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:

$$y = Xb + Z_a Q_a\, g_a + Z_n Q_n\, g_n + Z_a\, a_a + Z_n\, a_n + e$$

$$E[y] = Xb + Z_a Q_a\, g_a + Z_n Q_n\, g_n$$

$$\text{var}\begin{bmatrix} a_a \\ a_n \\ e \end{bmatrix} = \begin{bmatrix} G_a & 0 & 0 \\ 0 & G_n & 0 \\ 0 & 0 & R \end{bmatrix}$$

$$\Rightarrow \quad \text{var}(y) = Z_a G_a Z_a{}' + Z_n G_n Z_n{}' + R,$$

where

y = vector of animal records,

b = vector of unknown fixed effects (e.g., contemporary groups, sex of calf, age of dam),

g_a = vector of unknown direct and maternal additive group genetic effects (e.g., breed, breed $\times$ year of birth),

g_n = vector of unknown direct and maternal nonadditive group genetic effects (e.g., heterosis at 1 locus, heterosis at 2 loci),

a_a = vector of unknown random direct and maternal additive genetic effects (**DMAMBV**),

a_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_a = known incidence matrix relating records to elements of vector a_a,

Z_n = known incidence matrix relating records to elements of vector a_n,

Q_a =   known incidence matrix relating random direct and maternal additive genetic effects to

additive genetic groups in vector g_a,

Q_n = known incidence matrix relating random direct and maternal nonadditive genetic effects to nonadditive genetic groups in vector g_n,

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

G_n = diag{$A_m * V_{0nm}$, m = 1,..., N_m}, where A_m is the matrix of probabilities that pairs of animals received the same alleles at m loci, and V_{0nm} is the matrix of direct and maternal variances and covariances due to interaction effects among alleles at m loci. If m = 1, then $G_n = A * V_{0n1}$, where A = matrix of additive relationships and V_{0n1} = 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} = matrix of direct and maternal variances and covariances due to intralocus interbreed interaction effects = variance of random direct and maternal heterosis effects,

R = diag { σ_{ei}^2}, where σ_{ei}^2 = multibreed residual variance for animal i. 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 $R = I * \sigma_e^2$, where σ_e^2 = residual variance common to all animals in a multibreed population.

The mixed model equations (MME) for the **DMMAM** are:

$$
\begin{bmatrix}
X'R^{-1}X & X'R^{-1}Z_aQ_a & X'R^{-1}Z_nQ_n & X'R^{-1}Z_a & X'R^{-1}Z_n \\
Q_a'Z_a'R^{-1}X & Q_a'Z_a'R^{-1}Z_aQ_a & Q_a'Z_a'R^{-1}Z_nQ_n & Q_a'Z_a'R^{-1}Z_a & Q_a'Z_a'R^{-1}Z_n \\
Q_n'Z_n'R^{-1}X & Q_n'Z_n'R^{-1}Z_aQ_a & Q_n'Z_n'R^{-1}Z_nQ_n & Q_n'Z_n'R^{-1}Z_a & Q_n'Z_n'R^{-1}Z_n \\
Z_a'R^{-1}X & Z_a'R^{-1}Z_aQ_a & Z_a'R^{-1}Z_nQ_n & Z_a'R^{-1}Z_a+G_a^{-1} & Z_a'R^{-1}Z_n \\
Z_n'R^{-1}X & Z_n'R^{-1}Z_aQ_a & Z_n'R^{-1}Z_nQ_n & Z_n'R^{-1}Z_a & Z_n'R^{-1}Z_n+G_n^{-1}
\end{bmatrix}
\begin{bmatrix}
b \\ g_a \\ g_n \\ a_a \\ a_n
\end{bmatrix}
=
\begin{bmatrix}
X'R^{-1}y \\
Q_a'Z_a'R^{-1}y \\
Q_n'Z_n'R^{-1}y \\
Z_a'R^{-1}y \\
Z_n'R^{-1}y
\end{bmatrix}
$$

Example 1 of the DMMAM for a Non-inbred Multibreed Population

Animal	Breed Composn	Sex	Weaning weight (kg)	Sire	Breed Composn	Dam	Breed Composn
1	A	M	289	0	A	0	A
2	B	F	245	0	B	0	B
3	½ A ½ B	F	256	0	A	2	B
4	½ A ½ B	F	261	1	A	0	B
5	½ A ½ B	M	292	1	A	2	B
6	¾ A ¼ B	M	286	1	A	3	½ A ½ B

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:

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

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

$$
V_{aBB} = \begin{bmatrix} 9 & 2 \\ 2 & 4 \end{bmatrix} kg^2
$$

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

AB:

$$V_{aAB} = \begin{bmatrix} 4 & 1 \\ 1 & 3 \end{bmatrix} kg^2$$

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:

$$V_{nAA} = \begin{bmatrix} 4 & 1 \\ 1 & 2 \end{bmatrix} kg^2$$

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

$$V_{nBB} = \begin{bmatrix} 9 & 2 \\ 2 & 4 \end{bmatrix} kg^2$$

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

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

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

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

will be needed.

3) **Environmental variances:**

Environmental variance for breed A = σ_{eAA}^2 = 49 kg^2

Environmental variance for breed B = σ_{eBB}^2 = 16 kg^2

Environmental variance for combination of breeds AB = σ_{eAB}^2 = 25 kg^2

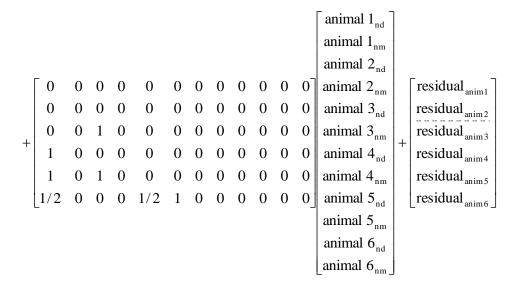4) **Environmental covariances among records of different animals are zero.**

Direct Maternal Multibreed Animal Model for the Example

Wean wt = overall mean + direct breed regression + maternal breed regression

+ direct heterosis regression + maternal heterosis regression + sex

+ animal direct additive genetic + animal maternal additive genetic

+ animal direct nonadditive genetic regression

+ animal maternal nonadditive genetic regression

+ residual

E [Wean wt] = overall mean + direct breed regression + maternal breed regression

+ direct heterosis regression + maternal heterosis regression + sex

Var (Wean wt) = var (animal direct additive genetic + animal maternal additive genetic)

+ var (animal direct nonadditive genetic regression + animal maternal

nonadditive genetic regression) + var (residual)

cov(Wean wt$_{ik}$, Wean wt$_{i'k'}$) = cov (animal direct add gen$_i$, animal direct add gen$_{i'}$)

+ cov (animal direct add gen$_i$, animal maternal add gen$_{i'}$)

+ cov (animal maternal add gen$_i$, animal direct add gen$_{i'}$)

+ cov (animal maternal add gen$_i$, animal maternal add gen$_{i'}$)

+ cov (animal direct nonadd gen$_i$, animal direct nonadd gen$_{i'}$)

$+$ cov (animal direct nonadd gen$_i$, animal maternal nonadd gen$_{i'}$)

$+$ cov (animal maternal nonadd gen$_i$, animal direct nonadd gen$_{i'}$)

$+$ cov (animal maternal nonadd gen$_i$, animal mat nonadd gen$_{i'}$)

$+$ cov (residual$_{ik}$, residual$_{i'k'}$)

The vectors and matrices of the **DMMAM** model are:

$$
\begin{bmatrix} 269 \\ 245 \\ 256 \\ 261 \\ 292 \\ 286 \end{bmatrix}
=
\begin{bmatrix}
1 & 1 & 1 & 0 & 0 & 0 & 0 & 1 & 0 \\
1 & 0 & 0 & 1 & 1 & 0 & 0 & 0 & 1 \\
1 & 1/2 & 0 & 1/2 & 1 & 1 & 0 & 0 & 1 \\
1 & 1/2 & 0 & 1/2 & 1 & 1 & 0 & 0 & 1 \\
1 & 1/2 & 0 & 1/2 & 1 & 1 & 0 & 1 & 0 \\
1 & 3/4 & 1/2 & 1/4 & 1/2 & 1/2 & 1 & 1 & 0
\end{bmatrix}
\begin{bmatrix}
\text{mean} \\
\text{breed}_{Ad} \\
\text{breed}_{Am} \\
\text{breed}_{Bd} \\
\text{breed}_{Bm} \\
\text{heterosis}_{ABd} \\
\text{heterosis}_{ABm} \\
\text{sex}_{M} \\
\text{sex}_{F}
\end{bmatrix}
$$

$$
+
\begin{bmatrix}
1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 0
\end{bmatrix}
\begin{bmatrix}
\text{animal } 1_{ad} \\
\text{animal } 1_{am} \\
\text{animal } 2_{ad} \\
\text{animal } 2_{am} \\
\text{animal } 3_{ad} \\
\text{animal } 3_{am} \\
\text{animal } 4_{ad} \\
\text{animal } 4_{am} \\
\text{animal } 5_{ad} \\
\text{animal } 5_{am} \\
\text{animal } 6_{ad} \\
\text{animal } 6_{am}
\end{bmatrix}
$$

$$+\begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1/2 & 0 & 0 & 0 & 1/2 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix} \begin{bmatrix} \text{animal } 1_{nd} \\ \text{animal } 1_{nm} \\ \text{animal } 2_{nd} \\ \text{animal } 2_{nm} \\ \text{animal } 3_{nd} \\ \text{animal } 3_{nm} \\ \text{animal } 4_{nd} \\ \text{animal } 4_{nm} \\ \text{animal } 5_{nd} \\ \text{animal } 5_{nm} \\ \text{animal } 6_{nd} \\ \text{animal } 6_{nm} \end{bmatrix} + \begin{bmatrix} \text{residual}_{anim1} \\ \text{residual}_{anim2} \\ \text{residual}_{anim3} \\ \text{residual}_{anim4} \\ \text{residual}_{anim5} \\ \text{residual}_{anim6} \end{bmatrix}$$

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:

$$V_{at} = E[var(t \mid b] + var(E[t \mid b])$$

$$V_{at} = \sum_{b=1}^{n_b} p_b^i (V_{at})_b + \sum_{b=1}^{n_b-1} \sum_{b'>b}^{n_b} (p_b^s p_{b'}^s + p_b^d p_{b'}^d)(V_{at})_{bb'}$$

where a = additive genetic, t = 2 x 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

n_b = number of breeds,

p_b^x = expected fraction of breed b in animal x, x = i, s, d,

$(V_{at})_b$ = matrix of direct and maternal additive intrabreed genetic variances and covariances for trait t in breed b,

$(V_{at})_{bb'}$ = matrix of direct and maternal additive interbreed genetic variances and covariances for trait t in pair of breeds b and b′.

The matrices of direct and maternal multibreed additive genetic variances and covariances for the 6 animals in the example are:

		Animal	
	Number	**Breed Group**	**Direct-Maternal Multibreed Additive Genetic Covariance Matrix**
Parents	1	A	$\begin{bmatrix} 36 & 8 \\ 8 & 24 \end{bmatrix}$
	2	B	$\begin{bmatrix} 9 & 2 \\ 2 & 4 \end{bmatrix}$
	3	½ A ½ B	$\tfrac{1}{2}\begin{bmatrix} 36 & 8 \\ 8 & 24 \end{bmatrix} + \tfrac{1}{2}\begin{bmatrix} 9 & 2 \\ 2 & 4 \end{bmatrix} = \begin{bmatrix} 22.5 & 5 \\ 5 & 14 \end{bmatrix}$
Non-parents	4	½ A ½ B	$\tfrac{1}{2}\begin{bmatrix} 36 & 8 \\ 8 & 24 \end{bmatrix} + \tfrac{1}{2}\begin{bmatrix} 9 & 2 \\ 2 & 4 \end{bmatrix} = \begin{bmatrix} 22.5 & 5 \\ 5 & 14 \end{bmatrix}$
	5	½ A ½ B	$\tfrac{1}{2}\begin{bmatrix} 36 & 8 \\ 8 & 24 \end{bmatrix} + \tfrac{1}{2}\begin{bmatrix} 9 & 2 \\ 2 & 4 \end{bmatrix} = \begin{bmatrix} 22.5 & 5 \\ 5 & 14 \end{bmatrix}$
	6	¾ A ¼ B	$\tfrac{3}{4}\begin{bmatrix} 36 & 8 \\ 8 & 24 \end{bmatrix} + \tfrac{1}{4}\begin{bmatrix} 9 & 2 \\ 2 & 4 \end{bmatrix} + [(1)(0) + (\tfrac{1}{2})(\tfrac{1}{2})]\begin{bmatrix} 4 & 1 \\ 1 & 3 \end{bmatrix}$ $= \begin{bmatrix} 30.25 & 6.75 \\ 6.75 & 19.75 \end{bmatrix}$

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, $\mathbf{G_a^{-1}}$, can be written as follows:

$$\mathbf{G_a^{-1}} = \{\mathbf{g_a^{ij}}\}$$

$$= \{\textstyle\sum_{k=1}^{K} \mathbf{t_{ik}} * \mathbf{d_{ak}^{-1}} * \mathbf{t_{kj}}\}$$

where **K** is the number of animals in the pedigree, $\mathbf{t_{ik}}$ are elements of **T' = (I – ½ P')**, $\mathbf{d_{ak}^{-1}}$ are $2 \times$ 2 direct-maternal submatrices of block-diagonal matrix $\mathbf{D_a^{-1}}$, and $\mathbf{t_{kj}}$ are elements of **T = (I – ½ P)**,

and

$\quad$ **I** $\quad$ = $\quad$ identity matrix,

$\quad$ **P** $\quad$ = $\quad$ matrix that relates animals to their sires and dams; each row of P contains up to 2

$\qquad\qquad\qquad$ nonzero elements: a 1 for the sire and a 1 for the dam of an animal,

$\quad$ **D_a^{-1}** $\quad$ = $\quad$ inverse of block-diagonal matrix of residual direct and maternal additive genetic

$\qquad\qquad\qquad$ variances and covariances. Because **D_a^{-1}** is block-diagonal, its inverse is equal to the

$\qquad\qquad\qquad$ inverse of its diagonal submatrices, i.e., **D_a^{-1}** = { **d_{aii}^{-1}** }.

The 2×2 direct-maternal submatrices of block-diagonal matrix **D_a^{-1}** are computed using the

expression:

$$d_{aii}^{-1} = \left[\left(V_{at} \right)_i - \tfrac{1}{4}\delta_s \left(\left(V_{at} \right)_s + \sum_{c=1}^{n_{cs}} F_{cs} \left(V_{at} \right)_{cs} \right) - \tfrac{1}{4}\delta_d \left(\left(V_{at} \right)_d + \sum_{c=1}^{n_{cd}} F_{cd} \left(V_{at} \right)_{cd} \right) \right]^{-1}$$

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:

$$d_{aii}^{-1} = \left[\left(V_{at} \right)_i - \tfrac{1}{4}\delta_s \left(V_{at} \right)_s - \tfrac{1}{4}\delta_d \left(V_{at} \right)_d \right]^{-1}$$

The **d_{aii}^{-1}** for the six animals in the example, computed using the formula for a non-inbred

multibreed population, are:

		Animal	
	Number	**Breed Group**	d_{aii}^{-1}
Parents	1	A	$\begin{bmatrix} 36 & 8 \\ 8 & 24 \end{bmatrix}^{-1}$
	2	B	$\begin{bmatrix} 9 & 2 \\ 2 & 4 \end{bmatrix}^{-1}$
	3	½ A ½ B	$\left[\begin{bmatrix} 22.5 & 5 \\ 5 & 14 \end{bmatrix} - ¼ \begin{bmatrix} 9 & 2 \\ 2 & 4 \end{bmatrix} \right]^{-1} = \begin{bmatrix} 20.25 & 4.5 \\ 4.5 & 13 \end{bmatrix}^{-1}$
Non-parents	4	½ A ½ B	$\left[\begin{bmatrix} 22.5 & 5 \\ 5 & 14 \end{bmatrix} - ¼ \begin{bmatrix} 36 & 8 \\ 8 & 24 \end{bmatrix} \right]^{-1} = \begin{bmatrix} 13.5 & 3 \\ 3 & 8 \end{bmatrix}^{-1}$
	5	½ A ½ B	$\left[\begin{bmatrix} 22.5 & 5 \\ 5 & 14 \end{bmatrix} - ¼ \begin{bmatrix} 36 & 8 \\ 8 & 24 \end{bmatrix} - ¼ \begin{bmatrix} 9 & 2 \\ 2 & 4 \end{bmatrix} \right]^{-1} =$ $\begin{bmatrix} 11.25 & 2.5 \\ 2.5 & 7 \end{bmatrix}^{-1}$
	6	¾ A ¼ B	$\left[\begin{bmatrix} 30.25 & 6.75 \\ 6.75 & 19.75 \end{bmatrix} - ¼ \begin{bmatrix} 36 & 8 \\ 8 & 24 \end{bmatrix} - ¼ \begin{bmatrix} 22.5 & 5 \\ 5 & 14 \end{bmatrix} \right]^{-1}$ $= \begin{bmatrix} 15.625 & 3.5 \\ 3.5 & 10.25 \end{bmatrix}^{-1}$

The lower-triangular matrix P is:

$$
P = \begin{bmatrix}
0 & & & | & & & \\
0 & 0 & & | & & & \\
0 & 1 & 0 & | & & & \\
- & - & - & | & - & - & - \\
1 & 0 & 0 & | & 0 & & \\
1 & 1 & 0 & | & 0 & 0 & \\
1 & 0 & 1 & | & 0 & 0 & 0
\end{bmatrix}
$$

The inverse of the block-diagonal matrix D_a is:

$$D_a^{-1} = \{d_{aii}^{-1}\}$$

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:

$$
G_a^{-1} = \left[
\begin{array}{ccc|ccc}
g_a^{11} & g_a^{12} & g_a^{13} & g_a^{14} & g_a^{15} & g_a^{16} \\
g_a^{12} & g_a^{22} & g_a^{23} & 0 & g_a^{25} & 0 \\
g_a^{13} & g_a^{23} & g_a^{33} & 0 & 0 & g_a^{36} \\
\hline
g_a^{14} & 0 & 0 & g_a^{44} & 0 & 0 \\
g_a^{15} & g_a^{25} & 0 & 0 & g_a^{55} & 0 \\
g_a^{16} & 0 & g_a^{36} & 0 & 0 & g_a^{66}
\end{array}
\right]
\begin{array}{l}
\\
\text{parents} \\
\\
\\
\\
\text{nonparents} \\
\end{array}
$$

$$\downarrow \qquad\qquad \downarrow$$

parents   non-parents

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

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

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

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

4) Add $\frac{1}{4} d_{aii}^{-1}$ 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 $\mathbf{G_a^{-1}}$ for direct and maternal effects are the same as those for single traits, except that the $\mathbf{d_{aii}^{-1}}$ are $\mathbf{2 \times 2}$ **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 $\mathbf{G_a^{-1}}$ for direct and maternal effects are in effect rules to obtain $\mathbf{G_a^{-1}}$ for multiple traits.**

Thus,

$$g_a^{11} = \begin{bmatrix} 36 & 8 \\ 8 & 24 \end{bmatrix}^{-1} + \frac{1}{4}\begin{bmatrix} 13.5 & 3 \\ 3 & 8 \end{bmatrix}^{-1} + \frac{1}{4}\begin{bmatrix} 11.25 & 2.5 \\ 2.5 & 12.75 \end{bmatrix}^{-1} + \frac{1}{4}\begin{bmatrix} 15.625 & 3.5 \\ 3.5 & 10.25 \end{bmatrix}^{-1}$$

$$g_a^{12} = \frac{1}{4}\begin{bmatrix} 11.25 & 2.5 \\ 2.5 & 12.75 \end{bmatrix}^{-1}$$

$$g_a^{13} = \frac{1}{4}\begin{bmatrix} 15.625 & 3.5 \\ 3.5 & 10.25 \end{bmatrix}^{-1}$$

$$g_a^{14} = -\frac{1}{2}\begin{bmatrix} 13.5 & 3 \\ 3 & 8 \end{bmatrix}^{-1}$$

$$g_a^{15} = -\frac{1}{2}\begin{bmatrix} 11.25 & 2.5 \\ 2.5 & 12.75 \end{bmatrix}^{-1}$$

$$g_a^{16} = -\frac{1}{2}\begin{bmatrix} 15.625 & 3.5 \\ 3.5 & 10.25 \end{bmatrix}^{-1}$$

$$g_a^{22} = \begin{bmatrix} 9 & 2 \\ 2 & 4 \end{bmatrix}^{-1} + \frac{1}{4}\begin{bmatrix} 20.25 & 4.5 \\ 4.5 & 13 \end{bmatrix}^{-1} + \frac{1}{4}\begin{bmatrix} 11.25 & 2.5 \\ 2.5 & 12.75 \end{bmatrix}^{-1}$$

$$g_a^{23} = -\frac{1}{2}\begin{bmatrix} 20.25 & 4.5 \\ 4.5 & 13 \end{bmatrix}^{-1}$$

$$g_a{}^{25} = -\frac{1}{2}\begin{bmatrix} 11.25 & 2.5 \\ 2.5 & 12.75 \end{bmatrix}^{-1}$$

$$g_a{}^{33} = \begin{bmatrix} 20.25 & 4.5 \\ 4.5 & 13 \end{bmatrix}^{-1} + \frac{1}{4}\begin{bmatrix} 11.25 & 2.5 \\ 2.5 & 12.75 \end{bmatrix}^{-1}$$

$$g_a{}^{36} = -\frac{1}{2}\begin{bmatrix} 15.625 & 3.5 \\ 3.5 & 10.25 \end{bmatrix}^{-1}$$

$$g_a{}^{44} = \begin{bmatrix} 13.5 & 3 \\ 3 & 8 \end{bmatrix}^{-1}$$

$$g_a{}^{55} = \begin{bmatrix} 11.25 & 2.5 \\ 2.5 & 12.75 \end{bmatrix}^{-1}$$

$$g_a{}^{66} = \begin{bmatrix} 15.625 & 3.5 \\ 3.5 & 10.25 \end{bmatrix}^{-1}$$

The **inverse of the direct and maternal multibreed additive genetic covariance matrix** is obtained by substituting submatrices $\{g_a{}^{ij}\}$, **i, j = 1, …, 6,** in matrix $\mathbf{G_a^{-1}}$.

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:

			Animal
	Number	**Breed Group**	**Direct-Maternal Multibreed Nonadditive Genetic Covariance Matrix**
Parents	1	A	$\begin{bmatrix} 16 & 6 \\ 6 & 12 \end{bmatrix}$
	2	B	$\begin{bmatrix} 16 & 6 \\ 6 & 12 \end{bmatrix}$
	3	½ A ½ B	$\begin{bmatrix} 16 & 6 \\ 6 & 12 \end{bmatrix}$
Non-parents	4	½ A ½ B	$\begin{bmatrix} 16 & 6 \\ 6 & 12 \end{bmatrix}$
	5	½ A ½ B	$\begin{bmatrix} 16 & 6 \\ 6 & 12 \end{bmatrix}$
	6	¾ A ¼ B	$\begin{bmatrix} 16 & 6 \\ 6 & 12 \end{bmatrix}$

Inverse of the Direct-Maternal Multibreed Nonadditive Genetic Covariance Matrix

Direct-maternal covariance matrices among sire × breed group of dam and dam × 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 × breed group of dam interaction and dam × breed group of sire interaction effects, G_n^{-1}, is:

$$G_n^{-1} \quad = \quad \{g_n^{ij}\}$$

$$= \{\textstyle\sum_{k=1}^{K} t_{ik} * d_{nk}^{-1} * t_{kj}\}$$

where **K** is the number of animals in the pedigree, t_{ik} are elements of **T' = (I − ½ P′)**, d_{nk}^{-1} are $2 \times$

2 direct-maternal submatrices of block-diagonal matrix D_n^{-1}, and t_{kj} are elements of **T = (I − ½ P)**,

and

$\quad$ **I** $\quad$ = $\quad$ identity matrix,

$\quad$ **P** $\quad$ = $\quad$ matrix that relates animals to their sires and dams; each row of P contains up to 2

$\qquad\qquad\qquad$ nonzero elements: a 1 for the sire and a 1 for the dam of an animal,

$\quad$ D_n^{-1} $\quad$ = inverse of block-diagonal matrix of residual direct and maternal nonadditive genetic

$\qquad\qquad\qquad$ 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:

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

because V_{nAB} is the same for all sire $\times$ 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 δ_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:

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

The diagonal elements of the D_n^{-1} matrix are:

			Animal
	Number	**Breed Group**	$(d_{nii})^{-1} * V_{nAB}^{-1}$
Parents	1	A	$[(1)]^{-1} * \begin{bmatrix} 16 & 6 \\ 6 & 12 \end{bmatrix}^{-1} = \begin{bmatrix} 16 & 6 \\ 6 & 12 \end{bmatrix}^{-1}$
	2	B	$[(1)]^{-1} * \begin{bmatrix} 16 & 6 \\ 6 & 12 \end{bmatrix}^{-1} = \begin{bmatrix} 16 & 6 \\ 6 & 12 \end{bmatrix}^{-1}$
	3	½ A ½ B	$[(1-¼)]^{-1} * \begin{bmatrix} 16 & 6 \\ 6 & 12 \end{bmatrix}^{-1} = \begin{bmatrix} 12 & 4.5 \\ 4.5 & 9 \end{bmatrix}^{-1}$
Non-parents	4	½ A ½ B	$[(1-¼)]^{-1} * \begin{bmatrix} 16 & 6 \\ 6 & 12 \end{bmatrix}^{-1} = \begin{bmatrix} 12 & 4.5 \\ 4.5 & 9 \end{bmatrix}^{-1}$
	5	½ A ½ B	$[(1-¼-¼)]^{-1} * \begin{bmatrix} 16 & 6 \\ 6 & 12 \end{bmatrix}^{-1} = \begin{bmatrix} 8 & 3 \\ 3 & 6 \end{bmatrix}^{-1}$
	6	¾ A ¼ B	$[(1-¼-¼)]^{-1} * \begin{bmatrix} 16 & 6 \\ 6 & 12 \end{bmatrix}^{-1} = \begin{bmatrix} 8 & 3 \\ 3 & 6 \end{bmatrix}^{-1}$

The P matrix is:

$$
P = \begin{bmatrix}
0 & & & | & & & \\
0 & 0 & & | & & & \\
0 & 1 & 0 & | & & & \\
- & - & - & | & - & - & - \\
1 & 0 & 0 & | & 0 & & \\
1 & 1 & 0 & | & 0 & 0 & \\
1 & 0 & 1 & | & 0 & 0 & 0
\end{bmatrix}
$$

The inverse of the block-diagonal matrix D_n is:

$$
D_n^{-1} = \{d_{nii}^{-1}\}
$$

where

$$
d_{n11}^{-1} = \begin{bmatrix} 16 & 6 \\ 6 & 12 \end{bmatrix}^{-1}
$$

$$d_{n22}^{-1} = \begin{bmatrix} 16 & 6 \\ 6 & 12 \end{bmatrix}^{-1}$$

$$d_{n33}^{-1} = \begin{bmatrix} 12 & 4.5 \\ 4.5 & 9 \end{bmatrix}^{-1}$$

$$d_{n44}^{-1} = \begin{bmatrix} 12 & 4.5 \\ 4.5 & 9 \end{bmatrix}^{-1}$$

$$d_{n55}^{-1} = \begin{bmatrix} 8 & 3 \\ 3 & 6 \end{bmatrix}^{-1}$$

$$d_{n66}^{-1} = \begin{bmatrix} 8 & 3 \\ 3 & 6 \end{bmatrix}^{-1}$$

The inverse of the direct-maternal multibreed nonadditive genetic covariance matrix is :

$$G_n^{-1} = (D_n^{-1} - \tfrac{1}{2} D_n^{-1} P - \tfrac{1}{2} P' D_n^{-1} + \tfrac{1}{4} P' D_n^{-1} P) * V_{nAB}^{-1}$$

$$G_n^{-1} = \left[\begin{array}{ccc|ccc}
g_n^{11} & g_n^{12} & g_n^{13} & g_n^{14} & g_n^{15} & g_n^{16} \\
g_n^{12} & g_n^{22} & g_n^{23} & 0 & g_n^{25} & 0 \\
g_n^{13} & g_n^{23} & g_n^{33} & 0 & 0 & g_n^{36} \\
\hline
g_n^{14} & 0 & 0 & g_n^{44} & 0 & 0 \\
g_n^{15} & g_n^{25} & 0 & 0 & g_n^{55} & 0 \\
g_n^{16} & 0 & g_n^{36} & 0 & 0 & g_n^{66}
\end{array}\right] \begin{array}{l} \\ \text{parents} \\ \\ \\ \\ \text{nonparents} \\ \end{array}$$

parents   non-parents

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

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

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

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

4) Add $\tfrac{1}{4} d_{nii}^{-1}$ 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}^{-1} are 2×2 submatrices of direct and maternal interbreed nonadditive genetic variances and covariances.

Thus,

$$g_n^{11} = \begin{bmatrix} 16 & 6 \\ 6 & 12 \end{bmatrix}^{-1} + \tfrac{1}{4}\begin{bmatrix} 12 & 4.5 \\ 4.5 & 9 \end{bmatrix}^{-1} + \tfrac{1}{4}\begin{bmatrix} 8 & 3 \\ 3 & 6 \end{bmatrix}^{-1} + \tfrac{1}{4}\begin{bmatrix} 8 & 3 \\ 3 & 6 \end{bmatrix}^{-1}$$

$$g_n^{12} = \tfrac{1}{4}\begin{bmatrix} 8 & 3 \\ 3 & 6 \end{bmatrix}^{-1}$$

$$g_n^{13} = \tfrac{1}{4}\begin{bmatrix} 8 & 3 \\ 3 & 6 \end{bmatrix}^{-1}$$

$$g_n^{14} = -\tfrac{1}{2}\begin{bmatrix} 12 & 4.5 \\ 4.5 & 9 \end{bmatrix}^{-1}$$

$$g_n^{15} = -\tfrac{1}{2}\begin{bmatrix} 8 & 3 \\ 3 & 6 \end{bmatrix}^{-1}$$

$$g_n^{16} = -\tfrac{1}{2}\begin{bmatrix} 8 & 3 \\ 3 & 6 \end{bmatrix}^{-1}$$

$$g_n^{22} = \begin{bmatrix} 16 & 6 \\ 6 & 12 \end{bmatrix}^{-1} + \tfrac{1}{4}\begin{bmatrix} 12 & 4.5 \\ 4.5 & 9 \end{bmatrix}^{-1} + \tfrac{1}{4}\begin{bmatrix} 8 & 3 \\ 3 & 6 \end{bmatrix}^{-1}$$

$$g_n^{23} = -\tfrac{1}{2}\begin{bmatrix} 12 & 4.5 \\ 4.5 & 9 \end{bmatrix}^{-1}$$

$$g_n^{25} = -\tfrac{1}{2}\begin{bmatrix} 8 & 3 \\ 3 & 6 \end{bmatrix}^{-1}$$

$$g_n^{33} = \begin{bmatrix} 12 & 4.5 \\ 4.5 & 9 \end{bmatrix}^{-1} + \tfrac{1}{4}\begin{bmatrix} 8 & 3 \\ 3 & 6 \end{bmatrix}^{-1}$$

$$g_n^{36} = -\tfrac{1}{2}\begin{bmatrix} 8 & 3 \\ 3 & 6 \end{bmatrix}^{-1}$$

$$g_n^{44} = \begin{bmatrix} 12 & 4.5 \\ 4.5 & 9 \end{bmatrix}^{-1}$$

$$g_n^{55} = \begin{bmatrix} 8 & 3 \\ 3 & 6 \end{bmatrix}^{-1}$$

$$g_n^{66} = \begin{bmatrix} 8 & 3 \\ 3 & 6 \end{bmatrix}^{-1}$$

The **inverse of the direct and maternal multibreed nonadditive genetic covariance matrix** is obtained by substituting submatrices $\{g_n^{ij}\}$, $i, j = 1, \ldots, 6$, 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:

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

where e = environmental, t = trait, superscripts i = individual, s = sire, and d = dam, subscripts b and b′ represent two breeds, and

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

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

		Animal	
	Number	**Breed Group**	**Multibreed Environmental Variance**
Parents	1	A	49
	2	B	16
	3	½ A ½ B	½ (49) + ½ (16) = 32.5
Non-parents	4	½ A ½ B	½ (49) + ½ (16) = 32.5
	5	½ A ½ B	½ (49) + ½ (16) = 32.5
	6	¾ A ¼ B	¾ (49) + ¼ (16) + [(1)(0) + (½)(½)](25) = 47.0

The left hand side of the **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 **MME_DMMAM** for Example 1 are:

Effect	RHS
Mean	52.19
$Breed_{Ad}$	22.91
$Breed_{Am}$	8.94
$Breed_{Bd}$	29.28
$Breed_{Bm}$	43.25
$Heterosis_{ABd}$	27.93
$Heterosis_{ABm}$	6.09
Sex_M	20.97
Sex_F	31.22
a_{ad1}	5.9
a_{am1}	0
a_{ad2}	15.31
a_{am2}	16.86
a_{ad3}	7.88
a_{am3}	6.09
a_{ad4}	8.03
a_{am4}	0
a_{ad5}	8.98

a_{am5}	0
a_{ad6}	6.09
a_{am6}	0
a_{nd1}	20.06
a_{nm1}	0
a_{nd2}	16.86
a_{nm2}	0
a_{nd3}	3.04
a_{nm3}	6.09
a_{nd4}	0
a_{nm4}	0
a_{nd5}	0
a_{nm5}	0
a_{nd6}	0
a_{nm6}	0

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.,

sol = ginvlhs * 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 **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_DMMAM**) are:

Effect	SOL	SESOL
Mean°	106.72	2.09
Breed$_{Ad}$°	58	3.92
Breed$_{Am}$°	53.62	4.12
Breed$_{Bd}$°	48.73	3.56
Breed$_{Bm}$°	53.1	3.22
Heterosis$_{ABd}$°	8.75	5.28
Heterosis$_{ABm}$°	-3.89	11.29
Sex$_{M}$°	70.05	4.74
Sex$_{F}$°	36.67	4.48
$\hat{a}_{ad1}$	0.61	5.81
$\hat{a}_{am1}$	0.14	4.89
$\hat{a}_{ad2}$	-0.22	2.95
$\hat{a}_{am2}$	-0.17	1.96
$\hat{a}_{ad3}$	-0.79	4.33
$\hat{a}_{am3}$	-0.24	3.7
$\hat{a}_{ad4}$	0.76	4.37
$\hat{a}_{am4}$	0.17	3.72
$\hat{a}_{ad5}$	0.19	4.72
$\hat{a}_{am5}$	-0.02	3.74

$\hat{a}_{ad6}$	-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

Direct and Maternal Additive Multibreed Genetic Predictions

The vector of **DMAMBV** for animal i, computed as deviations from breed B (chosen as the genetic

base), is:

$$DMAMBV_i \quad = \quad \hat{u}_{ai} \quad = \quad Prob_{Aanim\,i}*(Breed_A° - Breed_B°) + \hat{a}_{ai}$$

where

$Prob_{Aanim\,i}$ = expected fraction of breed A in animal i,

$Breed_A°$ = vector of generalized least squares solutions for direct and maternal effects for

breed A,

$Breed_B°$ = vector of generalized least squares solutions for direct and maternal effects for breed B,

$â_{ai}$ = 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:

$$VEP(DMAMBV) = var(û_a - u_a) = K_a*(ginvlhs)*K_a'$$

where

K_a = $n_{anim} \times n_{eq}$ matrix specifying the factors multiplying vector **DMAMBV**, where n_{anim} = number of animals, and n_{eq} = number of equations, and

ginvlhs = $n_{eq} \times n_{eq}$ 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 VEP(**DMAMBV**) matrix.

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

Animal	Effect	$Prob_{Ai}$	$Breed_A°$ - $Breed_B°$	$â_{ai}$	DMAMBV	SEP DMAMBV
1	Dir	1	9.27	0.61	9.88	7.69
1	Mat	1	0.52	0.14	0.66	8.32
2	Dir	0	9.27	-0.22	-0.22	2.95
2	Mat	0	0.52	-0.17	-0.17	1.96
3	Dir	0.5	9.27	-0.79	3.84	5.07

3	Mat	0.5	0.52	-0.24	0.03	5.17
4	Dir	0.5	9.27	0.76	5.4	4.57
4	Mat	0.5	0.52	0.17	0.43	5.01
5	Dir	0.5	9.27	0.19	4.83	6.04
5	Mat	0.5	0.52	-0.02	0.25	5.3
6	Dir	0.75	9.27	-0.09	6.86	6.7
6	Mat	0.75	0.52	-0.05	0.34	6.82

Direct and Maternal Nonadditive Multibreed Genetic Predictions

The vector of **DMNMBV** for animal i, computed assuming that males are mated to ½ A ½ B

females, and vice versa, is:

$$\text{DMNMBV}_i \quad = \quad \hat{u}_{ni} \quad = \quad (\text{Prob}_{\text{Aanim i}} * \text{Prob}_{\text{Bmate}} + \text{Prob}_{\text{Banim i}} * \text{Prob}_{\text{Amate}})(\text{Heterosis}_{\text{AB}}{}^\circ + \hat{a}_{ni})$$

where

$\text{Prob}_{\text{Aanim i}}$ =   expected fraction of breed A in animal i,

$\text{Prob}_{\text{Banim i}}$ =   expected fraction of breed B in animal i,

$\text{Prob}_{\text{Amate}}$ =   expected fraction of breed A in the mate of animal i,

$\text{Prob}_{\text{Bmate}}$ =   expected fraction of breed B in the mate of animal i,

$\text{Heterosis}_{\text{AB}}{}^\circ$ =   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,

$\hat{a}_{ni}$ =   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 **DMNMBV** is:

$$\text{VEP}(\textbf{DMNMBV}) = \quad \text{var}(\hat{u}_n - u_n) \quad = \quad K_n * (\text{ginvlhs}) * K_n{}'$$

where

K_n = $n_{anim} \times n_{eq}$ matrix specifying the factors multiplying vector **DMNMBV**, where

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

ginvlhs   = $n_{eq} \times n_{eq}$ 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 **DMNMBV** are computed as the

square roots of the diagonal elements of the VEP(**DMNMBV**) matrix.

The vector of **DMNMBV** and their SEP for the 6 animals in **DMMAM** Example 1 are:

Animal	Effect	$Prob_{Ai}*Prob_{Bmate} +$ $Prob_{Bi}*Prob_{Amate}$	$Heterosis_{AB}°$	$\hat{a}_{ni}$	DMNMBV	SEP DMNMBV
1	Dir	1*0.5 + 0*0.5	8.75	0.54	4.64	2.54
1	Mat	1*0.5 + 0*0.5	-3.89	0.2	-1.84	5.87
2	Dir	0*0.5 + 1*0.5	8.75	-0.54	4.1	2.57
2	Mat	0*0.5 + 1*0.5	-3.89	-0.2	-2.05	5.74
3	Dir	0.5*0.5 + 0.5*0.5	8.75	-0.27	4.24	2.98
3	Mat	0.5*0.5 + 0.5*0.5	-3.89	-0.1	-1.99	5.32
4	Dir	0.5*0.5 + 0.5*0.5	8.75	0.27	4.51	2.97
4	Mat	0.5*0.5 + 0.5*0.5	-3.89	0.1	-1.89	5.89
5	Dir	0.5*0.5 + 0.5*0.5	8.75	0	4.37	2.64
5	Mat	0.5*0.5 + 0.5*0.5	-3.89	0	-1.94	5.81
6	Dir	0.75*0.5 + 0.25*0.5	8.75	0.14	4.44	2.81
6	Mat	0.75*0.5 + 0.25*0.5	-3.89	0.05	-1.92	5.6

Direct and Maternal Total Multibreed Genetic Predictions

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

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

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

$$\text{VEP}(\textbf{DMTMBV}) = \quad \text{var}(\hat{u}_t - u_t) = \quad K_t*(\text{ginvlhs})*K_t{'}$$

where

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

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

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

Matrix K_t 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 **DMTMBV** are computed as the square roots of the diagonal elements of the VEP(**DMTMBV**) matrix.

The vector of **DMTMBV** and their SEP for the 6 animals in **DMMAM** Example 1 are:

Animal	Effect	DMAMBV	DMNMBV	DMTMBV	SEP DMTMBV
1	Dir	9.88	4.64	14.52	8.8
1	Mat	0.66	-1.84	-1.18	10.35
2	Dir	-0.22	4.1	3.88	4.1
2	Mat	-0.17	-2.05	-2.21	6.09
3	Dir	3.84	4.24	8.08	5.96
3	Mat	0.03	-1.99	-1.97	6.36

4	Dir	5.4	4.51	9.9	5.56
4	Mat	0.43	-1.89	-1.46	7.76
5	Dir	4.83	4.37	9.2	6.97
5	Mat	0.25	-1.94	-1.7	8.06
6	Dir	6.86	4.44	11.3	7.79
6	Mat	0.34	-1.92	-1.57	8.29

References

Henderson, C. R. 1976. A simple method for computing the inverse of a large numerator relationship matrix used in prediction of breeding values. Biometrics 32:69-83.

Elzo, M. A. 1990a. Recursive procedures to compute the inverse of the multiple trait additive genetic covariance matrix in inbred and noninbred multibreed populations. J. Anim. Sci. 68:1215-1228.

Elzo, M. A. 1990b. Covariances among sire $\times$ breed group of dam interaction effects in multibreed sire evaluation procedures. J. Anim. Sci. 68:4079-4099.

Elzo, M. A. 1994. Restricted maximum likelihood estimation of additive and nonadditive genetic variances and covariances in multibreed populations. J. Anim. Sci. 72:3055-3065.

Elzo, M. A. 1996. Animal Breeding Notes. University of Florida, Gainesville, Florida, USA.

Elzo, M. A. 2006. Animal Breeding Notes. Breeding value of animal for a single trait in a multibreed population. http://www.animal.ufl.edu/elzo/Publications/Animal%20Breeding%20Notes/Multibreed/MABN_14M/MABN_14M_Part%202_2007_a.pdf. Accessed December 16, 2007.

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

16.

Quaas, R. L. 1976. Computing the diagonal elements and inverse of a large numerator relationship matrix. Biometrics 32:949-953.