ANIMAL BREEDING NOTES

CHAPTER 21M

MULTIPLE TRAIT MULTIBREED ANIMAL MODEL

Multiple Trait Multibreed Animal Model (MTMAM)

Objective: to predict multiple-trait additive genetic effects (**MTAMBV**), nonadditive genetic effects (**MTNMBV**), and total genetic effects (**MTTMBV**) in a multibreed population, based on animals' own records and records from their relatives.

Assumptions

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

2) Animals have 1 or more records from several traits;

3) 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;

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

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

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

7) 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 **MTAMBV,** the relationship matrix was complete.

The **MTMAM** is:

$$y = Xb + Z_aQ_a\,g_a + Z_nQ_n\,g_n + Z_a\,a_a + Z_n\,a_n + e$$

$$E[y] = Xb + Z_aQ_a\,g_a + Z_nQ_n\,g_n$$

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

$$\Rightarrow \quad \text{var}(y) = Z_aG_aZ_a{}' + Z_nG_nZ_n{}' + R,$$

where

y = vector of animal records ordered by trait within animal (e.g., birth weight, weaning weight),

b = vector of unknown fixed effects (e.g., contemporary groups, sex of calf, age of dam) ordered by trait within effect,

g_a = vector of unknown additive group genetic effects (e.g., breed, breed $\times$ year of birth) ordered by trait within genetic group,

g_n = vector of unknown nonadditive group genetic effects (e.g., heterosis at 1 locus, heterosis at 2 loci) ordered by trait within genetic group,

a_a = vector of unknown random additive genetic effects (**MTAMBV**) ordered by trait within additive genetic effect,

a_n = vector of unknown random nonadditive genetic effects (**MTNMBV**) ordered by trait within nonadditive genetic effect,

e = vector of unknown random residual effects ordered by trait within animal,

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 additive genetic effects to additive genetic

groups in vector g_a,

Q_n = known incidence matrix relating random nonadditive genetic effects to nonadditive

genetic groups in vector g_n,

G_a = $\{G_{ij}\}$, where G_{ij} = matrix of multiple trait multibreed additive genetic covariances

between animals i and j, ordered by traits within animal,

G_n = $\text{diag}\{A_m * V_{0nm}, m = 1,..., N_m\}$, 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 multiple trait

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

multiple trait 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 multiple trait variances and covariances due to intralocus

interbreed interaction effects,

R = $\text{diag}\{V_{ei}\}$, where $V_{ei} = n_t \times n_t$ matrix of multiple trait multibreed residual variances and

covariances for animal i, where t = number of traits. Residual covariance matrices 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 $R = I * V_e$, where $V_e = n_t \times n_t$ matrix of multibreed residual variances and

covariances common to all animals in a multibreed population.

The mixed model equations (MME) for the **MTMAM** 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 MTMAM for a Non-inbred Multibreed Population

Animal	Breed Compsn	Sex	Birth weight (kg)	Weaning weight (kg)	Sire	Breed Compsn	Dam	Breed Compsn
1	A	M	33	289	0	A	0	A
2	B	F	29	245	0	B	0	B
3	½ A ½ B	F	32	256	0	A	2	B
4	½ A ½ B	F	30	261	1	A	0	B
5	½ A ½ B	M	38	292	1	A	2	B
6	¾ A ¼ B	M	35	286	1	A	3	½ A ½ B

Assumptions for the Example

1) **Matrices of multiple trait additive genetic variances and covariances:**

Intrabreed multiple trait additive genetic covariance matrix for breed A:

$$V_{aAA} = \begin{bmatrix} 12 & 10 \\ 10 & 36 \end{bmatrix} kg^2$$

Intrabreed multiple trait additive genetic covariance matrix for breed B:

$$V_{aBB} = \begin{bmatrix} 9 & 12 \\ 12 & 44 \end{bmatrix} kg^2$$

Interbreed multiple trait additive genetic covariance matrix for combination of breeds AB:

$$V_{aAB} = \begin{bmatrix} 4 & 1 \\ 1 & 22 \end{bmatrix} kg^2$$

2) **Matrices of multiple trait 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 multiple trait nonadditive genetic covariance matrix for breed A:

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

Intrabreed multiple trait nonadditive genetic covariance matrix for breed B:

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

Interbreed multiple trait additive genetic covariance matrix for combination of breeds AB:

$$V_{nAB} = \begin{bmatrix} 8 & 6 \\ 6 & 16 \end{bmatrix} kg^2$$

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

$$V_{nAB} = \begin{bmatrix} 8 & 6 \\ 6 & 16 \end{bmatrix} kg^2$$

will be needed.

3) **Matrices of multiple trait environmental variances and covariances:**

Environmental multiple trait covariance matrix for breed A:

$$V_{eAA} = \begin{bmatrix} 12 & 10 \\ 10 & 49 \end{bmatrix} kg^2$$

Environmental multiple trait covariance for breed B:

$$V_{eBB} = \begin{bmatrix} 8 & 6 \\ 6 & 16 \end{bmatrix} kg^2$$

Environmental multiple trait covariance for combination of breeds AB:

$$V_{eAB} = \begin{bmatrix} 16 & 14 \\ 14 & 25 \end{bmatrix} kg^2$$

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

Multiple Trait Multibreed Animal Model for the Example

$$\begin{Bmatrix} BW \\ WW \end{Bmatrix}_i = \begin{Bmatrix} Mean_{BW} \\ Mean_{WW} \end{Bmatrix}_i + \begin{Bmatrix} BreedReg_{BW} \\ BreedReg_{WW} \end{Bmatrix}_i + \begin{Bmatrix} DirectHet_{BW} \\ DirectHet_{WW} \end{Bmatrix}_i + \begin{Bmatrix} Sex_{BW} \\ Sex_{WW} \end{Bmatrix}_i$$

$$+ \begin{Bmatrix} AnimDirectAdd_{BW} \\ AnimDirectAdd_{WW} \end{Bmatrix}_i + \begin{Bmatrix} AnimDirectNonAdd_{BW} \\ AnimDirectNonAdd_{WW} \end{Bmatrix}_i$$

$$+ \begin{Bmatrix} Residual_{BW} \\ Residual_{WW} \end{Bmatrix}_i$$

$$E\begin{Bmatrix} BW \\ WW \end{Bmatrix}_i = \begin{Bmatrix} Mean_{BW} \\ Mean_{WW} \end{Bmatrix}_i + \begin{Bmatrix} BreedReg_{BW} \\ BreedReg_{WW} \end{Bmatrix}_i + \begin{Bmatrix} DirectHet_{BW} \\ DirectHet_{WW} \end{Bmatrix}_i + \begin{Bmatrix} Sex_{BW} \\ Sex_{WW} \end{Bmatrix}_i$$

$$Var\begin{Bmatrix} BW \\ WW \end{Bmatrix}_i = Var\begin{Bmatrix} AnimDirectAdd_{BW} \\ AnimDirectAdd_{WW} \end{Bmatrix}_i + Var\begin{Bmatrix} AnimDirectNonAdd_{BW} \\ AnimDirectNonAdd_{WW} \end{Bmatrix}_i$$

$$+ Var\begin{Bmatrix} Residual_{BW} \\ Residual_{WW} \end{Bmatrix}_i$$

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

$$
\begin{bmatrix} 33 \\ 289 \\ 29 \\ 245 \\ 32 \\ 256 \\ 30 \\ 261 \\ 38 \\ 292 \\ 35 \\ 286 \end{bmatrix}
=
\begin{bmatrix}
1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\
0 & 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\
1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\
0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 1 \\
1 & 0 & 1/2 & 0 & 1/2 & 0 & 1 & 0 & 0 & 0 & 1 & 0 \\
0 & 1 & 0 & 1/2 & 0 & 1/2 & 0 & 1 & 0 & 0 & 0 & 1 \\
1 & 0 & 1/2 & & 1/2 & 0 & 1 & 0 & 0 & 0 & 1 & 0 \\
0 & 1 & 0 & 1/2 & 0 & 1/2 & 0 & 1 & 0 & 0 & 0 & 1 \\
1 & 0 & 1/2 & & 1/2 & 0 & 1 & 0 & 1 & 0 & 0 & 0 \\
0 & 1 & 0 & 1/2 & 0 & 1/2 & 0 & 1 & 0 & 1 & 0 & 0 \\
1 & 0 & 3/4 & & 1/4 & 0 & 1/2 & 0 & 1 & 0 & 0 & 0 \\
0 & 1 & 0 & 3/4 & 0 & 1/4 & 0 & 1/2 & 0 & 1 & 0 & 0
\end{bmatrix}
\begin{bmatrix}
\text{mean}_{bw} \\
\text{mean}_{ww} \\
\text{breed}_{Abw} \\
\text{breed}_{Aww} \\
\text{breed}_{Bbw} \\
\text{breed}_{Bww} \\
\text{heterosis}_{ABbw} \\
\text{heterosis}_{ABww} \\
\text{sex}_{Mbw} \\
\text{sex}_{Mww} \\
\text{sex}_{Fbw} \\
\text{sex}_{Fww}
\end{bmatrix}
$$

$$
+
\begin{bmatrix}
1 & & & & & & & & & & & \\
& 1 & & & & & & & & & & \\
& & 1 & & & & & & & & & \\
& & & 1 & & & & & & & & \\
& & & & 1 & & & & & & & \\
& & & & & 1 & & & & & & \\
& & & & & & 1 & & & & & \\
& & & & & & & 1 & & & & \\
& & & & & & & & 1 & & & \\
& & & & & & & & & 1 & & \\
& & & & & & & & & & 1 & \\
& & & & & & & & & & & 1
\end{bmatrix}
\begin{bmatrix}
\text{animal 1}_{bwad} \\
\text{animal 1}_{wwad} \\
\text{animal 2}_{bwad} \\
\text{animal 2}_{wwad} \\
\text{animal 3}_{bwad} \\
\text{animal 3}_{wwad} \\
\text{animal 4}_{bwad} \\
\text{animal 4}_{wwad} \\
\text{animal 5}_{bwad} \\
\text{animal 5}_{wwad} \\
\text{animal 6}_{bwad} \\
\text{animal 6}_{wwad}
\end{bmatrix}
$$

$$
+ \begin{bmatrix}
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
1/2 & 0 & 0 & 0 & 1/2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 1/2 & 0 & 0 & 0 & 1/2 & 0 & 0 & 0 & 0 & 0 & 0
\end{bmatrix}
\begin{bmatrix}
\text{animal } 1_{bwnd} \\
\text{animal } 1_{wwnd} \\
\text{animal } 2_{bwnd} \\
\text{animal } 2_{wwnd} \\
\text{animal } 3_{bwnd} \\
\text{animal } 3_{wwnd} \\
\text{animal } 4_{bwnd} \\
\text{animal } 4_{wwnd} \\
\text{animal } 5_{bwnd} \\
\text{animal } 5_{wwnd} \\
\text{animal } 6_{bwnd} \\
\text{animal } 6_{wwnd}
\end{bmatrix}
+ \begin{bmatrix}
\text{residual } 1_{bw} \\
\text{residual } 1_{ww} \\
\text{residual } 2_{bw} \\
\text{residual } 2_{ww} \\
\text{residual } 3_{bw} \\
\text{residual } 3_{ww} \\
\text{residual } 4_{bw} \\
\text{residual } 4_{ww} \\
\text{residual } 5_{bw} \\
\text{residuall } 5_{ww} \\
\text{residual } 6_{bw} \\
\text{residual } 6_{ww}
\end{bmatrix}
$$

Matrices of Multiple Trait Multibreed Additive Genetic Variances and Covariances

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

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

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

where a = additive genetic, t = vector of traits, 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 multiple trait intrabreed additive genetic variances and covariances in breed b,

$(V_{at})_{bb'}$ = matrix of multiple trait interbreed additive genetic variances and covariances

in pair of breeds b and b′.

The matrices of multiple trait multibreed additive genetic variances and covariances for the 6

animals in the example are:

	Animal		
	Number	**Breed Group**	**Multiple Trait Multibreed Additive Genetic Covariance Matrix**
Parents	1	A	$\begin{bmatrix} 12 & 10 \\ 10 & 36 \end{bmatrix}$
	2	B	$\begin{bmatrix} 9 & 12 \\ 12 & 44 \end{bmatrix}$
	3	½ A ½ B	$\frac{1}{2}\begin{bmatrix} 12 & 10 \\ 10 & 36 \end{bmatrix} + \frac{1}{2}\begin{bmatrix} 9 & 12 \\ 12 & 44 \end{bmatrix} = \begin{bmatrix} 10.5 & 11 \\ 11 & 40 \end{bmatrix}$
Non-parents	4	½ A ½ B	$\frac{1}{2}\begin{bmatrix} 12 & 10 \\ 10 & 36 \end{bmatrix} + \frac{1}{2}\begin{bmatrix} 9 & 12 \\ 12 & 44 \end{bmatrix} = \begin{bmatrix} 10.5 & 11 \\ 11 & 40 \end{bmatrix}$
	5	½ A ½ B	$\frac{1}{2}\begin{bmatrix} 12 & 10 \\ 10 & 36 \end{bmatrix} + \frac{1}{2}\begin{bmatrix} 9 & 12 \\ 12 & 44 \end{bmatrix} = \begin{bmatrix} 10.5 & 11 \\ 11 & 40 \end{bmatrix}$
	6	¾ A ¼ B	$\frac{3}{4}\begin{bmatrix} 12 & 10 \\ 10 & 36 \end{bmatrix} + \frac{1}{4}\begin{bmatrix} 9 & 12 \\ 12 & 44 \end{bmatrix} + [(1)(0) + $ $(\frac{1}{2})(\frac{1}{2})]\begin{bmatrix} 4 & 1 \\ 1 & 22 \end{bmatrix} = \begin{bmatrix} 12.25 & 10.75 \\ 10.75 & 43.5 \end{bmatrix}$

Inverse of the Multiple Trait Multibreed Additive Genetic Covariance Matrix

The equation for the inverse of the multiple trait covariance matrix of multibreed additive genetic

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

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

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

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 $n_t \times$

n_t multiple trait submatrices of block-diagonal matrix $\mathbf{D_a}^{-1}$, and $\mathbf{t_{kj}}$ are elements of $\mathbf{T} = (\mathbf{I} - \frac{1}{2}\,\mathbf{P})$,

and

$\mathbf{I}$ = identity matrix,

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

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

$\mathbf{D_a}^{-1}$ = inverse of block-diagonal matrix of residual multiple trait additive genetic variances

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

its diagonal submatrices, i.e., $\mathbf{D_a}^{-1} = \{\, \mathbf{d_{aii}}^{-1}\}$.

The $n_t \times n_t$ multiple trait submatrices of block-diagonal matrix $\mathbf{D_a}^{-1}$ 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

$\mathbf{d_{aii}}^{-1}$ 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 $\mathbf{d_{aii}}^{-1}$ 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	$\begin{bmatrix} 12 & 10 \\ 10 & 36 \end{bmatrix}^{-1}$
	2	B	$\begin{bmatrix} 9 & 12 \\ 12 & 44 \end{bmatrix}^{-1}$
	3	½ A ½ B	$\left[\begin{bmatrix} 10.5 & 11 \\ 11 & 40 \end{bmatrix} - ¼\begin{bmatrix} 9 & 12 \\ 12 & 44 \end{bmatrix}\right]^{-1} = \begin{bmatrix} 8.25 & 8 \\ 8 & 29 \end{bmatrix}^{-1}$
Non-parents	4	½ A ½ B	$\left[\begin{bmatrix} 10.5 & 11 \\ 11 & 40 \end{bmatrix} - ¼\begin{bmatrix} 12 & 10 \\ 10 & 36 \end{bmatrix}\right]^{-1} = \begin{bmatrix} 7.5 & 8.5 \\ 8.5 & 31 \end{bmatrix}^{-1}$
	5	½ A ½ B	$\left[\begin{bmatrix} 10.5 & 11 \\ 11 & 40 \end{bmatrix} - ¼\begin{bmatrix} 12 & 10 \\ 10 & 36 \end{bmatrix} - ¼\begin{bmatrix} 9 & 12 \\ 12 & 44 \end{bmatrix}\right]^{-1} =$ $\begin{bmatrix} 5.25 & 5.5 \\ 5.5 & 20 \end{bmatrix}^{-1}$
	6	¾ A ¼ B	$\left[\begin{bmatrix} 12.25 & 10.75 \\ 10.75 & 43.5 \end{bmatrix} - ¼\begin{bmatrix} 12 & 10 \\ 10 & 36 \end{bmatrix} - ¼\begin{bmatrix} 10.5 & 11 \\ 11 & 40 \end{bmatrix}\right]^{-1}$ $= \begin{bmatrix} 6.625 & 5.5 \\ 5.5 & 24.5 \end{bmatrix}^{-1}$

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:

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

where

$$d_{a11}^{-1} = \begin{bmatrix} 12 & 10 \\ 10 & 36 \end{bmatrix}^{-1}$$

$$d_{a22}^{-1} = \begin{bmatrix} 9 & 12 \\ 12 & 44 \end{bmatrix}^{-1}$$

$$d_{a33}^{-1} = \begin{bmatrix} 8.25 & 8 \\ 8 & 29 \end{bmatrix}^{-1}$$

$$d_{a44}^{-1} = \begin{bmatrix} 7.5 & 8.5 \\ 8.5 & 31 \end{bmatrix}^{-1}$$

$$d_{a55}^{-1} = \begin{bmatrix} 5.25 & 5.5 \\ 5.5 & 20 \end{bmatrix}^{-1}$$

$$d_{a66}^{-1} = \begin{bmatrix} 6.625 & 5.5 \\ 5.5 & 24.5 \end{bmatrix}^{-1}$$

The inverse of the multiple trait multibreed additive genetic covariance matrix is:

$$
G_a^{-1} =
\left[
\begin{array}{ccc|ccc}
g_a^{11} & g_a^{12} & g_a^{13} & g_a^{14} & g_a^{15} & g_a^{16} \\
g_a^{12} & g_a^{22} & g_a^{23} & 0 & g_a^{25} & 0 \\
g_a^{13} & g_a^{23} & g_a^{33} & 0 & 0 & g_a^{36} \\
\hline
g_a^{14} & 0 & 0 & g_a^{44} & 0 & 0 \\
g_a^{15} & g_a^{25} & 0 & 0 & g_a^{55} & 0 \\
g_a^{16} & 0 & g_a^{36} & 0 & 0 & g_a^{66}
\end{array}
\right]
\begin{array}{l}
\\[-1.5ex] \text{parents} \\[4ex]
\\[2ex] \text{nonparents} \\
\end{array}
$$

$$
\begin{array}{cc}
\downarrow & \downarrow \\
\text{parents} & \text{non-parents}
\end{array}
$$

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

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

2) Add $-½\, d_{aii}^{-1}$ to $i \times s$ and $s \times i$ if the sire of animal i is identified,

3) Add $-½\, d_{aii}^{-1}$ to $i \times d$ and $d \times i$ if the dam of animal i is identified, and

4) Add $¼\, d_{aii}^{-1}$ 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 multiple traits effects are the same as those for single traits, except that the $\mathbf{d_{aii}}^{-1}$ are $\mathbf{n_t \times n_t}$ **submatrices multiple trait variances and covariances** instead of scalars.

Thus,

$$g_a{}^{11} = \begin{bmatrix} 12 & 10 \\ 10 & 36 \end{bmatrix}^{-1} + ¼ \begin{bmatrix} 7.5 & 8.5 \\ 8.5 & 31 \end{bmatrix}^{-1} + ¼ \begin{bmatrix} 5.25 & 5.5 \\ 5.5 & 20 \end{bmatrix}^{-1} + ¼ \begin{bmatrix} 6.625 & 5.5 \\ 5.5 & 24.5 \end{bmatrix}^{-1}$$

$$g_a{}^{12} = ¼ \begin{bmatrix} 5.25 & 5.5 \\ 5.5 & 20 \end{bmatrix}^{-1}$$

$$g_a{}^{13} = ¼ \begin{bmatrix} 6.625 & 5.5 \\ 5.5 & 24.5 \end{bmatrix}^{-1}$$

$$g_a{}^{14} = -½ \begin{bmatrix} 7.5 & 8.5 \\ 8.5 & 31 \end{bmatrix}^{-1}$$

$$g_a{}^{15} = -½ \begin{bmatrix} 5.25 & 5.5 \\ 5.5 & 20 \end{bmatrix}^{-1}$$

$$g_a{}^{16} = -½ \begin{bmatrix} 6.625 & 5.5 \\ 5.5 & 24.5 \end{bmatrix}^{-1}$$

$$g_a{}^{22} = \begin{bmatrix} 9 & 2 \\ 2 & 4 \end{bmatrix}^{-1} + ¼ \begin{bmatrix} 20.25 & 4.5 \\ 4.5 & 13 \end{bmatrix}^{-1} + ¼ \begin{bmatrix} 5.25 & 5.5 \\ 5.5 & 20 \end{bmatrix}^{-1}$$

$$g_a{}^{23} = -½ \begin{bmatrix} 20.25 & 4.5 \\ 4.5 & 13 \end{bmatrix}^{-1}$$

$$g_a{}^{25} = -½ \begin{bmatrix} 5.25 & 5.5 \\ 5.5 & 20 \end{bmatrix}^{-1}$$

$$g_a{}^{33} = \begin{bmatrix} 20.25 & 4.5 \\ 4.5 & 13 \end{bmatrix}^{-1} + ¼ \begin{bmatrix} 5.25 & 5.5 \\ 5.5 & 20 \end{bmatrix}^{-1}$$

$$g_a^{\ 36} = -\tfrac{1}{2}\begin{bmatrix} 6.625 & 5.5 \\ 5.5 & 24.5 \end{bmatrix}^{-1}$$

$$g_a^{\ 44} = \begin{bmatrix} 7.5 & 8.5 \\ 8.5 & 31 \end{bmatrix}^{-1}$$

$$g_a^{\ 55} = \begin{bmatrix} 5.25 & 5.5 \\ 5.5 & 20 \end{bmatrix}^{-1}$$

$$g_a^{\ 66} = \begin{bmatrix} 6.625 & 5.5 \\ 5.5 & 24.5 \end{bmatrix}^{-1}$$

The **inverse of the multiple trait 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 Multiple Trait Multibreed Nonadditive Genetic Variances and Covariances

Matrices of multiple trait 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 multiple trait 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 multiple trait 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 multiple trait variances and covariances needed for the example is the multiple trait covariance matrix of intralocus interbreed interaction effects, i.e., $V_{nAB} = \begin{bmatrix} 8 & 6 \\ 6 & 16 \end{bmatrix} \text{kg}^2$.

The multiple trait multibreed nonadditive genetic covariance matrices for the 6 animals in the

example is:

	Animal		
	Number	**Breed Group**	**Multiple Trait Multibreed Nonadditive Genetic Covariance Matrix**
Parents	1	A	$\begin{bmatrix} 8 & 6 \\ 6 & 16 \end{bmatrix}$
	2	B	$\begin{bmatrix} 8 & 6 \\ 6 & 16 \end{bmatrix}$
	3	½ A ½ B	$\begin{bmatrix} 8 & 6 \\ 6 & 16 \end{bmatrix}$
Non-parents	4	½ A ½ B	$\begin{bmatrix} 8 & 6 \\ 6 & 16 \end{bmatrix}$
	5	½ A ½ B	$\begin{bmatrix} 8 & 6 \\ 6 & 16 \end{bmatrix}$
	6	¾ A ¼ B	$\begin{bmatrix} 8 & 6 \\ 6 & 16 \end{bmatrix}$

Inverse of the Multiple Trait Multibreed Nonadditive Genetic Covariance Matrix

Multiple trait 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 multiple trait multibreed nonadditive genetic effects due to intralocus interbreed sire × breed group of dam interaction and dam × breed group of sire interaction effects, $\mathbf{G_n^{-1}}$, is:

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

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

where **K** is the number of animals in the pedigree, $\mathbf{t_{ik}}$ are elements of $\mathbf{T'} = (\mathbf{I} - ½\,\mathbf{P'})$, $\mathbf{d_{nk}^{-1}}$ are $n_t \times n_t$ multiple trait submatrices of block-diagonal matrix $\mathbf{D_n^{-1}}$, and $\mathbf{t_{kj}}$ are elements of $\mathbf{T} = (\mathbf{I} - ½\,\mathbf{P})$, and

I = identity matrix,

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

$\mathbf{D_n^{-1}}$ = inverse of block-diagonal matrix of residual multiple trait nonadditive genetic variances and covariances, where $\mathbf{D_n^{-1}} = \{ \mathbf{d_{nii}^{-1}} \}$.

The $n_t \times n_t$ multiple trait submatrices of block-diagonal matrix $\mathbf{D_n^{-1}}$ 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 × 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 $\mathbf{d_{nii}^{-1}}$ 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**	$\mathbf{(d_{nii})^{-1} * V_{nAB}^{-1}}$
Parents	1	A	$[(1)]^{-1} * \begin{bmatrix} 8 & 6 \\ 6 & 16 \end{bmatrix}^{-1} = \begin{bmatrix} 8 & 6 \\ 6 & 16 \end{bmatrix}^{-1}$
	2	B	$[(1)]^{-1} * \begin{bmatrix} 8 & 6 \\ 6 & 16 \end{bmatrix}^{-1} = \begin{bmatrix} 8 & 6 \\ 6 & 16 \end{bmatrix}^{-1}$

	3	½ A ½ B	$[(1- ¼)]^{-1} * \begin{bmatrix} 8 & 6 \\ 6 & 16 \end{bmatrix}^{-1} = \begin{bmatrix} 6 & 4.5 \\ 4.5 & 12 \end{bmatrix}^{-1}$
Non-parents	4	½ A ½ B	$[(1- ¼)]^{-1} * \begin{bmatrix} 8 & 6 \\ 6 & 16 \end{bmatrix}^{-1} = \begin{bmatrix} 6 & 4.5 \\ 4.5 & 12 \end{bmatrix}^{-1}$
	5	½ A ½ B	$[(1- ¼ - ¼)]^{-1} * \begin{bmatrix} 8 & 6 \\ 6 & 16 \end{bmatrix}^{-1} = \begin{bmatrix} 4 & 3 \\ 3 & 8 \end{bmatrix}^{-1}$
	6	¾ A ¼ B	$[(1- ¼ - ¼)]^{-1} * \begin{bmatrix} 8 & 6 \\ 6 & 16 \end{bmatrix}^{-1} = \begin{bmatrix} 4 & 3 \\ 3 & 8 \end{bmatrix}^{-1}$

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:

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

where

$$
d_{n11}^{-1} = \begin{bmatrix} 8 & 6 \\ 6 & 16 \end{bmatrix}^{-1}
$$

$$
d_{n22}^{-1} = \begin{bmatrix} 8 & 6 \\ 6 & 16 \end{bmatrix}^{-1}
$$

$$
d_{n33}^{-1} = \begin{bmatrix} 6 & 4.5 \\ 4.5 & 12 \end{bmatrix}^{-1}
$$

$$
d_{n44}^{-1} = \begin{bmatrix} 6 & 4.5 \\ 4.5 & 12 \end{bmatrix}^{-1}
$$

$$d_{n55}^{-1} = \begin{bmatrix} 4 & 3 \\ 3 & 8 \end{bmatrix}^{-1}$$

$$d_{n66}^{-1} = \begin{bmatrix} 4 & 3 \\ 3 & 8 \end{bmatrix}^{-1}$$

The inverse of the multiple trait multibreed nonadditive genetic covariance matrix is :

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

$$G_n^{-1} \quad = \quad \begin{bmatrix} g_n^{11} & g_n^{12} & g_n^{13} & | & g_n^{14} & g_n^{15} & g_n^{16} \\ g_n^{12} & g_n^{22} & g_n^{23} & | & 0 & g_n^{25} & 0 \\ g_n^{13} & g_n^{23} & g_n^{33} & | & 0 & 0 & g_n^{36} \\ - & - & - & | & - & - & - \\ g_n^{14} & 0 & 0 & | & g_n^{44} & 0 & 0 \\ g_n^{15} & g_n^{25} & 0 & | & 0 & g_n^{55} & 0 \\ g_n^{16} & 0 & g_n^{36} & | & 0 & 0 & g_n^{66} \end{bmatrix} \begin{matrix} \\ \\ \text{parents} \\ \\ \\ \\ \text{nonparents} \\ \\ \end{matrix}$$

<div align="center">parents   non-parents</div>

The rules used to compute the elements of matrix G_n^{-1} for multiple trait 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 $n_t \times n_t$ submatrices of multiple trait interbreed nonadditive genetic variances and covariances.

Thus,

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

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

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

$$g_n^{\ 14} = -\frac{1}{2}\begin{bmatrix} 6 & 4.5 \\ 4.5 & 12 \end{bmatrix}^{-1}$$

$$g_n^{\ 15} = -\frac{1}{2}\begin{bmatrix} 4 & 3 \\ 3 & 8 \end{bmatrix}^{-1}$$

$$g_n^{\ 16} = -\frac{1}{2}\begin{bmatrix} 4 & 3 \\ 3 & 8 \end{bmatrix}^{-1}$$

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

$$g_n^{\ 23} = -\frac{1}{2}\begin{bmatrix} 6 & 4.5 \\ 4.5 & 12 \end{bmatrix}^{-1}$$

$$g_n^{\ 25} = -\frac{1}{2}\begin{bmatrix} 4 & 3 \\ 3 & 8 \end{bmatrix}^{-1}$$

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

$$g_n^{\ 36} = -\frac{1}{2}\begin{bmatrix} 4 & 3 \\ 3 & 8 \end{bmatrix}^{-1}$$

$$g_n^{\ 44} = \begin{bmatrix} 6 & 4.5 \\ 4.5 & 12 \end{bmatrix}^{-1}$$

$$g_n^{\ 55} = \begin{bmatrix} 4 & 3 \\ 3 & 8 \end{bmatrix}^{-1}$$

$$g_n^{\ 66} = \begin{bmatrix} 4 & 3 \\ 3 & 8 \end{bmatrix}^{-1}$$

The **inverse of the multiple trait multibreed nonadditive genetic covariance matrix** is obtained by substituting submatrices $\{g_n^{\ ij}\}$, **i, j = 1, …, 6,** in matrix G_n^{-1}.

Multiple Trait Multibreed Environmental Variances

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

Thus, they are obtained using the expression:

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

where e = environmental, t = vector of traits, 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,

$\left(V_{et}\right)_b$ = matrix of multiple trait intrabreed environmental variances and covariances in breed b,

$\left(V_{et}\right)_{bb'}$ = matrix of multiple trait interbreed environmental variances and covariances in pair of breeds b and b′.

The matrices of multiple trait multibreed environmental variances and covariances for the 6 animals

in the example are:

			Animal
	Number	**Breed Group**	**Multiple Trait Multibreed Environmental Variance**
Parents	1	A	$\begin{bmatrix} 12 & 10 \\ 10 & 49 \end{bmatrix}$
	2	B	$\begin{bmatrix} 8 & 6 \\ 6 & 16 \end{bmatrix}$
	3	½ A ½ B	$\frac{1}{2}\begin{bmatrix} 12 & 10 \\ 10 & 49 \end{bmatrix} + \frac{1}{2}\begin{bmatrix} 8 & 6 \\ 6 & 16 \end{bmatrix} = \begin{bmatrix} 10 & 8 \\ 8 & 32.5 \end{bmatrix}$
Non-parents	4	½ A ½ B	$\frac{1}{2}\begin{bmatrix} 12 & 10 \\ 10 & 49 \end{bmatrix} + \frac{1}{2}\begin{bmatrix} 8 & 6 \\ 6 & 16 \end{bmatrix} = \begin{bmatrix} 10 & 8 \\ 8 & 32.5 \end{bmatrix}$

| | 5 | ½ A ½ B | $\frac{1}{2}\begin{bmatrix} 12 & 10 \\ 10 & 49 \end{bmatrix} + \frac{1}{2}\begin{bmatrix} 8 & 6 \\ 6 & 16 \end{bmatrix} = \begin{bmatrix} 10 & 8 \\ 8 & 32.5 \end{bmatrix}$ |
| | 6 | ¾ A ¼ B | $\frac{3}{4}\begin{bmatrix} 12 & 10 \\ 10 & 49 \end{bmatrix} + \frac{1}{4}\begin{bmatrix} 8 & 6 \\ 6 & 16 \end{bmatrix} + [(1)(0) + (\frac{1}{2})(\frac{1}{2})]\begin{bmatrix} 16 & 14 \\ 14 & 25 \end{bmatrix}$ $= \begin{bmatrix} 15 & 12.5 \\ 12.5 & 47 \end{bmatrix}$ |

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

Effect	RHS
Mean$_{bw}$	-29.405
Mean$_{ww}$	60.7949
Breed$_{Abw}$	-11.419
Breed$_{Aww}$	25.6612
Breed$_{Bbw}$	-17.986
Breed$_{Bww}$	35.1337
Heterosis$_{ABbw}$	-14.103
Heterosis$_{ABww}$	31.4413
Sex$_{Mbw}$	-10.344
Sex$_{Mww}$	23.4738
Sex$_{Fbw}$	-19.061
Sex$_{Fww}$	37.3211
a$_{abw1}$	-2.6086
a$_{aww1}$	6.43033

a_{abw2}	-10.935
a_{aww2}	19.413
a_{abw3}	-3.8621
a_{am3}	8.82759
a_{abw4}	-4.2644
a_{aww4}	9.08046
a_{abw5}	-4.2184
a_{aww5}	10.023
a_{abw6}	-3.5171
a_{aww6}	7.0205
a_{nbw1}	-10.241
a_{nww1}	22.6137
a_{nbw2}	-8.0805
a_{nww2}	18.8506
a_{nbw3}	-1.7585
a_{nww3}	3.51025
a_{nbw4}	0
a_{nww4}	0
a_{nbw5}	0
a_{nww5}	0
a_{nbw6}	0
a_{nww6}	0

Remarks:

1) The rank of the left hand side matrix of the MME is $(36 - 4) = 32$.

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

3) The set of **MME_MTMAM** 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 36 and the rank of the left hand side of the **MME_MTMAM** is 32, thus restrictions need to be imposed to obtain solutions. These 4 restrictions could be:

   i. Set the solution for the mean for each trait to zero, and

   ii. Set the solution for breed B for each trait to zero. These restrictions are useful because the expectation of the multiple trait 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 multiple trait additive multibreed genetic effects.

4) Fixed heterosis effects here are estimates of the difference between multiple trait interbreed (AB and BA) interaction effects relative to the average of multiple trait intrabreed interaction effects (AA and BB). Thus, multiple trait 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_MTMAM**) are:

Effect	SOL	SESOL
$\text{Mean}_{bw}°$	15.5	1.55
$\text{Mean}_{ww}°$	133.21	2.9
$\text{Breed}_{Abw}°$	6.39	4.2
$\text{Breed}_{Aww}°$	71.38	7.87
$\text{Breed}_{Bbw}°$	9.11	4.13
$\text{Breed}_{Bww}°$	61.83	7.74
$\text{Heterosis}_{ABbw}°$	3.45	4.51
$\text{Heterosis}_{ABww}°$	8.27	7.51
$\text{Sex}_{Mbw}°$	11.18	2.69
$\text{Sex}_{Mww}°$	82.69	4.9
$\text{Sex}_{Fbw}°$	4.32	2.59
$\text{Sex}_{Fww}°$	50.52	4.69
$\hat{a}_{abw1}$	-0.18	3.34
$\hat{a}_{aww1}$	0.79	5.8
$\hat{a}_{abw2}$	0.07	2.93
$\hat{a}_{aww2}$	-0.57	6.42
$\hat{a}_{abw3}$	0.2	2.86
$\hat{a}_{aww3}$	-1.56	5.46

$\hat{a}_{abw4}$	-0.27	2.92
$\hat{a}_{aww4}$	1.19	5.56
$\hat{a}_{abw5}$	0.01	3.16
$\hat{a}_{aww5}$	0.48	6.16
$\hat{a}_{abw6}$	-0.1	3.26
$\hat{a}_{aww6}$	-1.3	6.04
$\hat{a}_{nbw1}$	-0.34	2.62
$\hat{a}_{nww1}$	0.29	3.81
$\hat{a}_{nbw2}$	0.37	2.58
$\hat{a}_{nww2}$	-0.15	3.77
$\hat{a}_{nbw3}$	0.14	2.76
$\hat{a}_{nww3}$	-0.28	3.94
$\hat{a}_{nbw4}$	-0.17	2.78
$\hat{a}_{nww4}$	0.14	3.95
$\hat{a}_{nbw5}$	0.01	2.82
$\hat{a}_{nww5}$	0.07	4
$\hat{a}_{nbw6}$	-0.1	2.81
$\hat{a}_{nww6}$	0	3.98

Multiple Trait Additive Multibreed Genetic Predictions

The vector of **MTAMBV** for animal i, computed as deviations from breed B (chosen as the genetic base), is:

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

where

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

$Breed_A°$ = vector of multiple trait generalized least squares solutions for breed A,

$Breed_B°$ = vector of multiple trait generalized least squares solutions for breed B,

$\hat{a}_{ai}$ = vector of multiple trait additive genetic BLUP for animal i.

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

$$VEP(MTAMBV) = var(\hat{u}_a - u_a) = K_a*(ginvlhs)*K_a'$$

where

K_a = $n_{anim} \times n_{eq}$ matrix specifying the factors multiplying vector **MTAMBV**, 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 **MTMAM** Example 1 is shown in the output of the SAS IML program.

The standard errors of prediction (SEP) of the elements of vector **MTAMBV** are computed as the square root of the diagonal elements of the VEP(**MTAMBV**) matrix.

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

Animal	Trait	Prob$_{Ai}$	Breed$_A$° - Breed$_B$°	â$_{ai}$	MTAMBV	SEP MTAMBV
1	BW	1	-2.72	-0.18	-2.89	7.85
1	WW	1	9.55	0.79	10.34	14.91
2	BW	0	-2.72	0.07	0.07	2.93
2	WW	0	9.55	-0.57	-0.57	6.42
3	BW	0.5	-2.72	0.2	-1.15	4.99
3	WW	0.5	9.55	-1.56	3.22	9.64
4	BW	0.5	-2.72	-0.27	-1.63	4.33
4	WW	0.5	9.55	1.19	5.97	8.37
5	BW	0.5	-2.72	0.01	-1.34	5.73
5	WW	0.5	9.55	0.48	5.25	11.37
6	BW	0.75	-2.72	-0.1	-2.14	6.56
6	WW	0.75	9.55	-1.3	5.86	12.53

Multiple Trait Nonadditive Multibreed Genetic Predictions

The vector of **MTNMBV** for animal i, computed assuming that males are mated to ½ A ½ B females, and vice versa, is:

$$\text{MTNMBV}_i \; = \; û_{ni} \; = \; (\text{Prob}_{\text{Aanim }i} * \text{Prob}_{\text{Bmate}} + \text{Prob}_{\text{Banim }i} * \text{Prob}_{\text{Amate}})(\text{Heterosis}_{AB}° + â_{ni})$$

where

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

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,

$\text{Heterosis}_{\text{AB}}°$ =   vector of multiple trait generalized least squares solutions heterosis effects

                    due to interaction between alleles of breeds A and B in 1 locus,

$\hat{a}_{\text{ni}}$ =   vector of multiple trait nonadditive genetic BLUP for animal i.

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

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

where

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

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

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

Matrix K_n for **MTMAM** Example 1 is shown in the output of the SAS IML program.

The standard errors of prediction (SEP) of the elements of vector **MTNMBV** are computed as the

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

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

Animal	Trait	$\text{Prob}_{\text{Ai}}*\text{Prob}_{\text{Bmate}}$ + $\text{Prob}_{\text{Bi}}*\text{Prob}_{\text{Amate}}$	$\text{Heterosis}_{\text{AB}}°$	$\hat{a}_{\text{ni}}$	MTNMBV	SEP MTNMBV
1	BW	1*0.5 + 0*0.5	3.45	-0.34	1.55	1.94
1	WW	1*0.5 + 0*0.5	8.27	0.29	4.28	3.43
2	BW	0*0.5 + 1*0.5	3.45	0.37	1.91	1.95
2	WW	0*0.5 + 1*0.5	8.27	-0.15	4.06	3.41

3	BW	0.5*0.5 + 0.5*0.5	3.45	0.14	1.79	2.34
3	WW	0.5*0.5 + 0.5*0.5	8.27	-0.28	3.99	3.87
4	BW	0.5*0.5 + 0.5*0.5	3.45	-0.17	1.64	2.34
4	WW	0.5*0.5 + 0.5*0.5	8.27	0.14	4.21	3.88
5	BW	0.5*0.5 + 0.5*0.5	3.45	0.01	1.73	2.02
5	WW	0.5*0.5 + 0.5*0.5	8.27	0.07	4.17	3.48
6	BW	0.75*0.5 + 0.25*0.5	3.45	-0.1	1.67	2.19
6	WW	0.75*0.5 + 0.25*0.5	8.27	0	4.14	3.68

Multiple Trait Total Multibreed Genetic Predictions

The vector of **MTTMBV** for animal i is equal to the sum of its vectors of predicted multiple trait

multibreed additive (**MTAMBV**) and nonadditive (**MTNMBV**) genetic effects, i.e.,

$$\text{MTTMBV}_i \quad = \quad \text{MTAMBV}_i + \text{MTNMBV}_i = \quad \hat{u}_{ai} + \hat{u}_{ni}$$

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

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

where

$K_t \qquad = \qquad n_{anim} \times n_{eq}$ matrix specifying the factors multiplying vector **MTTMBV**, 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 **MTMAM** Example 1 is shown in the output of the SAS IML program.

The standard errors of prediction (SEP) of the elements of vector **MTTMBV** are computed as the

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

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

Animal	Trait	MTAMBV	MTNMBV	MTTMBV	SEP MTTMBV
1	BW	-2.89	1.55	-1.34	7.8
1	WW	10.34	4.28	14.61	14.6
2	BW	0.07	1.91	1.98	3.6
2	WW	-0.57	4.06	3.49	7.49
3	BW	-1.15	1.79	0.64	4.83
3	WW	3.22	3.99	7.21	9.18
4	BW	-1.63	1.64	0.01	4.29
4	WW	5.97	4.21	10.17	7.94
5	BW	-1.34	1.73	0.39	5.67
5	WW	5.25	4.17	9.42	11.04
6	BW	-2.14	1.67	-0.47	6.48
6	WW	5.86	4.14	9.99	12.21

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