environmental variances are also computed by conditioning them on breeds of origin.

Thus, they are obtained using the expression:

\[
\sigma_{et}^2 = \sum_{b=1}^{n_b} p_b^i \left( \sigma_{et}^2 \right)_b + \sum_{b=1}^{n_b-1} \sum_{b'>b} (p_b^i p_{b'}^i + p_b^d p_{b'}^d) \left( \sigma_{et}^2 \right)_{bb'}
\]

where \( e = \) environmental, \( t = \) trait, superscripts \( i = \) individual, \( s = \) sire, and \( d = \) dam, subscripts \( b \) and \( b' \) represent two breeds, and

\[
\begin{align*}
n_b & = \text{number of breeds}, \\
p_b^x & = \text{expected fraction of breed } b \text{ in animal } x, \ x = i, s, d, \\
(\sigma_{et}^2)_b & = \text{intrabreed environmental variance for trait } t \text{ for breed } b, \\
(\sigma_{et}^2)_{bb'} & = \text{interbreed environmental variance for trait } t \text{ for the pair of breeds } b \text{ and } b'.
\end{align*}
\]

The multibreed environmental variances for the 6 animals in the example are:

<table>
<thead>
<tr>
<th>Animal</th>
<th>Number</th>
<th>Breed Group</th>
<th>Multibreed Environmental Variance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parents</td>
<td>1</td>
<td>A</td>
<td>49</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>B</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>( \frac{1}{2} ) A ( \frac{1}{2} ) B</td>
<td>( \frac{1}{2} ) (49) + ( \frac{1}{2} ) (16) = 32.5</td>
</tr>
<tr>
<td>Non-parents</td>
<td>4</td>
<td>( \frac{1}{2} ) A ( \frac{1}{2} ) B</td>
<td>( \frac{1}{2} ) (49) + ( \frac{1}{2} ) (16) = 32.5</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>( \frac{1}{2} ) A ( \frac{1}{2} ) B</td>
<td>( \frac{1}{2} ) (49) + ( \frac{1}{2} ) (16) = 32.5</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>( \frac{3}{4} ) A ( \frac{1}{4} ) B</td>
<td>( \frac{3}{4} ) (49) + ( \frac{1}{4} ) (16) + <a href="25">(1)(0) + (( \frac{1}{2} ))(( \frac{1}{2} ))</a> = 47.0</td>
</tr>
</tbody>
</table>
The left hand side of the \texttt{MME\_DMMAM} for Example 1 is shown in the output of the SAS IML program.

The vector of effects and the right hand side (RHS) of the \texttt{MME\_DMMAM} for Example 1 are:

\begin{table}[h]
\centering
\begin{tabular}{|l|l|}
\hline
\textbf{Effect} & \textbf{RHS} \\
\hline
 Mean & 52.19 \\
 Breed\textsubscript{Ad} & 22.91 \\
 Breed\textsubscript{Am} & 8.94 \\
 Breed\textsubscript{Bd} & 29.28 \\
 Breed\textsubscript{Bm} & 43.25 \\
 Heterosis\textsubscript{ABd} & 27.93 \\
 Heterosis\textsubscript{ABm} & 6.09 \\
 Sex\textsubscript{M} & 20.97 \\
 Sex\textsubscript{F} & 31.22 \\
 a\textsubscript{ad1} & 5.9 \\
 a\textsubscript{am1} & 0 \\
 a\textsubscript{ad2} & 15.31 \\
 a\textsubscript{am2} & 16.86 \\
 a\textsubscript{ad3} & 7.88 \\
 a\textsubscript{am3} & 6.09 \\
 a\textsubscript{ad4} & 8.03 \\
 a\textsubscript{am4} & 0 \\
 a\textsubscript{ad5} & 8.98 \\
\hline
\end{tabular}
\end{table}
### Remarks:

1) The rank of the left hand side matrix of the MME is $(33 - 3) = 30$.

2) Differences between breed effects, heterosis, and differences between sex effects are estimable.

3) The set of **MME_DMMAM** can be solved directly by:

   a. Obtaining the generalized inverse of the left hand side (ginvlhs) and multiplying it by
the right hand side (rhs), i.e.,

\[ \text{sol} = \text{ginvlhs} \times \text{rhs} \]

b. Imposing restrictions on the solutions. The number of equations in Example 1 is 33 and the rank of the left hand side of the \text{MME\_DMMAM} is 30, thus 3 restrictions need to be imposed to obtain solutions. These 3 restrictions could be:

i. Set the solution of the mean to zero, and

ii. Set the solution for breed B to zero for direct and maternal effects. These restrictions are useful because the expectation of the direct and maternal solutions for breed A estimate the difference between breeds A and B for these effects. Thus, breed B can be used as the genetic base of comparison for direct and maternal additive multibreed genetic effects.

iii. Insufficient numbers of records from straightbred and crossbred matings may cause confounding among breed direct, breed maternal effects, and heterosis effects, which in turn, may prevent differences between breeds and heterosis effects from being estimable (unbiasedly). In Example 1, breed effects are confounded with heterosis effects, thus the rank of the left hand side matrix of the MME is 29 instead of 30.

4) Fixed heterosis effects here are estimates of the difference between direct and maternal interbreed (AB and BA) interaction effects relative to the average of direct and maternal intrabreed interaction effects (AA and BB). Thus, direct and maternal fixed heterosis effects can be used as the genetic base for comparison of nonadditive multibreed genetic effects.

The vector of solutions (SOL; obtained without imposing restrictions on the solutions), and the standard error of solutions (SESOL; computed as the square root of the diagonals of the
generalized inverse of the left hand side of the MME\textsubscript{DMMAM}) are:

<table>
<thead>
<tr>
<th>Effect</th>
<th>SOL</th>
<th>SESOL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean\textdegree</td>
<td>106.72</td>
<td>2.09</td>
</tr>
<tr>
<td>Breed\textsubscript{AD} \textdegree</td>
<td>58</td>
<td>3.92</td>
</tr>
<tr>
<td>Breed\textsubscript{AM} \textdegree</td>
<td>53.62</td>
<td>4.12</td>
</tr>
<tr>
<td>Breed\textsubscript{BD} \textdegree</td>
<td>48.73</td>
<td>3.56</td>
</tr>
<tr>
<td>Breed\textsubscript{BM} \textdegree</td>
<td>53.1</td>
<td>3.22</td>
</tr>
<tr>
<td>Heterosis\textsubscript{ABD} \textdegree</td>
<td>8.75</td>
<td>5.28</td>
</tr>
<tr>
<td>Heterosis\textsubscript{ABM} \textdegree</td>
<td>-3.89</td>
<td>11.29</td>
</tr>
<tr>
<td>Sex\textsubscript{M} \textdegree</td>
<td>70.05</td>
<td>4.74</td>
</tr>
<tr>
<td>Sex\textsubscript{F} \textdegree</td>
<td>36.67</td>
<td>4.48</td>
</tr>
<tr>
<td>\textalpha\textsubscript{AD1}</td>
<td>0.61</td>
<td>5.81</td>
</tr>
<tr>
<td>\textalpha\textsubscript{AM1}</td>
<td>0.14</td>
<td>4.89</td>
</tr>
<tr>
<td>\textalpha\textsubscript{AD2}</td>
<td>-0.22</td>
<td>2.95</td>
</tr>
<tr>
<td>\textalpha\textsubscript{AM2}</td>
<td>-0.17</td>
<td>1.96</td>
</tr>
<tr>
<td>\textalpha\textsubscript{AD3}</td>
<td>-0.79</td>
<td>4.33</td>
</tr>
<tr>
<td>\textalpha\textsubscript{AM3}</td>
<td>-0.24</td>
<td>3.7</td>
</tr>
<tr>
<td>\textalpha\textsubscript{AD4}</td>
<td>0.76</td>
<td>4.37</td>
</tr>
<tr>
<td>\textalpha\textsubscript{AM4}</td>
<td>0.17</td>
<td>3.72</td>
</tr>
<tr>
<td>\textalpha\textsubscript{AD5}</td>
<td>0.19</td>
<td>4.72</td>
</tr>
<tr>
<td>\textalpha\textsubscript{AM5}</td>
<td>-0.02</td>
<td>3.74</td>
</tr>
</tbody>
</table>
The vector of $\text{DMAMBV}$ for animal $i$, computed as deviations from breed $B$ (chosen as the genetic base), is:

$$\text{DMAMBV}_i = \hat{u}_{ai} = \text{Prob}_{\text{Anim}_i}^{A}(\text{Breed}_A^\circ - \text{Breed}_B^\circ) + \hat{a}_{ai}$$

where

- $\text{Prob}_{\text{Anim}_i}^{A}$ = expected fraction of breed $A$ in animal $i$,

- $\text{Breed}_A^\circ$ = vector of generalized least squares solutions for direct and maternal effects for breed $A$,  

| $\hat{a}_{ad6}$ | -0.09 | 5.5  |
| $\hat{a}_{am6}$ | -0.05 | 4.44 |
| $\hat{a}_{nd1}$ |  0.54 | 3.78 |
| $\hat{a}_{nm1}$ |   0.2 | 3.43 |
| $\hat{a}_{nd2}$ | -0.54 | 3.78 |
| $\hat{a}_{nm2}$ |  -0.2 | 3.43 |
| $\hat{a}_{nd3}$ | -0.27 | 3.95 |
| $\hat{a}_{nm3}$ |  -0.1 | 3.46 |
| $\hat{a}_{nd4}$ |  0.27 | 3.95 |
| $\hat{a}_{nm4}$ |   0.1 | 3.46 |
| $\hat{a}_{nd5}$ |   0  |  4   |
| $\hat{a}_{nm5}$ |   0  | 3.46 |
| $\hat{a}_{nd6}$ |  0.14 | 3.99 |
| $\hat{a}_{nm6}$ |  0.05 | 3.46 |
Breed$_B^\circ$ = vector of generalized least squares solutions for direct and maternal effects for breed B,

$\hat{a}_{ai} = \text{vector of BLUP for direct and maternal multibreed additive genetic effects for animal i.}$

The matrix of variances and covariances of errors of prediction (VEP) for vector DMAMBV is:

$$\text{VEP(}DMAMBV\text{)} = \text{var}(\hat{u}_a - u_a) = K_a^*(\text{ginvlhs})^*K_a,'$$

where

$$K_a = n_{anim} \times n_{eq} \text{ matrix specifying the factors multiplying vector DMAMBV, where } n_{anim}$$

= number of animals, and $n_{eq}$ = number of equations, and $\text{ginvlhs} = n_{eq} \times n_{eq} \text{ generalized inverse matrix of the left hand side of the MME.}$

Matrix $K_a$ for DMMAM Example 1 is shown in the output of the SAS IML program.

The standard errors of prediction (SEP) of the elements of vector DMAMBV are computed as the square root of the diagonal elements of the $\text{VEP(}DMAMBV\text{)}$ matrix.

The vector of DMAMBV and their SEP for the 6 animals in Example 1 are:

<table>
<thead>
<tr>
<th>Animal</th>
<th>Effect</th>
<th>Prob$_{Ai}$</th>
<th>Breed$_A^\circ$ - Breed$_B^\circ$</th>
<th>$\hat{a}_{ai}$</th>
<th>DMAMBV</th>
<th>SEP DMAMBV</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Dir</td>
<td>1</td>
<td>9.27</td>
<td>0.61</td>
<td>9.88</td>
<td>7.69</td>
</tr>
<tr>
<td>1</td>
<td>Mat</td>
<td>1</td>
<td>0.52</td>
<td>0.14</td>
<td>0.66</td>
<td>8.32</td>
</tr>
<tr>
<td>2</td>
<td>Dir</td>
<td>0</td>
<td>9.27</td>
<td>-0.22</td>
<td>-0.22</td>
<td>2.95</td>
</tr>
<tr>
<td>2</td>
<td>Mat</td>
<td>0</td>
<td>0.52</td>
<td>-0.17</td>
<td>-0.17</td>
<td>1.96</td>
</tr>
<tr>
<td>3</td>
<td>Dir</td>
<td>0.5</td>
<td>9.27</td>
<td>-0.79</td>
<td>3.84</td>
<td>5.07</td>
</tr>
</tbody>
</table>
### Direct and Maternal Nonadditive Multibreed Genetic Predictions

The vector of $\text{DMNMBV}$ for animal $i$, computed assuming that males are mated to $\frac{1}{2} A \frac{1}{2} B$ females, and vice versa, is:

$$\text{DMNMBV}_i = \mathbf{u}_n = (\text{Prob}_{A\text{anim }i} \cdot \text{Prob}_{B\text{mate}} + \text{Prob}_{B\text{anim }i} \cdot \text{Prob}_{A\text{mate}})(\text{Heterosis}_{AB}^\circ + \mathbf{\hat{u}}_n)$$

where

- $\text{Prob}_{A\text{anim }i}$ = expected fraction of breed A in animal $i$,
- $\text{Prob}_{B\text{anim }i}$ = expected fraction of breed B in animal $i$,
- $\text{Prob}_{A\text{mate}}$ = expected fraction of breed A in the mate of animal $i$,
- $\text{Prob}_{B\text{mate}}$ = expected fraction of breed B in the mate of animal $i$,
- $\text{Heterosis}_{AB}^\circ$ = vector of generalized least squares solutions for direct and maternal heterosis effect due to the interaction between alleles of breeds A and B in 1 locus,
- $\mathbf{\hat{u}}_n$ = vector of BLUP for direct and maternal nonadditive genetic effects for animal $i$.

The matrix of variances and covariances of errors of prediction (VEP) for vector $\text{DMNMBV}$ is:

$$\text{VEP}(\text{DMNMBV}) = \text{var}(\mathbf{u}_n - \mathbf{u}_n) = \mathbf{K}_n^* (\mathbf{ginvlhs})^* \mathbf{K}_n^*$$

<p>| | | | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>Mat</td>
<td>0.5</td>
<td>0.52</td>
<td>-0.24</td>
<td>0.03</td>
</tr>
<tr>
<td>4</td>
<td>Dir</td>
<td>0.5</td>
<td>9.27</td>
<td>0.76</td>
<td>5.4</td>
</tr>
<tr>
<td>4</td>
<td>Mat</td>
<td>0.5</td>
<td>0.52</td>
<td>0.17</td>
<td>0.43</td>
</tr>
<tr>
<td>5</td>
<td>Dir</td>
<td>0.5</td>
<td>9.27</td>
<td>0.19</td>
<td>4.83</td>
</tr>
<tr>
<td>5</td>
<td>Mat</td>
<td>0.5</td>
<td>0.52</td>
<td>-0.02</td>
<td>0.25</td>
</tr>
<tr>
<td>6</td>
<td>Dir</td>
<td>0.75</td>
<td>9.27</td>
<td>-0.09</td>
<td>6.86</td>
</tr>
<tr>
<td>6</td>
<td>Mat</td>
<td>0.75</td>
<td>0.52</td>
<td>-0.05</td>
<td>0.34</td>
</tr>
</tbody>
</table>
where

\[ K_n = n_{anim} \times n_{eq} \] matrix specifying the factors multiplying vector \( \text{DMNMBV} \), where

\[ n_{anim} = \text{number of animals}, \quad n_{eq} = \text{number of equations}, \quad \text{and} \]

\[ \text{ginvlhs} = n_{eq} \times n_{eq} \text{ generalized inverse matrix of the left hand side of MME}_{DMMAM}. \]

Matrix \( K_n \) for DMMAM Example 1 is shown in the output of the SAS IML program.

The standard errors of prediction (SEP) of the elements of vector \( \text{DMNMBV} \) are computed as the square roots of the diagonal elements of the VEP(\( \text{DMNMBV} \)) matrix.

The vector of \( \text{DMNMBV} \) and their SEP for the 6 animals in DMMAM Example 1 are:

<table>
<thead>
<tr>
<th>Animal</th>
<th>Effect</th>
<th>( \text{Prob}<em>{Ai} \times \text{Prob}</em>{B\text{mate}} + \text{Prob}<em>{Bi} \times \text{Prob}</em>{A\text{mate}} )</th>
<th>( \text{Heterosis}_{AB} \circ )</th>
<th>( \hat{a}_{ni} )</th>
<th>DMNMBV</th>
<th>SEP ( \text{DMNMBV} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Dir</td>
<td>( 1<em>0.5 + 0</em>0.5 )</td>
<td>8.75</td>
<td>0.54</td>
<td>4.64</td>
<td>2.54</td>
</tr>
<tr>
<td>1</td>
<td>Mat</td>
<td>( 1<em>0.5 + 0</em>0.5 )</td>
<td>-3.89</td>
<td>0.2</td>
<td>-1.84</td>
<td>5.87</td>
</tr>
<tr>
<td>2</td>
<td>Dir</td>
<td>( 0<em>0.5 + 1</em>0.5 )</td>
<td>8.75</td>
<td>-0.54</td>
<td>4.1</td>
<td>2.57</td>
</tr>
<tr>
<td>2</td>
<td>Mat</td>
<td>( 0<em>0.5 + 1</em>0.5 )</td>
<td>-3.89</td>
<td>-0.2</td>
<td>-2.05</td>
<td>5.74</td>
</tr>
<tr>
<td>3</td>
<td>Dir</td>
<td>( 0.5<em>0.5 + 0.5</em>0.5 )</td>
<td>8.75</td>
<td>-0.27</td>
<td>4.24</td>
<td>2.98</td>
</tr>
<tr>
<td>3</td>
<td>Mat</td>
<td>( 0.5<em>0.5 + 0.5</em>0.5 )</td>
<td>-3.89</td>
<td>-0.1</td>
<td>-1.99</td>
<td>5.32</td>
</tr>
<tr>
<td>4</td>
<td>Dir</td>
<td>( 0.5<em>0.5 + 0.5</em>0.5 )</td>
<td>8.75</td>
<td>0.27</td>
<td>4.51</td>
<td>2.97</td>
</tr>
<tr>
<td>4</td>
<td>Mat</td>
<td>( 0.5<em>0.5 + 0.5</em>0.5 )</td>
<td>-3.89</td>
<td>0.1</td>
<td>-1.89</td>
<td>5.89</td>
</tr>
<tr>
<td>5</td>
<td>Dir</td>
<td>( 0.5<em>0.5 + 0.5</em>0.5 )</td>
<td>8.75</td>
<td>0</td>
<td>4.37</td>
<td>2.64</td>
</tr>
<tr>
<td>5</td>
<td>Mat</td>
<td>( 0.5<em>0.5 + 0.5</em>0.5 )</td>
<td>-3.89</td>
<td>0</td>
<td>-1.94</td>
<td>5.81</td>
</tr>
<tr>
<td>6</td>
<td>Dir</td>
<td>( 0.75<em>0.5 + 0.25</em>0.5 )</td>
<td>8.75</td>
<td>0.14</td>
<td>4.44</td>
<td>2.81</td>
</tr>
<tr>
<td>6</td>
<td>Mat</td>
<td>( 0.75<em>0.5 + 0.25</em>0.5 )</td>
<td>-3.89</td>
<td>0.05</td>
<td>-1.92</td>
<td>5.6</td>
</tr>
</tbody>
</table>
Direct and Maternal Total Multibreed Genetic Predictions

The vector of $\text{DMTMBV}$ for animal $i$ is equal to the sum of its vectors of predicted direct and maternal multibreed additive ($\text{DMAMBV}$) and nonadditive ($\text{DMNMBV}$) genetic effects, i.e.,

$$\text{DMTMBV}_i = \text{DMAMBV}_i + \text{DMNMBV}_i = \hat{u}_i + \hat{u}_{ni}$$

The matrix of variances and covariances of errors of prediction (VEP) for vector $\text{DMTMBV}$ is:

$$\text{VEP}( \text{DMTMBV}) = \text{var}(\hat{u} - u) = K_t^t(\text{ginvlhs}) K_t'$$

where

$$K_t = n_{anim} \times n_{eq} \text{ matrix specifying the factors multiplying vector } \text{DMTMBV}, \text{ where}$$

$$n_{anim} = \text{number of animals, and } n_{eq} = \text{number of equations, and}$$

$$\text{ginvlhs} = n_{eq} \times n_{eq} \text{ generalized inverse matrix of the left hand side of the MME.}$$

Matrix $K_t$ for $\text{DMMAM Example 1}$ is shown in the output of the SAS IML program.

The standard errors of prediction (SEP) of the elements of vector $\text{DMTMBV}$ are computed as the square roots of the diagonal elements of the $\text{VEP}(\text{DMTMBV})$ matrix.

The vector of $\text{DMTMBV}$ and their SEP for the 6 animals in $\text{DMMAM Example 1}$ are:

<table>
<thead>
<tr>
<th>Animal</th>
<th>Effect</th>
<th>DMAMBV</th>
<th>DMNMBV</th>
<th>DMTMBV</th>
<th>SEP DMTMBV</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Dir</td>
<td>9.88</td>
<td>4.64</td>
<td>14.52</td>
<td>8.8</td>
</tr>
<tr>
<td>1</td>
<td>Mat</td>
<td>0.66</td>
<td>-1.84</td>
<td>-1.18</td>
<td>10.35</td>
</tr>
<tr>
<td>2</td>
<td>Dir</td>
<td>-0.22</td>
<td>4.1</td>
<td>3.88</td>
<td>4.1</td>
</tr>
<tr>
<td>2</td>
<td>Mat</td>
<td>-0.17</td>
<td>-2.05</td>
<td>-2.21</td>
<td>6.09</td>
</tr>
<tr>
<td>3</td>
<td>Dir</td>
<td>3.84</td>
<td>4.24</td>
<td>8.08</td>
<td>5.96</td>
</tr>
<tr>
<td>3</td>
<td>Mat</td>
<td>0.03</td>
<td>-1.99</td>
<td>-1.97</td>
<td>6.36</td>
</tr>
</tbody>
</table>


<table>
<thead>
<tr>
<th>4</th>
<th>Dir</th>
<th>5.4</th>
<th>4.51</th>
<th>9.9</th>
<th>5.56</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>Mat</td>
<td>0.43</td>
<td>-1.89</td>
<td>-1.46</td>
<td>7.76</td>
</tr>
<tr>
<td>5</td>
<td>Dir</td>
<td>4.83</td>
<td>4.37</td>
<td>9.2</td>
<td>6.97</td>
</tr>
<tr>
<td>5</td>
<td>Mat</td>
<td>0.25</td>
<td>-1.94</td>
<td>-1.7</td>
<td>8.06</td>
</tr>
<tr>
<td>6</td>
<td>Dir</td>
<td>6.86</td>
<td>4.44</td>
<td>11.3</td>
<td>7.79</td>
</tr>
<tr>
<td>6</td>
<td>Mat</td>
<td>0.34</td>
<td>-1.92</td>
<td>-1.57</td>
<td>8.29</td>
</tr>
</tbody>
</table>

References


Quaas, R. L. 1975. From Mendel's laws to the A inverse. Mimeograph, Cornell University, p 1-