

ANIMAL BREEDING NOTES

CHAPTER 16M

MULTIBREED ANIMAL MODEL

Multibreed Animal Model (MAM)

Objective: to predict additive genetic effects (**AMBV**), nonadditive genetic effects (**NMBV**), and total genetic effects (**TMBV**) of 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) 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 **AMBV**, the relationship matrix was complete.

The MAM is:

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

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

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

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

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 additive group genetic effects (e.g., breed, breed \times year of birth),

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

a_a = vector of unknown random additive genetic effects (AMBV),

a_n = vector of unknown random nonadditive genetic effects (NMBV),

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 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} = multibreed additive genetic covariance between animals i and j ,

$G_n = \text{diag}\{A_m * \sigma_{nm}^2, m = 1, \dots, N_m\}$, where A_m is the matrix of probabilities that pairs of animals received the same alleles at m loci, and σ_{nm}^2 is the variance of interaction effects among alleles at m loci. If $m = 1$, then $G_n = A * \sigma_{n1}^2$, where A = matrix of additive relationships and σ_{n1}^2 = variance of intralocus interaction effects (intra-breed and inter-breed). Further, if only inter-breed intralocus effects are included in the model, then σ_{n1}^2 = variance of intralocus inter-breed interaction effects = variance of random heterosis effects,

$R = \text{diag}\{\sigma_{ei}^2\}$, where σ_{ei}^2 = multibreed residual variance for animal i . The multibreed residual variance is 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 MAM are:

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

Example 1 of the MAM 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) Additive genetic variances:**

$$\text{Intrabreed additive genetic variance for breed A} = \sigma_{aAA}^2 = 36 \text{ kg}^2$$

$$\text{Intrabreed additive genetic variance for breed B} = \sigma_{aBB}^2 = 9 \text{ kg}^2$$

$$\text{Interbreed additive genetic variance for combination of breeds AB} = \sigma_{aAB}^2 = 4 \text{ kg}^2$$

2) Nonadditive genetic variances 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.

$$\text{Intrabreed nonadditive genetic variance for breed A} = \sigma_{nAA}^2 = 4 \text{ kg}^2$$

$$\text{Intrabreed nonadditive genetic variance for breed B} = \sigma_{nBB}^2 = 9 \text{ kg}^2$$

$$\text{Interbreed nonadditive genetic variance for combination of breeds AB} = \sigma_{nAB}^2 = 16 \text{ kg}^2$$

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 \times breed group of dam and dam \times 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 $\sigma_{nAB}^2 = 16 \text{ kg}^2$ will be needed.

3) Environmental variances:

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

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

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

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

Multibreed Animal Model for the Example

$$\begin{aligned} \text{Wean wt} = & \text{overall mean} + \text{breed regression} + \text{heterosis regression} + \text{sex} \\ & + \text{animal additive genetic} + \text{animal nonadditive genetic regression} \\ & + \text{residual} \end{aligned}$$

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

$$\begin{aligned} \text{Var}(\text{Wean wt}) = & \text{var}(\text{animal additive genetic}) + \text{var}(\text{animal nonadditive genetic regression}) \\ & + \text{var}(\text{residual}) \end{aligned}$$

$$\begin{aligned} \text{cov}(\text{Wean wt}_{ik}, \text{Wean wt}_{i'k'}) = & \text{cov}(\text{animal additive genetic}_i, \text{animal additive genetic}_{i'}) \\ & + \text{cov}(\text{animal nonadditive genetic}_i, \text{animal nonadditive} \\ & \text{genetic}_{i'}) + \text{cov}(\text{residual}_{ik}, \text{residual}_{i'k'}) \end{aligned}$$

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

$$\begin{bmatrix} 289 \\ 245 \\ 256 \\ 261 \\ 292 \\ 286 \end{bmatrix} = \begin{bmatrix} 1 & 1 & 0 & 0 & 1 & 0 \\ 1 & 0 & 1 & 0 & 0 & 1 \\ 1 & \frac{1}{2} & \frac{1}{2} & 1 & 0 & 1 \\ 1 & \frac{1}{2} & \frac{1}{2} & 1 & 0 & 1 \\ 1 & \frac{1}{2} & \frac{1}{2} & 1 & 1 & 0 \\ 1 & \frac{3}{4} & \frac{1}{4} & \frac{1}{2} & 1 & 0 \end{bmatrix} \begin{bmatrix} \text{mean} \\ \text{breed}_A \\ \text{breed}_B \\ \text{heterosis}_{AB} \\ \text{sex}_M \\ \text{sex}_F \end{bmatrix} + \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} \text{animal 1}_{\text{add}} \\ \text{animal 2}_{\text{add}} \\ \text{animal 3}_{\text{add}} \\ \text{animal 4}_{\text{add}} \\ \text{animal 5}_{\text{add}} \\ \text{animal 6}_{\text{add}} \end{bmatrix}$$

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

Multibreed Additive Genetic Variances

Multibreed additive genetic variances are computed by conditioning them on breed of origin of alleles using the expression:

$$\sigma_{\text{at}}^2 = E[\text{var}(t | \mathbf{b}) + \text{var}(E[t | \mathbf{b}])]$$

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

where a = additive genetic, 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,
- $(\sigma_{\text{at}}^2)_b$ = additive intrabreed genetic variance for trait t in breed b,
- $(\sigma_{\text{at}}^2)_{bb'}$ = additive interbreed genetic variance for trait t in pair of breeds b and b' (non-

zero only when one or both parents are crossbreds).

The multibreed additive genetic variances for the 6 animals in the example are:

	Animal		
	Number	Breed Group	Multibreed Additive Genetic Variance
Parents	1	A	36
	2	B	9
	3	½ A ½ B	½ (36) + ½ (9) = 22.5
Non-parents	4	½ A ½ B	½ (36) + ½ (9) = 22.5
	5	½ A ½ B	½ (36) + ½ (9) = 22.5
	6	¾ A ¼ B	¾ (36) + ¼ (9) + [(1)(0) + (½)(½)](4) = 30.25

Inverse of the Multibreed Additive Genetic Covariance Matrix

The equation for the inverse of the covariance matrix of multibreed additive genetic effects, G_a^{-1} , is:

$$G_a^{-1} = (I - \frac{1}{2} P') D_a^{-1} (I - \frac{1}{2} P)$$

where

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,

D_a = diagonal matrix of residual additive genetic variances.

The diagonal elements of the D_a^{-1} matrix are computed using the expression:

$$d_{a_{ii}}^{-1} = \left[\left(\sigma_{at_i}^2 \right) - \frac{1}{4} \delta_s \left(\left(\sigma_{at_s}^2 \right) + \sum_{c=1}^{n_{cs}} F_{cs} \left(\sigma_{at_{cs}}^2 \right) \right) - \frac{1}{4} \delta_d \left(\left(\sigma_{at_d}^2 \right) + \sum_{c=1}^{n_{cd}} F_{cd} \left(\sigma_{at_{cd}}^2 \right) \right) \right]^{-1}$$

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 $d_{a_{ii}}^{-1}$ simplifies to:

$$d_{a_{ii}}^{-1} = \left[(\sigma_{at}^2)_i - \frac{1}{4} \delta_s (\sigma_{at}^2)_s - \frac{1}{4} \delta_d (\sigma_{at}^2)_d \right]^{-1}$$

Thus, the $d_{a_{ii}}^{-1}$ for the six animals in the example, computed using the formula for a non-inbred multibreed population, are:

	Animal		
	Number	Breed Group	$d_{a_{ii}}^{-1}$
Parents	1	A	$(36)^{-1}$
	2	B	$(9)^{-1}$
	3	½ A ½ B	$[22.5 - \frac{1}{4} (9)]^{-1} = (20.25)^{-1}$
Non-parents	4	½ A ½ B	$[22.5 - \frac{1}{4} (36)]^{-1} = (13.5)^{-1}$
	5	½ A ½ B	$[22.5 - \frac{1}{4} (36) - \frac{1}{4} (9)]^{-1} = (11.25)^{-1}$
	6	¾ A ¼ B	$[30.25 - \frac{1}{4} (36) - \frac{1}{4} (20.25)]^{-1} = (15.1875)^{-1}$

The P matrix is:

$$P = \left[\begin{array}{ccc|ccc} 0 & & & & & \\ 0 & 0 & & & & \\ 0 & 1 & 0 & & & \\ - & - & - & - & - & - \\ 1 & 0 & 0 & 0 & & \\ 1 & 1 & 0 & 0 & 0 & \\ 1 & 0 & 1 & 0 & 0 & 0 \end{array} \right]$$

$$D_a^{-1} = \left[\begin{array}{ccc|ccc} (36)^{-1} & & & & & \\ & (9)^{-1} & & & & \\ & & (20.25)^{-1} & & & \\ - & - & - & - & - & - \\ & & & (13.5)^{-1} & & \\ & & & & (11.25)^{-1} & \\ & & & & & (16.1875)^{-1} \end{array} \right]$$

The inverse of the multibreed additive genetic covariance matrix, in terms of parental and non-parental terms, is :

$$G_a^{-1} = D_a^{-1} - \frac{1}{2} D_a^{-1} P - \frac{1}{2} P' D_a^{-1} + \frac{1}{4} P' D_a^{-1} P$$

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

\downarrow \downarrow
 parents non-parents

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.

Thus,

$$g_a^{11} = (36)^{-1} + \frac{1}{4} (13.5)^{-1} + \frac{1}{4} (11.25)^{-1} + \frac{1}{4} (16.1875)^{-1} = 0.084$$

$$\begin{aligned}
g_a^{12} &= \frac{1}{4} (11.25)^{-1} = 0.022 \\
g_a^{13} &= \frac{1}{4} (16.1875)^{-1} = 0.015 \\
g_a^{14} &= -\frac{1}{2} (13.5)^{-1} = -0.037 \\
g_a^{15} &= -\frac{1}{2} (11.25)^{-1} = -0.044 \\
g_a^{16} &= -\frac{1}{2} (16.1875)^{-1} = -0.031 \\
g_a^{22} &= (9)^{-1} + \frac{1}{4} (20.25)^{-1} + \frac{1}{4} (11.25)^{-1} = 0.146 \\
g_a^{23} &= -\frac{1}{2} (20.25)^{-1} = -0.025 \\
g_a^{25} &= -\frac{1}{2} (11.25)^{-1} = -0.044 \\
g_a^{33} &= (20.25)^{-1} + \frac{1}{4} (16.1875)^{-1} = 0.065 \\
g_a^{36} &= -\frac{1}{2} (16.1875)^{-1} = -0.031 \\
g_a^{44} &= (13.5)^{-1} = 0.074 \\
g_a^{55} &= (11.25)^{-1} = 0.089 \\
g_a^{66} &= (16.1875)^{-1} = 0.062
\end{aligned}$$

Consequently, G_a^{-1} is equal to :

$$G_a^{-1} = \begin{bmatrix} 0.084 & 0.022 & 0.015 & -0.037 & -0.044 & -0.031 \\ 0.022 & 0.146 & -0.025 & 0 & -0.044 & 0 \\ 0.015 & -0.025 & 0.065 & 0 & 0 & -0.031 \\ \hline -0.037 & 0 & 0 & 0.074 & 0 & 0 \\ -0.044 & -0.044 & 0 & 0 & 0.089 & 0 \\ -0.031 & 0 & -0.031 & 0 & 0 & 0.062 \end{bmatrix}$$

Multibreed Nonadditive Genetic Variances

Multibreed nonadditive genetic variances in a regression model that accounts for sire \times breed group of dam and dam \times breed group of sire interaction effects are equal to the intrabreed and interbreed

interaction variances 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 multibreed nonadditive genetic variances would be block diagonal, 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 variance needed for the example here is the variance of intralocus interbreed interaction effects, $\sigma_{nAB}^2 = 16 \text{ kg}^2$.

Thus, the multibreed nonadditive genetic variances for the 6 animals in the example is:

	Animal		
	Number	Breed Group	Multibreed Nonadditive Genetic Variance
Parents	1	A	16
	2	B	16
	3	½ A ½ B	16
Non-parents	4	½ A ½ B	16
	5	½ A ½ B	16
	6	¾ A ¼ B	16

Inverse of the Multibreed Nonadditive Genetic Covariance Matrix

Covariances 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 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:

$$G_n^{-1} = (I - \frac{1}{2} P') D_n^{-1} (I - \frac{1}{2} P)$$

where

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,

D_n = diagonal matrix of residual nonadditive genetic variances.

The diagonal elements of the D_n⁻¹ matrix are computed using the expression:

$$d_{nii}^{-1} = \left[\left(1 - \frac{1}{4}\delta_s(1 + F_s) - \frac{1}{4}\delta_d(1 + F_d) \right) * \sigma_{nAB}^2 \right]^{-1}$$

where F_s and F_d are the coefficients of inbreeding of the sire and the dam of animal i, and δ_s = 1 if the sire is known, else δ_s = 0, and δ_d = 1 if the dam is known, else δ_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:

$$d_{nii}^{-1} = \left[\left(1 - \frac{1}{4}\delta_s - \frac{1}{4}\delta_d \right) * \sigma_{nAB}^2 \right]^{-1}$$

The diagonal elements of the D_n⁻¹ matrix are:

	Animal		
	Number	Breed Group	d _{nii} ⁻¹
Parents	1	A	[(1)*(16)] ⁻¹ = (16) ⁻¹
	2	B	[(1)*(16)] ⁻¹ = (16) ⁻¹
	3	½ A ½ B	[(1 - ¼) (16)] ⁻¹ = (12) ⁻¹
Non-parents	4	½ A ½ B	[(1 - ¼) (16)] ⁻¹ = (12) ⁻¹
	5	½ A ½ B	[(1 - ¼ - ¼) (16)] ⁻¹ = (8) ⁻¹
	6	¾ A ¼ B	[(1 - ¼ - ¼) (16)] ⁻¹ = (8) ⁻¹

The P matrix is:

$$P = \left[\begin{array}{ccc|ccc} 0 & & & & & \\ 0 & 0 & & & & \\ 0 & 1 & 0 & & & \\ - & - & - & - & - & - \\ 1 & 0 & 0 & 0 & & \\ 1 & 1 & 0 & 0 & 0 & \\ 1 & 0 & 1 & 0 & 0 & 0 \end{array} \right]$$

$$D_n^{-1} = \left[\begin{array}{ccc|ccc} (16)^{-1} & & & & & \\ & (16)^{-1} & & & & \\ & & (12)^{-1} & & & \\ - & - & - & - & - & - \\ & & & (12)^{-1} & & \\ & & & & (8)^{-1} & \\ & & & & & (8)^{-1} \end{array} \right]$$

The inverse of the multibreed nonadditive genetic covariance matrix is :

$$G_n^{-1} = D_n^{-1} - 1/2 D_n^{-1} P - 1/2 P' D_n^{-1} + 1/4 P' D_n^{-1} P$$

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

parents non-parents

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

- 1) Add d_{nii}^{-1} to $i \times i$,
- 2) Add $-1/2 d_{nii}^{-1}$ to $i \times s$ and $s \times i$ if the sire of animal i is identified,
- 3) Add $-1/2 d_{nii}^{-1}$ to $i \times d$ and $d \times i$ if the dam of animal i is identified, and
- 4) Add $1/4 d_{nii}^{-1}$ to $s \times s$, $s \times d$, $d \times s$, and $d \times d$ if the sire and dam of animal i are identified.

Thus,

$$g_n^{11} = (16)^{-1} + 1/4 (12)^{-1} + 1/4 (8)^{-1} + 1/4 (8)^{-1} = 0.146$$

$$g_n^{12} = 1/4 (8)^{-1} = 0.031$$

$$g_n^{13} = 1/4 (8)^{-1} = 0.031$$

$$g_n^{14} = -1/2 (12)^{-1} = -0.042$$

$$g_n^{15} = -1/2 (8)^{-1} = -0.063$$

$$g_n^{16} = -1/2 (8)^{-1} = -0.063$$

$$g_n^{22} = (16)^{-1} + 1/4 (12)^{-1} + 1/4 (8)^{-1} = 0.115$$

$$g_n^{23} = -1/2 (12)^{-1} = -0.042$$

$$g_n^{25} = -1/2 (8)^{-1} = -0.063$$

$$g_n^{33} = (12)^{-1} + 1/4 (8)^{-1} = 0.115$$

$$g_n^{36} = -1/2 (8)^{-1} = -0.063$$

$$g_n^{44} = (12)^{-1} = 0.083$$

$$g_n^{55} = (8)^{-1} = 0.125$$

$$g_n^{66} = (8)^{-1} = 0.125$$

Thus, G_n^{-1} is equal to :

$$G_n^{-1} = \begin{bmatrix} 0.146 & 0.031 & 0.031 & -0.042 & -0.063 & -0.063 \\ 0.031 & 0.115 & -0.042 & 0 & -0.063 & 0 \\ 0.031 & -0.042 & 0.115 & 0 & 0 & -0.063 \\ \hline -0.042 & -0.042 & 0 & 0.083 & 0 & 0 \\ -0.063 & -0.063 & 0 & 0 & 0.125 & 0 \\ -0.063 & 0 & -0.063 & 0 & 0 & 0.125 \end{bmatrix}$$

Multibreed Environmental Variances

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

Thus, they are obtained using the expression:

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

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'

(non-zero only when one or both parents are crossbreds).

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	$\frac{1}{2}$ A $\frac{1}{2}$ B	$\frac{1}{2} (49) + \frac{1}{2} (16) = 32.5$
Non-parents	4	$\frac{1}{2}$ A $\frac{1}{2}$ B	$\frac{1}{2} (49) + \frac{1}{2} (16) = 32.5$
	5	$\frac{1}{2}$ A $\frac{1}{2}$ B	$\frac{1}{2} (49) + \frac{1}{2} (16) = 32.5$
	6	$\frac{3}{4}$ A $\frac{1}{4}$ B	$\frac{3}{4} (49) + \frac{1}{4} (16) + [(1)(0) + (\frac{1}{2})(\frac{1}{2})](25) = 47.0$

The mixed model equations are now constructed with the contributions of each animal to the effects in the model. The resulting left-hand side and right-hand side of the mixed model equations, as well as the vector of unknowns for the **MAM** in Example 1 are as follows.

The left hand side of the **MME_MAM** for Example 1 is:

lhs																	
0.196	0.083	0.114	0.103	0.072	0.124	0.020	0.063	0.031	0.031	0.031	0.021	0.072	0.062	0.011	0.000	0.000	0.000
0.083	0.055	0.027	0.054	0.052	0.031	0.020	0.000	0.015	0.015	0.015	0.016	0.039	0.031	0.008	0.000	0.000	0.000
0.114	0.027	0.087	0.049	0.021	0.093	0.000	0.063	0.015	0.015	0.015	0.005	0.033	0.031	0.003	0.000	0.000	0.000
0.103	0.054	0.049	0.098	0.041	0.062	0.000	0.000	0.031	0.031	0.031	0.011	0.067	0.062	0.005	0.000	0.000	0.000
0.072	0.052	0.021	0.041	0.072	0.000	0.020	0.000	0.000	0.000	0.031	0.021	0.041	0.031	0.011	0.000	0.000	0.000
0.124	0.031	0.093	0.062	0.000	0.124	0.000	0.063	0.031	0.031	0.000	0.000	0.031	0.031	0.000	0.000	0.000	0.000
0.020	0.020	0.000	0.000	0.020	0.000	0.104	0.022	0.015	-0.037	-0.044	-0.031	0.000	0.000	0.000	0.000	0.000	0.000
0.063	0.000	0.063	0.000	0.000	0.063	0.022	0.208	-0.025	0.000	-0.044	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.031	0.015	0.015	0.031	0.000	0.031	0.015	-0.025	0.096	0.000	0.000	-0.031	0.000	0.031	0.000	0.000	0.000	0.000
0.031	0.015	0.015	0.031	0.000	0.031	-0.037	0.000	0.000	0.105	0.000	0.000	0.031	0.000	0.000	0.000	0.000	0.000
0.031	0.015	0.015	0.031	0.031	0.000	-0.044	-0.044	0.000	0.000	0.120	0.000	0.031	0.031	0.000	0.000	0.000	0.000
0.021	0.016	0.005	0.011	0.021	0.000	-0.031	0.000	-0.031	0.000	0.000	0.083	0.011	0.000	0.011	0.000	0.000	0.000
0.072	0.039	0.033	0.067	0.041	0.031	0.000	0.000	0.000	0.031	0.031	0.011	0.213	0.062	0.037	-0.042	-0.063	-0.063
0.062	0.031	0.031	0.062	0.031	0.031	0.000	0.000	0.031	0.000	0.031	0.000	0.062	0.176	-0.042	0.000	-0.063	0.000
0.011	0.008	0.003	0.005	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.011	0.037	-0.042	0.120	0.000	0.000	-0.063
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-0.042	0.000	0.000	0.083	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-0.063	-0.063	0.000	0.000	0.125	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-0.063	0.000	-0.063	0.000	0.000	0.125

The vector of effects and the right hand side (RHS) of the **MME_MAM** for Example 1 are:

Effect	RHS
Mean	52.19
Breed _A	22.91
Breed _B	29.28
Heterosis _{AB}	27.93
Sex _M	20.97
Sex _F	31.22
a _{a1}	5.90
a _{a2}	15.31
a _{a3}	7.88
a _{a4}	8.03
a _{a5}	8.98
a _{a6}	6.09
a _{n1}	20.06
a _{n2}	16.86
a _{n3}	3.04
a _{n4}	0.00
a _{n5}	0.00
a _{n6}	0.00

Remarks:

- 1) The rank of the left hand side matrix of the MME is 16.
- 2) Differences between breed effects, heterosis, and differences between sex effects are estimable.
- 3) The set of **MME_MAM** 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.,
$$\text{sol} = \text{ginvlhs} * \text{rhs}$$
 - b. Imposing restrictions on the solutions. The number of equations in Example 1 is 18 and the rank of the left hand side of the **MME_MAM** is 16, thus 2 restrictions need to be imposed to obtain solutions. These 2 restrictions could be:
 - i. Set the solution of the mean to zero, and
 - ii. Set the solution for breed B to zero. This restriction is useful because the expectation of the solution for breed A estimates the difference between the effects of breed A and breed B. Thus, breed B can be used as the genetic base of comparison for additive multibreed genetic effects.
- 4) Fixed heterosis effects here are an estimate of the difference between the interbreed (AB and BA) interaction effects relative to the average of intrabreed interaction effects (AA and BB). Thus, fixed heterosis effects can be used as the genetic base of comparison for 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_MAM**) are:

Effect	SOL	SESOL
Mean ^o	133.04	2.47
Breed _A ^o	71.47	7.13
Breed _B ^o	61.57	6.26
Heterosis _{AB} ^o	8.44	7.21
Sex _M ^o	82.50	4.34
Sex _F ^o	50.54	4.33
\hat{a}_{a1}	0.96	5.75
\hat{a}_{a2}	-0.14	2.98
\hat{a}_{a3}	-1.15	4.27
\hat{a}_{a4}	0.91	4.34
\hat{a}_{a5}	0.65	4.61
\hat{a}_{a6}	-0.79	5.29
\hat{a}_{n1}	0.51	3.77
\hat{a}_{n2}	-0.34	3.73
\hat{a}_{n3}	-0.43	3.93
\hat{a}_{n4}	0.26	3.94
\hat{a}_{n5}	0.09	3.99
\hat{a}_{n6}	0.04	3.98

The standard errors of prediction (SEP) of the **AMBV** are computed as the square roots of the diagonal elements of the $VEP(\mathbf{AMBV})$ matrix.

The **AMBV** and their **SEP** for the 6 animals in Example 1 are:

Animal	Prob_{Aanim}	Breed_A^o - Breed_B^o	\hat{a}_{add}	AMBV	SEP AMBV
1	1	9.99	0.96	10.86	12.54
2	0	9.99	-0.14	-0.14	2.98
3	0.5	9.99	-1.15	3.80	7.39
4	0.5	9.99	0.91	5.86	6.68
5	0.5	9.99	0.65	5.60	8.30
6	0.75	9.99	-0.79	6.64	10.08

Nonadditive Multibreed Genetic Predictions

The **NMBV** computed assuming that males are mated to $\frac{1}{2}$ A $\frac{1}{2}$ B females, and vice versa, are:

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

where

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

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

Prob_{Amate} = expected fraction of breed A in the mate of animal i,

Prob_{Bmate} = expected fraction of breed B in the mate of animal i,

Heterosis_{AB}^o = generalized least squares solution for the heterosis due to interaction between alleles of breeds A and B in 1 locus,

$$\hat{a}_{ni} = \text{BLUP solution for } a_{ni}.$$

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

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

where

$K_n = n_{\text{anim}} \times n_{\text{eq}}$ matrix specifying the factors multiplying the components of the

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

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

Matrix K_n for **MAM** Example 1 is:

KN																	
0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00
0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00
0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00
0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50
0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50

The standard errors of prediction (SEP) of the **NMBV** are computed as the square roots of the diagonal elements of the **VEP(NMBV)** matrix.

The **NMBV** and their **SEP** for the 6 animals in **MAM** Example 1 are:

Animal	$\text{Prob}_{A_{\text{anim}}} * \text{Prob}_{B_{\text{mate}}}$ + $\text{Prob}_{B_{\text{anim}}} * \text{Prob}_{A_{\text{mate}}}$	Heterosis _{AB} ^o	\hat{a}_{nadd}	NMBV	SEP NMBV
1	1*0.5 + 0*0.5	8.44	0.51	4.48	3.22
2	0*0.5 + 1*0.5	8.44	-0.34	4.05	3.26
3	0.5*0.5 + 0.5*0.5	8.44	-0.43	4.01	3.74
4	0.5*0.5 + 0.5*0.5	8.44	0.26	4.35	3.71
5	0.5*0.5 + 0.5*0.5	8.44	0.09	4.26	3.31
6	0.75*0.5 + 0.25*0.5	8.44	0.04	4.24	3.52

Total Multibreed Genetic Predictions

The **TMBV** are the sum of **AMBV** and **NMBV**, i.e.,

$$\text{TMBV}_i = \text{AMBV}_i + \text{NMBV}_i = \hat{u}_{ai} + \hat{u}_{ni}$$

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

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

where

$$K_t = n_{\text{anim}} \times n_{\text{eq}} \text{ matrix specifying the factors multiplying the components of the}$$

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

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

Matrix K_t for **MAM** Example 1 is:

KT																	
0.00	1.00	-1.00	0.50	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.50	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00
0.00	0.50	-0.50	0.50	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00
0.00	0.50	-0.50	0.50	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00
0.00	0.50	-0.50	0.50	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00
0.00	0.75	-0.75	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.50

The standard errors of prediction (SEP) of the **TMBV** are computed as the square roots of the diagonal elements of the $VEP(\mathbf{TMBV})$ matrix.

The **TMBV** and their SEP for the 6 animals in **MAM** Example 1 are:

Animal	AMBV	NMBV	TMBV	SEP TMBV
1	10.86	4.48	15.33	11.82
2	-0.14	4.05	3.91	4.49
3	3.80	4.01	7.80	6.70
4	5.86	4.35	10.21	6.17
5	5.60	4.26	9.86	7.80
6	6.64	4.24	10.88	9.44

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.