

GENETIC AND GENOMIC EVALUATION NOTES

CHAPTER 02

POLYGENIC-GENOMIC MODELS WITH COMPLETE GENOTYPE INFORMATION

Genetic Evaluation Model

Polygenic-Genomic Models with Complete Genotype Information

- a. Polygenic -Genomic Marker Model with a single fixed marker effect
- b. Polygenic –Genomic Marker Model with a small number of fixed marker effects
- c. Polygenic -Genomic Marker Model with a small number of random marker effects
- d. Polygenic-Genomic Marker Model with a large number of random marker effects
- e. Polygenic-Genomic Animal Model with a large number of random marker effects

Genetic Evaluation Model

A typical polygenic genetic evaluation model has the following components:

- 1) A trait of interest (e.g., weaning weight, marbling, milk yield)
- 2) Some fixed environmental effects (e.g., contemporary group, age of dam, sex of calf), genetic effects (e.g., breed group, heterosis), or both.
- 3) Some random polygenic genetic effects (e.g., animal, sire, dam), and
- 4) A residual effect.

Example

Prediction of the genetic value of animals for weaning weight using the following phenotypic information on 6 calves.

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

Additive Genetic and Residual Variances

Variance	Additive Genetic	Residual
Intrabreed AA	36 kg ²	49 kg ²
Intrabreed BB	44 kg ²	16 kg ²
Interbreed AB	22 kg ²	25 kg ²

Genetic Model

$$\text{Wean wt} = \text{overall mean} + \text{breed regression} + \text{heterosis regression} + \text{sex} \\ + \text{animal additive genetic} + \text{residual}$$

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

$$\text{Var}(\text{Wean wt}) = \text{var}(\text{animal additive genetic}) + \text{var}(\text{residual})$$

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

The genetic model, in matrix notation, is:

$$y = Xb + Z_a Q_a g_a + Z_n Q_n g_n + Z_a a_a + \varepsilon$$

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

$$\text{var} \begin{bmatrix} a_a \\ \varepsilon \end{bmatrix} = \begin{bmatrix} G_a & 0 \\ 0 & R \end{bmatrix}$$

$$\text{var}(y) = Z_a G_a Z_a' + R$$

where

y = vector of animal records,

b = vector of unknown fixed effects (mean, sex of calf),

g_a = vector of unknown additive group genetic effects (breed),

g_n = vector of unknown nonadditive group genetic effects (heterosis at 1 locus),

a_a = vector of unknown random additive genetic effects,

ε = 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 random nonadditive genetic effects in vector a_n (a_n is assumed to be part of the residual),

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 = matrix of additive genetic variances and covariances among animals (purebred and crossbred) in the multibreed population; covariances are due to additive relationships

among animals.

R = matrix of residual variances for purebred and crossbred animals (sums of nonadditive genetic and environmental variances).

The mixed model with the information of the 6 calves can be written as follows:

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

To obtain solutions for the effects in the mixed model we need to solve the mixed model equations (MME). The mixed model equations were derived by C. R. Henderson (Henderson et al., 1959) by maximizing the joint function of records and random effects written as the product of the conditional distribution of the records given the random effects times the distribution of the random effects, i.e., $f(\text{records, random effects}) = f(\text{records} | \text{random effects}) * f(\text{random effects})$.

Constructing and Solving the Mixed Model Equations (MME)

The mixed model equations can be constructed as follows:

- 1) Define v = vector of unknowns:

$$v = \begin{bmatrix} b \\ g_a \\ g_n \\ a_a \end{bmatrix}$$

2) Compute R^{-1} , the inverse of the residual covariance matrix R ,

invr = R^{-1}					
0.0204082	0	0	0	0	0
0	0.0625	0	0	0	0
0	0	0.0307692	0	0	0
0	0	0	0.0307692	0	0
0	0	0	0	0.0307692	0
0	0	0	0	0	0.0212766

3) Compute G_a^{-1} , the inverse of the additive genetic covariance matrix among animal effects,

gainv = G_a^{-1}					
0.0585464	0.0125	0.0102041	-0.016129	-0.025	-0.020408
0.0125	0.043848	-0.017241	0	-0.025	0
0.0102041	-0.017241	0.0446868	0	0	-0.020408
-0.016129	0	0	0.0322581	0	0
-0.025	-0.025	0	0	0.05	0
-0.020408	0	-0.020408	0	0	0.0408163

4) Compute the fixed part of left hand side of the mixed model equations (Fixed part of LHS)

by:

- a. Multiplying the transposes of the coefficient matrices in the model times R^{-1} times the coefficient matrices in the model, i.e.,

$$\text{Fixed part of LHS} = \begin{bmatrix} X' \\ Q_a'Z_a' \\ Q_n'Z_n' \\ Z_a' \end{bmatrix} [R^{-1}][X \quad Z_aQ_a \quad Z_nQ_n \quad Z_a]$$

$$= \begin{bmatrix} X'R^{-1}X & X'R^{-1}Z_aQ_a & X'R^{-1}Z_nQ_n & X'R^{-1}Z_a \\ Q_a'Z_a'R^{-1}X & Q_a'Z_a'R^{-1}Z_aQ_a & Q_a'Z_a'R^{-1}Z_nQ_n & Q_a'Z_a'R^{-1}Z_a \\ Q_n'Z_n'R^{-1}X & Q_n'Z_n'R^{-1}Z_aQ_a & Q_n'Z_n'R^{-1}Z_nQ_n & Q_n'Z_n'R^{-1}Z_a \\ Z_a'R^{-1}X & Z_a'R^{-1}Z_aQ_a & Z_a'R^{-1}Z_nQ_n & Z_a'R^{-1}Z_a \end{bmatrix}$$

Matrix $[X \quad Z_aQ_a \quad Z_nQ_n \quad Z_a]$ is:

$xf = [X \quad Z_aQ_a \quad Z_nQ_n \quad Z_a]$											
1	1	0	0	1	0	1	0	0	0	0	0
1	0	1	0	0	1	0	1	0	0	0	0
1	0.5	0.5	1	0	1	0	0	1	0	0	0
1	0.5	0.5	1	0	1	0	0	0	1	0	0
1	0.5	0.5	1	1	0	0	0	0	0	1	0
1	0.75	0.25	0.5	1	0	0	0	0	0	0	1

The fixed part of the LHS (i.e., the LHS before adding G_a^{-1}) is:

xtinvrx = Fixed part of LHS											
0.1964925	0.0825195	0.113973	0.102946	0.072454	0.1240385	0.0204082	0.0625	0.0307692	0.0307692	0.0307692	0.0212766
0.0825195	0.0554532	0.0270663	0.0541326	0.0517502	0.0307692	0.0204082	0	0.0153846	0.0153846	0.0153846	0.0159574
0.113973	0.0270663	0.0869067	0.0488134	0.0207038	0.0932692	0	0.0625	0.0153846	0.0153846	0.0153846	0.0053191
0.102946	0.0541326	0.0488134	0.0976268	0.0414075	0.0615385	0	0	0.0307692	0.0307692	0.0307692	0.0106383
0.072454	0.0517502	0.0207038	0.0414075	0.072454	0	0.0204082	0	0	0	0.0307692	0.0212766
0.1240385	0.0307692	0.0932692	0.0615385	0	0.1240385	0	0.0625	0.0307692	0.0307692	0	0
0.0204082	0.0204082	0	0	0.0204082	0	0.0204082	0	0	0	0	0
0.0625	0	0.0625	0	0	0.0625	0	0.0625	0	0	0	0

xtinvrx = Fixed part of LHS											
0.0307692	0.0153846	0.0153846	0.0307692	0	0.0307692	0	0	0.0307692	0	0	0
0.0307692	0.0153846	0.0153846	0.0307692	0	0.0307692	0	0	0	0.0307692	0	0
0.0307692	0.0153846	0.0153846	0.0307692	0.0307692	0	0	0	0	0	0.0307692	0
0.0212766	0.0159574	0.0053191	0.0106383	0.0212766	0	0	0	0	0	0	0.0212766

b. Adding G_a^{-1} to the diagonal equations corresponding to the random effects in the fixed part of the LHS. Thus, the LHS of the mixed model equations is:

$$LHS = \begin{bmatrix} X'R^{-1}X & X'R^{-1}Z_aQ_a & X'R^{-1}Z_nQ_n & X'R^{-1}Z_a \\ Q_a'Z_a'R^{-1}X & Q_a'Z_a'R^{-1}Z_aQ_a & Q_a'Z_a'R^{-1}Z_nQ_n & Q_a'Z_a'R^{-1}Z_a \\ Q_n'Z_n'R^{-1}X & Q_n'Z_n'R^{-1}Z_aQ_a & Q_n'Z_n'R^{-1}Z_nQ_n & Q_n'Z_n'R^{-1}Z_a \\ Z_a'R^{-1}X & Z_a'R^{-1}Z_aQ_a & Z_a'R^{-1}Z_nQ_n & Z_a'R^{-1}Z_a + G_a^{-1} \end{bmatrix}$$

The left-hand side matrix is:

LHS											
0.1964925	0.0825195	0.113973	0.102946	0.072454	0.1240385	0.0204082	0.0625	0.0307692	0.0307692	0.0307692	0.0212766
0.0825195	0.0554532	0.0270663	0.0541326	0.0517502	0.0307692	0.0204082	0	0.0153846	0.0153846	0.0153846	0.0159574
0.113973	0.0270663	0.0869067	0.0488134	0.0207038	0.0932692	0	0.0625	0.0153846	0.0153846	0.0153846	0.0053191
0.102946	0.0541326	0.0488134	0.0976268	0.0414075	0.0615385	0	0	0.0307692	0.0307692	0.0307692	0.0106383
0.072454	0.0517502	0.0207038	0.0414075	0.072454	0	0.0204082	0	0	0	0.0307692	0.0212766
0.1240385	0.0307692	0.0932692	0.0615385	0	0.1240385	0	0.0625	0.0307692	0.0307692	0	0
0.0204082	0.0204082	0	0	0.0204082	0	0.0789545	0.0125	0.0102041	-0.016129	-0.025	-0.020408
0.0625	0	0.0625	0	0	0.0625	0.0125	0.106348	-0.017241	0	-0.025	0
0.0307692	0.0153846	0.0153846	0.0307692	0	0.0307692	0.0102041	-0.017241	0.0754561	0	0	-0.020408
0.0307692	0.0153846	0.0153846	0.0307692	0	0.0307692	-0.016129	0	0	0.0630273	0	0
0.0307692	0.0153846	0.0153846	0.0307692	0.0307692	0	-0.025	-0.025	0	0	0.0807692	0
0.0212766	0.0159574	0.0053191	0.0106383	0.0212766	0	-0.020408	0	-0.020408	0	0	0.0620929

- 5) Compute the right hand side of the mixed model equation (RHS) by multiplying the transposes of the coefficient matrices in the model times R^{-1} times the vector of records, i.e.,

$$RHS = \begin{bmatrix} X' \\ Q_a'Z_a' \\ Q_n'Z_n' \\ Z_a' \end{bmatrix} [R^{-1}]y = \begin{bmatrix} X'R^{-1}y \\ Q_a'Z_a'R^{-1}y \\ Q_n'Z_n'R^{-1}y \\ Z_a'R^{-1}y \end{bmatrix}$$

The right-hand side vector is:

RHS
52.187873
22.907943
29.27993
27.934861
20.967681
31.220192
5.8979592
15.3125
7.8769231
8.0307692
8.9846154
6.0851064

- 6) Construct the mixed model equations by multiplying the left hand side times the vector of unknowns and making it equal to the right hand side, i.e., $LHS v = RHS$. Explicitly, the mixed model equations (MME) are:

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

7) Solutions to the vector of unknowns of the mixed model equations can be obtained directly or iteratively. Direct solutions are usually obtained when the mixed model equations are small (e.g., 1000 equations) and a generalized inverse of the LHS or other numerical approach is feasible, else solutions are obtained by iterative procedures (e.g., Gauss-Seidel, Jacobi). **If the computation of a generalized inverse is feasible, the vector of solutions can be obtained as the product of the generalized inverse of the LHS times the RHS, i.e.,**

$$\hat{v} = (LHS)^{-} RHS$$

or

$$\begin{bmatrix} b^\circ \\ g_a^\circ \\ g_n^\circ \\ \hat{a}_a \end{bmatrix} = \begin{bmatrix} X'R^{-1}X & X'R^{-1}Z_aQ_a & X'R^{-1}Z_nQ_n & X'R^{-1}Z_a \\ Q_a'Z_a'R^{-1}X & Q_a'Z_a'R^{-1}Z_aQ_a & Q_a'Z_a'R^{-1}Z_nQ_n & Q_a'Z_a'R^{-1}Z_a \\ Q_n'Z_n'R^{-1}X & Q_n'Z_n'R^{-1}Z_aQ_a & Q_n'Z_n'R^{-1}Z_nQ_n & Q_n'Z_n'R^{-1}Z_a \\ Z_a'R^{-1}X & Z_a'R^{-1}Z_aQ_a & Z_a'R^{-1}Z_nQ_n & Z_a'R^{-1}Z_a + G_a^{-1} \end{bmatrix}^{-1} \begin{bmatrix} X'R^{-1}y \\ Q_a'Z_a'R^{-1}y \\ Q_n'Z_n'R^{-1}y \\ Z_a'R^{-1}y \end{bmatrix}$$

The vector of solutions, the generalized inverse of the LHS, and the RHS for the example are:

Effect	ginvlhs = Generalized Inverse of LHS													RHS
Mean°	8.359	52.19	3.092	-10.29	5.198	3.161	-8.580	-10.61	-5.982	-4.837	-8.778	-9.287	52.19	
Breed _A °	5.267	22.91	-54.16	-17.25	-18.73	23.995	-15.43	18.900	-1.939	-11.10	11.771	-8.774	22.91	
Breed _B °	3.092	29.28	57.254	6.962	23.926	-20.83	6.851	-29.51	-4.044	6.261	-20.55	-0.514	29.28	
Heterosis _{AB} °	-10.29	27.93	6.962	38.276	-0.381	-9.909	4.368	5.237	-4.419	-5.196	-5.583	0.919	27.93	

Effect	ginvlhs = Generalized Inverse of LHS													RHS
Sex _M ^o	5.198	20.97	23.926	-0.381	22.168	-16.97	-7.763	-10.15	0.180	2.677	-16.82	-9.041	20.97	
Sex _F ^o	3.161	31.22	-20.83	-9.909	-16.97	20.131	-0.817	-0.458	-6.162	-7.514	8.039	-0.246	31.22	
\hat{a}_{a1}	-8.580	5.90	6.851	4.368	-7.763	-0.817	33.341	2.547	5.557	13.082	17.305	21.015	5.90	
\hat{a}_{a2}	-10.61	15.31	-29.51	5.237	-10.15	-0.458	2.547	40.582	16.188	6.090	21.287	10.047	15.31	
\hat{a}_{a3}	-5.982	7.88	-4.044	-4.419	0.180	-6.162	5.557	16.188	28.140	10.968	11.764	14.665	7.88	
\hat{a}_{a4}	-4.837	8.03	6.261	-5.196	2.677	-7.514	13.082	6.090	10.968	28.960	9.657	11.850	8.03	
\hat{a}_{a5}	-8.778	8.98	-20.55	-5.583	-16.82	8.039	17.305	21.287	11.764	9.657	37.875	18.016	8.98	
\hat{a}_{a6}	-9.287	6.09	-0.514	0.919	-9.041	-0.246	21.015	10.047	14.665	11.850	18.016	36.254	6.09	

Solutions to the mixed model equations were computed as the product of the generalized inverse of the LHS times the RHS. Standard errors of solutions were computed as square roots of the diagonal elements of the generalized inverse of the LHS.

The vector of solutions and their standard errors for the example are:

Effect	SOL	SESOL
Mean ^o	133.22	2.89
Breed _A ^o	71.28	7.71
Breed _B ^o	61.94	7.57
Heterosis _{AB} ^o	8.36	6.19
Sex _M ^o	82.73	4.71
Sex _F ^o	50.49	4.49

\hat{a}_{a1}	0.87	5.77
\hat{a}_{a2}	-0.65	6.37
\hat{a}_{a3}	-1.72	5.30
\hat{a}_{a4}	1.35	5.38
\hat{a}_{a5}	0.48	6.15
\hat{a}_{a6}	-1.33	6.02

Prediction of genetic values

Predictions of additive genetic values (\hat{u}_{ai}) are computed as the sum of the breed effect and the animal additive genetic deviation from the breed effect, i.e.,

$$\hat{u}_{ai} = \text{Prob}_{A\text{anim } i} * (\text{Breed}_A^\circ - \text{Breed}_B^\circ) + \hat{a}_{ai}$$

where

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

Breed_A° = generalized least squares solution for breed A,

Breed_B° = generalized least squares solution for breed B, and

\hat{a}_{ai} = BLUP of a_{ai} .

The matrix of variances of errors of prediction (VEP) for the vector of predicted genetic values (\hat{u}_a) is:

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

where

K_a = $n_{\text{anim}} \times n_{\text{eq}}$ matrix specifying multipliers for breed differences and random animal deviations, 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.

The standard errors of prediction (SEP) of the \hat{u}_{ai} are computed as the square roots of the diagonal elements of the $VEP(\hat{u}_{ai})$ matrix.

Matrix K_a for the Example is:

ka											
0.00	1.00	-1.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
0.00	0.50	-0.50	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
0.00	0.50	-0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
0.00	0.50	-0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
0.00	0.75	-0.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00

The \hat{u}_{ai} and their SEP for the animals in Example are:

Animal	Prob _{Aanim}	Breed _A ^o - Breed _B ^o	\hat{a}_{add}	\hat{u}_a	SEP (\hat{u}_a)
1	1	9.34	0.87	10.21	14.62
2	0	9.34	-0.65	-0.65	6.37
3	0.5	9.34	-1.72	2.95	9.30
4	0.5	9.34	1.35	6.02	8.24
5	0.5	9.34	0.48	5.15	11.24
6	0.75	9.34	-1.33	5.67	12.26

Polygenic-Genomic Marker Model with a single fixed marker locus effect

Example

Prediction of the polygenic-genomic values of animals for weaning weight using the following phenotypic and genomic information for a single marker locus on 6 calves.

Animal	Breed Compsn	Leptin Promoter Genotype ¹	Sex	Weaning weight (kg)	Sire	Breed Compsn	Dam	Breed Compsn
1	A	GG	M	289	0	A	0	A
2	B	CC	F	245	0	B	0	B
3	½ A ½ B	CG	F	256	0	A	2	B
4	½ A ½ B	GC	F	261	1	A	0	B
5	½ A ½ B	GC	M	292	1	A	2	B
6	¾ A ¼ B	GG	M	286	1	A	3	½ A ½ B

¹Nkrumah et al. (2005)

Additive Genetic and Residual Variances

Variance	Additive Genetic	Residual
Intrabreed AA	36 kg ²	49 kg ²
Intrabreed BB	44 kg ²	16 kg ²
Interbreed AB	22 kg ²	25 kg ²

Polygenic-Genomic Marker Model

Wean wt = overall mean + breed regression + heterosis regression + sex + marker 1 regression + animal additive genetic + residual

$$E[\text{Wean wt}] = \text{overall mean} + \text{breed regression} + \text{heterosis regression} + \text{sex} + \text{marker 1 regression}$$

$$\text{Var}(\text{Wean wt}) = \text{var}(\text{animal additive genetic}) + \text{var}(\text{residual})$$

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

The polygenic-genomic marker model, in matrix notation, is:

$$y = Xb + Z_a Q_a g_a + Z_{ma} g_{ma} + Z_n Q_n g_n + Z_a a_a + \varepsilon$$

$$E[y] = Xb + Z_a Q_a g_a + Z_{ma} g_{ma} + Z_n Q_n g_n$$

$$\text{var} \begin{bmatrix} a_a \\ \varepsilon \end{bmatrix} = \begin{bmatrix} G_a & 0 \\ 0 & R \end{bmatrix}$$

$$\text{var}(y) = Z_a G_a Z_a' + R$$

where

y = vector of animal records,

b = vector of unknown fixed effects (mean, sex of calf),

g_a = vector of unknown additive group genetic effects (breed),

g_n = vector of unknown nonadditive group genetic effects (heterosis at 1 locus),

g_{ma} = vector of unknown fixed marker locus 1 additive genetic effect,

a_a = vector of unknown random polygenic additive genetic effects,

ε = 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 random polygenic nonadditive genetic effects in vector a_n (a_n is assumed to be part of the residual),

Z_{ma} = known incidence matrix relating records to elements of vector g_{ma} ; elements of Z_{ma} will be 0, 1, 2 depending on the number of G alleles in marker 1,

Q_a = known incidence matrix relating random polygenic additive genetic effects to additive genetic groups in vector g_a ,

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

G_a = matrix of polygenic additive genetic variances and covariances among animals (purebred and crossbred) in the multibreed population; covariances are due to additive relationships among animals.

R = matrix of residual variances for purebred and crossbred animals (sums of nonadditive genetic and environmental variances).

The mixed model with the information of the 6 calves can be written as follows:

$$\begin{bmatrix} 289 \\ 245 \\ 256 \\ 261 \\ 292 \\ 286 \end{bmatrix} = \begin{bmatrix} 1 & 1 & 0 & 0 & 1 & 0 \\ 1 & 0 & 1 & 0 & 0 & 1 \\ 1 & 1/2 & 1/2 & 1 & 0 & 1 \\ 1 & 1/2 & 1/2 & 1 & 0 & 1 \\ 1 & 1/2 & 1/2 & 1 & 1 & 0 \\ 1 & 3/4 & 1/4 & 1/2 & 1 & 0 \end{bmatrix} \begin{bmatrix} mean \\ breed_A \\ breed_B \\ heterosis_{AB} \\ sex_M \\ sex_F \end{bmatrix} + \begin{bmatrix} 2 \\ 0 \\ 1 \\ 1 \\ 1 \\ -2 \end{bmatrix} [ma_1]$$

$$+ \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} animal\ 1_{add} \\ animal\ 2_{add} \\ animal\ 3_{add} \\ animal\ 4_{add} \\ animal\ 5_{add} \\ animal\ 6_{add} \end{bmatrix} + \begin{bmatrix} residual_{anim\ 1} \\ residual_{anim\ 2} \\ residual_{anim\ 3} \\ residual_{anim\ 4} \\ residual_{anim\ 5} \\ residual_{anim\ 6} \end{bmatrix}$$

The mixed model equations (MME) are:

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z_aQ_a & X'R^{-1}Z_nQ_n & X'R^{-1}Z_{ma} & X'R^{-1}Z_a \\ Q'_aZ'_aR^{-1}X & Q'_aZ'_aR^{-1}Z_aQ_a & Q'_aZ'_aR^{-1}Z_nQ_n & Q'_aZ'_aR^{-1}Z_{ma} & Q'_aZ'_aR^{-1}Z_a \\ Q'_nZ'_nR^{-1}X & Q'_nZ'_nR^{-1}Z_aQ_a & Q'_nZ'_nR^{-1}Z_nQ_n & Q'_nZ'_nR^{-1}Z_{ma} & Q'_nZ'_nR^{-1}Z_a \\ Z'_{ma}R^{-1}X & Z'_{ma}R^{-1}Z_aQ_a & Z'_{ma}R^{-1}Z_nQ_n & Z'_{ma}R^{-1}Z_{ma} & Z'_{ma}R^{-1}Z_a \\ Z'_aR^{-1}X & Z'_aR^{-1}Z_aQ_a & Z'_aR^{-1}Z_nQ_n & Z'_aR^{-1}Z_{ma} & Z'_aR^{-1}Z_a + G_a^{-1} \end{bmatrix} \begin{bmatrix} b \\ g_a \\ g_n \\ g_{ma} \\ a_a \end{bmatrix}$$

$$= \begin{bmatrix} X'R^{-1}y \\ Q'_aZ'_aR^{-1}y \\ Q'_nZ'_nR^{-1}y \\ Z'_{ma}R^{-1}y \\ Z'_aR^{-1}y \end{bmatrix}$$

Matrix $[X \ Z_aQ_a \ Z_nQ_n \ Z_{ma} \ Z_a]$ is:

xf = [X Z _a Q _a Z _n Q _n Z _{ma} Z _a]											
1	1	0	0	1	0	2	1	0	0	0	0
1	0	1	0	0	1	0	0	1	0	0	0
1	0.5	0.5	1	0	1	1	0	0	1	0	0
1	0.5	0.5	1	0	1	1	0	0	0	1	0
1	0.5	0.5	1	1	0	1	0	0	0	0	1
1	0.75	0.25	0.5	1	0	2	0	0	0	0	1

The inverse of the matrix of residual effects, R^{-1} , is:

invr = R ⁻¹					
0.0204082	0	0	0	0	0
0	0.0625	0	0	0	0
0	0	0.0307692	0	0	0
0	0	0	0.0307692	0	0
0	0	0	0	0.0307692	0
0	0	0	0	0	0.0212766

The inverse of the matrix of covariances among animal effects, G_a^{-1} , is:

gainv = G_a^{-1}					
0.0585464	0.0125	0.0102041	-0.016129	-0.025	-0.020408
0.0125	0.043848	-0.017241	0	-0.025	0
0.0102041	-0.017241	0.0446868	0	0	-0.020408
-0.016129	0	0	0.0322581	0	0
-0.025	-0.025	0	0	0.05	0
-0.020408	0	-0.020408	0	0	0.0408163

The LHS matrix, the vector of effects, and the RHS vector of the mixed model equations are:

LHS													Effect	RHS
0.196	0.083	0.114	0.103	0.072	0.124	0.176	0.020	0.063	0.031	0.031	0.031	0.021	Mean	52.19
0.083	0.055	0.027	0.054	0.052	0.031	0.119	0.020	0.000	0.015	0.015	0.015	0.016	Breed _A	22.91
0.114	0.027	0.087	0.049	0.021	0.093	0.057	0.000	0.063	0.015	0.015	0.015	0.005	Breed _B	29.28
0.103	0.054	0.049	0.098	0.041	0.062	0.114	0.000	0.000	0.031	0.031	0.031	0.011	Heterosis _{AB}	27.93
0.072	0.052	0.021	0.041	0.072	0.000	0.114	0.020	0.000	0.000	0.000	0.031	0.021	Sex _M	20.97
0.124	0.031	0.093	0.062	0.000	0.124	0.062	0.000	0.063	0.031	0.031	0.000	0.000	Sex _F	31.22
0.176	0.119	0.057	0.114	0.114	0.062	0.259	0.041	0.000	0.031	0.031	0.031	0.043	ma ₁	48.86
0.020	0.020	0.000	0.000	0.020	0.000	0.041	0.078	0.012	0.010	-0.016	-0.024	-0.020	a ₁	5.90
0.063	0.000	0.063	0.000	0.000	0.063	0.000	0.012	0.105	-0.017	0.000	-0.024	0.000	a ₂	15.31
0.031	0.015	0.015	0.031	0.000	0.031	0.031	0.010	-0.017	0.074	0.000	0.000	-0.020	a ₃	7.88
0.031	0.015	0.015	0.031	0.000	0.031	0.031	-0.016	0.000	0.000	0.063	0.000	0.000	a ₄	8.03
0.031	0.015	0.015	0.031	0.031	0.000	0.031	-0.024	-0.024	0.000	0.000	0.078	0.000	a ₅	8.98
0.021	0.016	0.005	0.011	0.021	0.000	0.043	-0.020	0.000	-0.020	0.000	0.000	0.062	a ₆	6.09

The vector of **solutions** and their **standard errors** are:

Effect	SOL	SESOL
Mean ^o	137.38	11.40
Breed _A ^o	80.91	26.66
Breed _B ^o	56.47	16.35
Heterosis _{AB} ^o	8.22	6.20
Sex _M ^o	85.47	8.67
Sex _F ^o	51.91	5.85
ma1^o	-7.69	20.38
\hat{a}_{a1}	0.62	5.81
\hat{a}_{a2}	-0.76	6.38
\hat{a}_{a3}	-1.38	5.38
\hat{a}_{a4}	1.38	5.38
\hat{a}_{a5}	-0.07	6.32
\hat{a}_{a6}	-0.38	6.53

Prediction of polygenic-genomic values

Predictions of additive polygenic-genomic values (\hat{u}_{ai}) are computed as the sum of the breed effect, the fixed effect of the single marker, and the animal additive genetic deviation from the breed effect, i.e.,

$$\hat{u}_{ai} = \text{Prob}_{A_{\text{anim } i}} * (\text{Breed}_A^o - \text{Breed}_B^o) + \text{W}_{\text{ma1Anim } i} * \text{g}_{\text{ma1}}^o + \hat{a}_{ai}$$

where

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

Breed_A° = generalized least squares solution for breed A,

Breed_B° = generalized least squares solution for breed B,

$\mathbf{W}_{\text{ma1Anim } i}$ = number of G alleles in marker locus 1 of animal i ,

$\mathbf{g}_{\text{ma1}}^\circ$ = generalized least squares solution for the difference between alleles G and C in marker locus 1, and

\hat{a}_{ai} = BLUP of a_{ai} .

The matrix of variances of errors of prediction (VEP) for the vector of predicted genetic values ($\hat{\mathbf{u}}_a$) is:

$$\text{VEP}(\hat{\mathbf{u}}_a) = \text{var}(\hat{\mathbf{u}}_a - \mathbf{u}_a) = \mathbf{K}_a * (\text{ginvlhs}) * \mathbf{K}_a'$$

where

\mathbf{K}_a = $n_{\text{anim}} \times n_{\text{eq}}$ matrix specifying multipliers for breed differences, **allele difference within marker locus 1**, and random animal deviations, 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 the MME.

The standard errors of prediction (SEP) of the \hat{u}_{ai} are computed as the square roots of the diagonal elements of the $\text{VEP}(\hat{\mathbf{u}}_{ai})$ matrix.

Matrix K_a for the Example is:

ka												
0.00	1.00	-1.00	0.00	0.00	0.00	2.00	1.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
0.00	0.50	-0.50	0.00	0.00	0.00	1.00	0.00	0.00	1.00	0.00	0.00	0.00
0.00	0.50	-0.50	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00
0.00	0.50	-0.50	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	1.00	0.00
0.00	0.75	-0.75	0.00	0.00	0.00	2.00	0.00	0.00	0.00	0.00	0.00	1.00

The \hat{u}_{ai} and their **SEP** for the animals in the Example are:

Animal	Prob _{Aanim}	Breed _A ^o - Breed _B ^o	Weight marker 1	g_{mal}^o	\hat{a}_{add}	\hat{u}_a	SEP (\hat{u}_a)
1	1	24.44	2	-7.69	0.62	9.67	14.69
2	0	24.44	0	-7.69	-0.76	-0.76	6.38
3	0.5	24.44	1	-7.69	-1.38	3.15	9.32
4	0.5	24.44	1	-7.69	1.38	5.91	8.24
5	0.5	24.44	1	-7.69	-0.07	4.46	11.39
6	0.75	24.44	2	-7.69	-0.38	2.56	14.77

Polygenic-Genomic Marker Model with a small number of fixed marker locus effects

Example

Prediction of the polygenic-genomic values of animals for weaning weight using the following phenotypic and genomic information for 4 marker loci on 6 calves.

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

¹Number of “second” alleles (VanRaden, 2008).

Additive Genetic and Residual Variances

Variance	Additive Genetic	Residual
Intrabreed AA	36 kg ²	49 kg ²
Intrabreed BB	44 kg ²	16 kg ²
Interbreed AB	22 kg ²	25 kg ²

Polygenic-Genomic Marker Model

$$\text{Wean wt} = \text{overall mean} + \text{breed regression} + \text{heterosis regression} + \text{sex} + \text{sum regression markers 1 to 4} + \text{animal additive genetic} + \text{residual}$$

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

regression markers 1 to 4

$$\text{Var}(\text{Wean wt}) = \text{var}(\text{animal additive genetic}) + \text{var}(\text{residual})$$

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

The **polygenic-genomic marker model**, in matrix notation, is:

$$y = Xb + Z_a Q_a g_a + Z_{ma} g_{ma} + Z_n Q_n g_n + Z_a a_a + \varepsilon$$

$$E[y] = Xb + Z_a Q_a g_a + Z_{ma} g_{ma} + Z_n Q_n g_n$$

$$\text{var} \begin{bmatrix} a_a \\ \varepsilon \end{bmatrix} = \begin{bmatrix} G_a & 0 \\ 0 & R \end{bmatrix}$$

$$\text{var}(y) = Z_a G_a Z_a' + R$$

where

y = vector of animal records,

b = vector of unknown fixed effects (mean, sex of calf),

g_a = vector of unknown additive group genetic effects (breed),

g_n = vector of unknown nonadditive group genetic effects (heterosis at 1 locus),

g_{ma} = vector of unknown fixed marker loci additive genetic effects,

a_a = vector of unknown random polygenic additive genetic effects,

ε = 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 random polygenic nonadditive genetic effects in vector a_n (a_n is assumed to be part of the residual),

Z_{ma} = known incidence matrix relating records to elements of vector g_{ma} ; elements of Z_{ma} will

be 0, 1, 2 depending on the number of “second” alleles in marker j , $j = 1, \dots, 4$,

Q_a = known incidence matrix relating random polygenic additive genetic effects to additive genetic groups in vector g_a ,

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

G_a = matrix of polygenic additive genetic variances and covariances among animals (purebred and crossbred) in the multibreed population; covariances are due to additive relationships among animals.

R = matrix of residual variances for purebred and crossbred animals (sums of nonadditive genetic and environmental variances).

The mixed model with the information of the 6 calves can be written as follows:

$$\begin{bmatrix} 289 \\ 245 \\ 256 \\ 261 \\ 292 \\ 286 \end{bmatrix} = \begin{bmatrix} 1 & 1 & 0 & 0 & 1 & 0 \\ 1 & 0 & 1 & 0 & 0 & 1 \\ 1 & 1/2 & 1/2 & 1 & 0 & 1 \\ 1 & 1/2 & 1/2 & 1 & 0 & 1 \\ 1 & 1/2 & 1/2 & 1 & 1 & 0 \\ 1 & 3/4 & 1/4 & 1/2 & 1 & 0 \end{bmatrix} \begin{bmatrix} \text{mean} \\ \text{breed}_A \\ \text{breed}_B \\ \text{heterosis}_{AB} \\ \text{sex}_M \\ \text{sex}_F \end{bmatrix} + \begin{bmatrix} 2 & 1 & 1 & 2 \\ 0 & 1 & 2 & 0 \\ 1 & 2 & 0 & 0 \\ 1 & 2 & 0 & 0 \\ 1 & 2 & 0 & 1 \\ 2 & 1 & 2 & 2 \end{bmatrix} \begin{bmatrix} ma_1 \\ ma_2 \\ ma_3 \\ ma_4 \end{bmatrix} \\ + \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} \text{animal } 1_{add} \\ \text{animal } 2_{add} \\ \text{animal } 3_{add} \\ \text{animal } 4_{add} \\ \text{animal } 5_{add} \\ \text{animal } 6_{add} \end{bmatrix} + \begin{bmatrix} \text{residual}_{anim 1} \\ \text{residual}_{anim 2} \\ \text{residual}_{anim 3} \\ \text{residual}_{anim 4} \\ \text{residual}_{anim 5} \\ \text{residual}_{anim 6} \end{bmatrix}$$

The mixed model equations (MME) are:

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z_aQ_a & X'R^{-1}Z_nQ_n & X'R^{-1}Z_{ma} & X'R^{-1}Z_a \\ Q'_aZ'_aR^{-1}X & Q'_aZ'_aR^{-1}Z_aQ_a & Q'_aZ'_aR^{-1}Z_nQ_n & Q'_aZ'_aR^{-1}Z_{ma} & Q'_aZ'_aR^{-1}Z_a \\ Q'_nZ'_nR^{-1}X & Q'_nZ'_nR^{-1}Z_aQ_a & Q'_nZ'_nR^{-1}Z_nQ_n & Q'_nZ'_nR^{-1}Z_{ma} & Q'_nZ'_nR^{-1}Z_a \\ Z'_{ma}R^{-1}X & Z'_{ma}R^{-1}Z_aQ_a & Z'_{ma}R^{-1}Z_nQ_n & Z'_{ma}R^{-1}Z_{ma} & Z'_{ma}R^{-1}Z_a \\ Z'_aR^{-1}X & Z'_aR^{-1}Z_aQ_a & Z'_aR^{-1}Z_nQ_n & Z'_aR^{-1}Z_{ma} & Z'_aR^{-1}Z_a + G_a^{-1} \end{bmatrix} \begin{bmatrix} b \\ g_a \\ g_n \\ g_{ma} \\ a_a \end{bmatrix}$$

$$= \begin{bmatrix} X'R^{-1}y \\ Q'_aZ'_aR^{-1}y \\ Q'_nZ'_nR^{-1}y \\ Z'_{ma}R^{-1}y \\ Z'_aR^{-1}y \end{bmatrix}$$

Matrix $[X \ Z_aQ_a \ Z_nQ_n \ Z_{ma} \ Z_a]$ is:

$xf = [X \ Z_aQ_a \ Z_nQ_n \ Z_{ma} \ Z_a]$														
1	1	0	0	1	0	2	1	1	2	1	0	0	0	0
1	0	1	0	0	1	0	1	2	0	0	1	0	0	0
1	0.5	0.5	1	0	1	1	2	0	0	0	0	1	0	0
1	0.5	0.5	1	0	1	1	2	0	0	0	0	0	1	0
1	0.5	0.5	1	1	0	1	2	0	1	0	0	0	0	1
1	0.75	0.25	0.5	1	0	2	1	2	2	0	0	0	0	1

The inverse of the matrix of residual effects, R^{-1} , is:

$invr = R^{-1}$					
0.0204082	0	0	0	0	0
0	0.0625	0	0	0	0
0	0	0.0307692	0	0	0
0	0	0	0.0307692	0	0
0	0	0	0	0.0307692	0
0	0	0	0	0	0.0212766

The inverse of the matrix of covariances among animal effects, G_a^{-1} , is:

gainv = G_a^{-1}					
0.0585464	0.0125	0.0102041	-0.016129	-0.025	-0.020408
0.0125	0.043848	-0.017241	0	-0.025	0
0.0102041	-0.017241	0.0446868	0	0	-0.020408
-0.016129	0	0	0.0322581	0	0
-0.025	-0.025	0	0	0.05	0
-0.020408	0	-0.020408	0	0	0.0408163

The LHS matrix, the vector of effects, and the RHS vector of the mixed model equations are:

lhs																Effect	rhs
0.196	0.083	0.114	0.103	0.072	0.124	0.176	0.289	0.188	0.114	0.020	0.063	0.031	0.031	0.031	0.021	Mean	52.19
0.083	0.055	0.027	0.054	0.052	0.031	0.119	0.129	0.052	0.088	0.020	0.000	0.015	0.015	0.015	0.016	Breed _A	22.91
0.114	0.027	0.087	0.049	0.021	0.093	0.057	0.160	0.136	0.026	0.000	0.063	0.015	0.015	0.015	0.005	Breed _B	29.28
0.103	0.054	0.049	0.098	0.041	0.062	0.114	0.195	0.021	0.052	0.000	0.000	0.031	0.031	0.031	0.011	Heterosis _{AB}	27.93
0.072	0.052	0.021	0.041	0.072	0.000	0.114	0.103	0.063	0.114	0.020	0.000	0.000	0.000	0.031	0.021	Sex _M	20.97
0.124	0.031	0.093	0.062	0.000	0.124	0.062	0.186	0.125	0.000	0.000	0.063	0.031	0.031	0.000	0.000	Sex _F	31.22
0.176	0.119	0.057	0.114	0.114	0.062	0.259	0.268	0.126	0.198	0.041	0.000	0.031	0.031	0.031	0.043	ma ₁	48.86
0.289	0.129	0.160	0.195	0.103	0.186	0.268	0.473	0.188	0.145	0.020	0.063	0.062	0.062	0.062	0.021	ma ₂	77.08
0.188	0.052	0.136	0.021	0.063	0.125	0.126	0.188	0.356	0.126	0.020	0.125	0.000	0.000	0.000	0.043	ma ₃	48.69
0.114	0.088	0.026	0.052	0.114	0.000	0.198	0.145	0.126	0.198	0.041	0.000	0.000	0.000	0.031	0.043	ma ₄	32.95
0.020	0.020	0.000	0.000	0.020	0.000	0.041	0.020	0.020	0.041	0.078	0.012	0.010	-0.016	-0.024	-0.020	a _{a1}	5.90
0.063	0.000	0.063	0.000	0.000	0.063	0.000	0.063	0.125	0.000	0.012	0.105	-0.017	0.000	-0.024	0.000	a _{a2}	15.31
0.031	0.015	0.015	0.031	0.000	0.031	0.031	0.062	0.000	0.000	0.010	-0.017	0.074	0.000	0.000	-0.020	a _{a3}	7.88
0.031	0.015	0.015	0.031	0.000	0.031	0.031	0.062	0.000	0.000	-0.016	0.000	0.000	0.063	0.000	0.000	a _{a4}	8.03
0.031	0.015	0.015	0.031	0.031	0.000	0.031	0.062	0.000	0.031	-0.024	-0.024	0.000	0.000	0.078	0.000	a _{a5}	8.98
0.021	0.016	0.005	0.011	0.021	0.000	0.043	0.021	0.043	0.043	-0.020	0.000	-0.020	0.000	0.000	0.062	a _{a6}	6.09

The vector of **solutions** and their **standard errors** are:

Effect	SOL	SESOL
Mean ^o	67.11	4.79
Breed _A ^o	26.54	3.85
Breed _B ^o	40.57	3.24
Heterosis _{AB} ^o	-37.15	11.84
Sex _M ^o	35.23	4.80
Sex _F ^o	31.88	4.31
ma₁^o	2.96	5.79
ma₂^o	80.07	3.57
ma₃^o	13.06	5.37
ma₄^o	30.22	2.68
\hat{a}_{a1}	0.62	5.81
\hat{a}_{a2}	-0.76	6.38
\hat{a}_{a3}	-1.38	5.38
\hat{a}_{a4}	1.38	5.38
\hat{a}_{a5}	-0.07	6.32
\hat{a}_{a6}	-0.38	6.53

Prediction of polygenic-genomic values

Predictions of additive polygenic-genomic values (\hat{u}_{ai}) are computed as the sum of the breed effect, the sum of the fixed effects of the 4 markers, and the animal additive polygenic deviation from the breed effect, i.e.,

$$\hat{u}_{ai} = \text{Prob}_{A_{\text{anim } i}} * (\text{Breed}_A^\circ - \text{Breed}_B^\circ) + \sum_{j=1}^{j=4} W_{\text{ma } j \text{ Anim } i} * g_{\text{ma } j}^\circ + \hat{a}_{ai}$$

where

- $\text{Prob}_{A_{\text{anim } i}}$ = expected fraction of breed A in animal i,
 Breed_A° = generalized least squares solution for breed A,
 Breed_B° = generalized least squares solution for breed B,
 $W_{\text{ma } j \text{ Anim } i}$ = number of “second” alleles in marker locus j of animal i,
 $g_{\text{ma } j}^\circ$ = generalized least squares solution for marker locus j, and
 \hat{a}_{ai} = BLUP of a_{ai} .

The matrix of variances of errors of prediction (VEP) for the vector of predicted genetic values (\hat{u}_a) is:

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

where

- K_a = $n_{\text{anim}} \times n_{\text{eq}}$ matrix specifying multipliers for breed differences, **allele difference in marker locus j, j = 1, 2, 3, 4**, and random animal deviations, 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 the MME.

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

Matrix K_a for the Example is:

ka															
0.00	1.00	-1.00	0.00	0.00	0.00	2.00	1.00	1.00	2.00	1.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	2.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
0.00	0.50	-0.50	0.00	0.00	0.00	1.00	2.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
0.00	0.50	-0.50	0.00	0.00	0.00	1.00	2.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
0.00	0.50	-0.50	0.00	0.00	0.00	1.00	2.00	0.00	1.00	0.00	0.00	0.00	0.00	1.00	0.00
0.00	0.75	-0.75	0.00	0.00	0.00	2.00	1.00	2.00	2.00	0.00	0.00	0.00	0.00	0.00	1.00

Remarks: marker loci 1, 2, 3, and 4 regression effects were **confounded** with other effects in the model. This can be verified by multiplying matrix $K_a * \text{ginvlhs} * \text{lhs}$. If multipliers for markers $j, j = 1, 2, 3, 4$ in matrix K_a are recreated exactly in matrix $(K_a * \text{ginvlhs} * \text{lhs})$, then markers $j, j = 1, 2, 3, 4$ are estimable, else they are not. Matrix $K_a * \text{ginvlhs} * \text{lhs}$ was:

kagl															
0.50	0.99	-0.49	0.17	0.42	0.08	2.32	0.33	-0.78	1.66	1.00	-0.00	0.00	0.00	0.00	0.00
0.42	-0.14	0.56	0.29	0.11	0.31	0.09	0.34	-1.68	0.20	0.00	1.00	0.00	0.00	0.00	-0.00
0.58	0.52	0.06	0.46	0.13	0.45	0.93	1.15	-0.37	0.31	0.00	0.00	1.00	0.00	0.00	0.00
0.58	0.52	0.06	0.46	0.13	0.45	0.93	1.15	-0.37	0.31	0.00	0.00	0.00	1.00	0.00	0.00
0.66	0.65	0.01	0.35	0.44	0.22	1.16	1.14	-0.26	0.78	0.00	0.00	0.00	0.00	1.00	0.00
0.58	0.82	-0.24	0.26	0.43	0.15	2.24	0.24	-1.76	1.72	0.00	-0.00	0.00	0.00	0.00	1.00

Thus, **neither breed differences nor marker regression effects were estimable**. Consequently, **polygenic-genomic predictions for animal $i, i = 1, \dots, 6$, were biased**. The prediction for each animal contains a linear combination of the overall mean, $\text{breed}_A, \text{breed}_B, \text{heterosis}_{AB}, \text{sex}, \text{ma1}, \text{ma2}, \text{ma3},$ and ma4 effects plus its own random deviation.

The (biased) \hat{u}_{ai} and their SEP for the animals in the Example are:

Anim	Prob_A	Br_A^o - Br_B^o	w_{ma1}	w_{ma2}	w_{ma3}	w_{ma4}	g_{ma1}^o	g_{ma2}^o	g_{ma3}^o	g_{ma4}^o	â_{add}	û_a	SEP (û_a)
1	1	-14.03	2	1	1	2	2.96	80.07	13.06	30.22	0.62	146.10	11.67
2	0	-14.03	0	1	2	0	2.96	80.07	13.06	30.22	-0.76	105.44	8.79
3	0.5	-14.03	1	2	0	0	2.96	80.07	13.06	30.22	-1.38	154.71	6.40
4	0.5	-14.03	1	2	0	0	2.96	80.07	13.06	30.22	1.38	157.47	5.40
5	0.5	-14.03	1	2	0	1	2.96	80.07	13.06	30.22	-0.07	186.24	7.56
6	0.75	-14.03	2	1	2	2	2.96	80.07	13.06	30.22	-0.38	161.67	11.74

Polygenic-Genomic Marker Model with a small number of random marker locus effects

Example

Prediction of the polygenic-genomic values of animals for weaning weight using the following phenotypic and genomic information for 4 marker loci on 6 calves.

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

¹Number of “second” alleles (VanRaden, 2008).

Additive Genetic and Residual Variances

Variance	Additive Genetic	Residual
Intrabreed AA	36 kg ²	49 kg ²
Intrabreed BB	44 kg ²	16 kg ²
Interbreed AB	22 kg ²	25 kg ²

Polygenic-Genomic Marker Model

Wean wt = overall mean + breed regression + heterosis regression + sex + sum
regression markers 1 to 4 + animal polygenic additive genetic + residual

E [Wean wt] = overall mean + breed regression + heterosis regression + sex

$$\begin{aligned} \text{Var}(\text{Wean wt}) &= \text{sum} [\text{var}(\text{ma } j \text{ regression}), j = 1 \text{ to } 4] + \text{var}(\text{animal polygenic additive genetic}) + \text{var}(\text{residual}) \\ \text{cov}(\text{Wean wt}_{ik}, \text{Wean wt}_{i'k'}) &= \text{sum} [\text{cov}(\text{ma } j \text{ regression}, \text{ma } j' \text{ regression}), j, j' = 1 \text{ to } 4] + \\ &\quad \text{cov}(\text{animal additive genetic}_i, \text{animal additive genetic}_{i'}) \\ &\quad + \text{cov}(\text{residual}_{ik}, \text{residual}_{i'k'}) \\ \text{cov}(\text{Wean wt}_{ik}, \text{Wean wt}_{i'k'}) &= 0 + \text{cov}(\text{animal additive genetic}_i, \text{animal additive genetic}_{i'}) \\ &\quad + \text{cov}(\text{residual}_{ik}, \text{residual}_{i'k'}) \\ \text{cov}(\text{Wean wt}_{ik}, \text{Wean wt}_{i'k'}) &= \text{cov}(\text{animal additive genetic}_i, \text{animal additive genetic}_{i'}) \\ &\quad + \text{cov}(\text{residual}_{ik}, \text{residual}_{i'k'}) \end{aligned}$$

The polygenic-genomic marker model, in matrix notation, is:

$$y = Xb + Z_a Q_a g_a + Z_n Q_n g_n + Z_{ma} m_a + Z_a a_a + \varepsilon$$

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

$$\text{var} \begin{bmatrix} m_a \\ a_a \\ \varepsilon \end{bmatrix} = \begin{bmatrix} G_{ma} & 0 & 0 \\ 0 & G_a & 0 \\ 0 & 0 & R \end{bmatrix}$$

$$\text{var}(y) = Z_{ma} G_{ma} Z_{ma}' + Z_a G_a Z_a' + R$$

where

y = vector of animal records,

b = vector of unknown fixed effects (mean, sex of calf),

g_a = vector of unknown additive group genetic effects (breed),

g_n = vector of unknown nonadditive group genetic effects (heterosis at 1 locus),

m_a = vector of unknown random marker locus additive genomic effects,

a_a = vector of unknown random polygenic additive genetic effects,

- ε = 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 random polygenic nonadditive genetic effects in vector a_n (a_n is assumed to be part of the residual),
- Z_{ma} = known incidence matrix relating records to elements of vector ma ; elements of Z_{ma} will be 0, 1, 2 depending on the number of “second” alleles in marker locus j , $j = 1, \dots, 4$,
- Q_a = known incidence matrix relating random polygenic additive genetic effects to additive genetic groups in vector g_a ,
- Q_n = known incidence matrix relating random polygenic nonadditive genetic effects to nonadditive genetic groups in vector g_n ,
- G_{ma} = $nma \times nma$ diagonal matrix of marker locus additive genomic variances (assumed to be equal for all markers associated with a trait),
- = $I * \sigma_{ma}^2$
- = $I * \{ \sigma_a^2 / 2 \sum_{j=1}^{j=nma} p_j (1 - p_j) \}$, where σ_a^2 = polygenic additive genetic variance, nma = number of marker loci (in linkage disequilibrium with QTL), and p_j = frequency of “second” allele in marker j ,
- G_a = matrix of polygenic additive genetic variances and covariances among animals (purebred and crossbred) in the multibreed population; covariances are due to additive relationships among animals.
- R = matrix of residual variances for purebred and crossbred animals (sums of nonadditive

genetic and environmental variances).

The mixed model with the information of the 6 calves can be written as follows:

$$\begin{bmatrix} 289 \\ 245 \\ 256 \\ 261 \\ 292 \\ 286 \end{bmatrix} = \begin{bmatrix} 1 & 1 & 0 & 0 & 1 & 0 \\ 1 & 0 & 1 & 0 & 0 & 1 \\ 1 & 1/2 & 1/2 & 1 & 0 & 1 \\ 1 & 1/2 & 1/2 & 1 & 0 & 1 \\ 1 & 1/2 & 1/2 & 1 & 1 & 0 \\ 1 & 3/4 & 1/4 & 1/2 & 1 & 0 \end{bmatrix} \begin{bmatrix} \textit{mean} \\ \textit{breed}_A \\ \textit{breed}_B \\ \textit{heterosis}_{AB} \\ \textit{sex}_M \\ \textit{sex}_F \end{bmatrix} + \begin{bmatrix} 2 & 1 & 1 & 2 \\ 0 & 1 & 2 & 0 \\ 1 & 2 & 0 & 0 \\ 1 & 2 & 0 & 0 \\ 1 & 2 & 0 & 1 \\ 2 & 1 & 2 & 2 \end{bmatrix} \begin{bmatrix} \textit{ma}_1 \\ \textit{ma}_2 \\ \textit{ma}_3 \\ \textit{ma}_4 \end{bmatrix} \\
 + \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} \textit{animal 1}_{add} \\ \textit{animal 2}_{add} \\ \textit{animal 3}_{add} \\ \textit{animal 4}_{add} \\ \textit{animal 5}_{add} \\ \textit{animal 6}_{add} \end{bmatrix} + \begin{bmatrix} \textit{residual}_{anim 1} \\ \textit{residual}_{anim 2} \\ \textit{residual}_{anim 3} \\ \textit{residual}_{anim 4} \\ \textit{residual}_{anim 5} \\ \textit{residual}_{anim 6} \end{bmatrix}$$

The mixed model equations (MME) are:

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z_aQ_a & X'R^{-1}Z_nQ_n & X'R^{-1}Z_{ma} & X'R^{-1}Z_a \\ Q'_aZ'_aR^{-1}X & Q'_aZ'_aR^{-1}Z_aQ_a & Q'_aZ'_aR^{-1}Z_nQ_n & Q'_aZ'_aR^{-1}Z_{ma} & Q'_aZ'_aR^{-1}Z_a \\ Q'_nZ'_nR^{-1}X & Q'_nZ'_nR^{-1}Z_aQ_a & Q'_nZ'_nR^{-1}Z_nQ_n & Q'_nZ'_nR^{-1}Z_{ma} & Q'_nZ'_nR^{-1}Z_a \\ Z'_{ma}R^{-1}X & Z'_{ma}R^{-1}Z_aQ_a & Z'_{ma}R^{-1}Z_nQ_n & Z'_{ma}R^{-1}Z_{ma} + G_{ma}^{-1} & Z'_{ma}R^{-1}Z_a \\ Z'_aR^{-1}X & Z'_aR^{-1}Z_aQ_a & Z'_aR^{-1}Z_nQ_n & Z'_aR^{-1}Z_{ma} & Z'_aR^{-1}Z_a + G_a^{-1} \end{bmatrix} \begin{bmatrix} b \\ g_a \\ g_n \\ \textit{ma}_a \\ a_a \end{bmatrix} \\
 = \begin{bmatrix} X'R^{-1}y \\ Q'_aZ'_aR^{-1}y \\ Q'_nZ'_nR^{-1}y \\ Z'_{ma}R^{-1}y \\ Z'_aR^{-1}y \end{bmatrix}$$

Matrix $[X \ Z_aQ_a \ Z_nQ_n \ Z_{ma} \ Z_a]$ is:

$xf = [X \ Z_a Q_a \ Z_n Q_n \ Z_{ma} \ Z_a]$															
1	1	0	0	1	0	2	1	1	2	1	0	0	0	0	0
1	0	1	0	0	1	0	1	2	0	0	1	0	0	0	0
1	0.5	0.5	1	0	1	1	2	0	0	0	0	1	0	0	0
1	0.5	0.5	1	0	1	1	2	0	0	0	0	0	1	0	0
1	0.5	0.5	1	1	0	1	2	0	1	0	0	0	0	1	0
1	0.75	0.25	0.5	1	0	2	1	2	2	0	0	0	0	0	1

The inverse of the matrix of residual effects, R^{-1} , is:

$invr = R^{-1}$					
0.0204082	0	0	0	0	0
0	0.0625	0	0	0	0
0	0	0.0307692	0	0	0
0	0	0	0.0307692	0	0
0	0	0	0	0.0307692	0
0	0	0	0	0	0.0212766

The diagonal matrix of marker locus additive genomic variances is equal to:

$$G_{ma} = I * \{ \sigma_a^2 / 2 \sum_{j=1}^{j=60} p_j (1 - p_j) \} = I * \{ 36 / 20.974159 \} = 1.7163978$$

Thus, matrix G_{ma} is equal to:

$gma = G_{ma}$			
1.7163978	0	0	0
0	1.7163978	0	0
0	0	1.7163978	0
0	0	0	1.7163978

and G_{ma}^{-1} is equal to:

$gmainv = G_{ma}^{-1}$			
0.5826155	0	0	0
0	0.5826155	0	0
0	0	0.5826155	0
0	0	0	0.5826155

The inverse of the matrix of covariances among animal effects, G_a^{-1} , is:

$gainv = G_a^{-1}$					
0.0585464	0.0125	0.0102041	-0.016129	-0.025	-0.020408
0.0125	0.043848	-0.017241	0	-0.025	0
0.0102041	-0.017241	0.0446868	0	0	-0.020408
-0.016129	0	0	0.0322581	0	0
-0.025	-0.025	0	0	0.05	0
-0.020408	0	-0.020408	0	0	0.0408163

The LHS matrix, the vector of effects, and the RHS vector of the mixed model equations are:

lhs																Effect	rhs
0.196	0.083	0.114	0.103	0.072	0.124	0.176	0.289	0.188	0.114	0.020	0.063	0.031	0.031	0.031	0.021	Mean	52.19
0.083	0.055	0.027	0.054	0.052	0.031	0.119	0.129	0.052	0.088	0.020	0.000	0.015	0.015	0.015	0.016	Breed _A	22.91
0.114	0.027	0.087	0.049	0.021	0.093	0.057	0.160	0.136	0.026	0.000	0.063	0.015	0.015	0.015	0.005	Breed _B	29.28
0.103	0.054	0.049	0.098	0.041	0.062	0.114	0.195	0.021	0.052	0.000	0.000	0.031	0.031	0.031	0.011	Heterosis _{AB}	27.93
0.072	0.052	0.021	0.041	0.072	0.000	0.114	0.103	0.063	0.114	0.020	0.000	0.000	0.000	0.031	0.021	Sex _M	20.97
0.124	0.031	0.093	0.062	0.000	0.124	0.062	0.186	0.125	0.000	0.000	0.063	0.031	0.031	0.000	0.000	Sex _F	31.22
0.176	0.119	0.057	0.114	0.114	0.062	0.842	0.268	0.126	0.198	0.041	0.000	0.031	0.031	0.031	0.043	ma ₁	48.86
0.289	0.129	0.160	0.195	0.103	0.186	0.268	1.056	0.188	0.145	0.020	0.063	0.062	0.062	0.062	0.021	ma ₂	77.08

lhs															Effect	rhs	
0.188	0.052	0.136	0.021	0.063	0.125	0.126	0.188	0.938	0.126	0.020	0.125	0.000	0.000	0.000	0.043	ma ₃	48.69
0.114	0.088	0.026	0.052	0.114	0.000	0.198	0.145	0.126	0.780	0.041	0.000	0.000	0.000	0.031	0.043	ma ₄	32.95
0.020	0.020	0.000	0.000	0.020	0.000	0.041	0.020	0.020	0.041	0.079	0.013	0.010	-0.016	-0.025	-0.020	a _{a1}	5.90
0.063	0.000	0.063	0.000	0.000	0.063	0.000	0.063	0.125	0.000	0.013	0.106	-0.017	0.000	-0.025	0.000	a _{a2}	15.31
0.031	0.015	0.015	0.031	0.000	0.031	0.031	0.062	0.000	0.000	0.010	-0.017	0.075	0.000	0.000	-0.020	a _{a3}	7.88
0.031	0.015	0.015	0.031	0.000	0.031	0.031	0.062	0.000	0.000	-0.016	0.000	0.000	0.063	0.000	0.000	a _{a4}	8.03
0.031	0.015	0.015	0.031	0.031	0.000	0.031	0.062	0.000	0.031	-0.025	-0.025	0.000	0.000	0.081	0.000	a _{a5}	8.98
0.021	0.016	0.005	0.011	0.021	0.000	0.043	0.021	0.043	0.043	-0.020	0.000	-0.020	0.000	0.000	0.062	a _{a6}	6.09

The vector of solutions and their standard errors are:

Effect	SOL	SESOL
Mean ^o	133.32	3.31
Breed _A ^o	71.32	7.95
Breed _B ^o	62.00	7.74
Heterosis _{AB} ^o	8.18	6.67
Sex _M ^o	82.82	4.94
Sex _F ^o	50.49	4.54
ma ₁ ^o	-0.03	1.31
ma ₂ ^o	0.03	1.31
ma ₃ ^o	-0.09	1.29
ma ₄ ^o	-0.03	1.31
â _{a1}	0.85	5.78
â _{a2}	-0.66	6.37

\hat{a}_{a3}	-1.71	5.31
\hat{a}_{a4}	1.35	5.38
\hat{a}_{a5}	0.45	6.16
\hat{a}_{a6}	-1.29	6.05

Prediction of polygenic-genomic values

Predictions of additive polygenic-genomic values (\hat{u}_{ai}) are computed as the sum of the breed effect, the sum of the random effects of the 4 markers, and the animal polygenic deviation from the breed effect, i.e.,

$$\hat{u}_{ai} = \text{Prob}_{A\text{anim } i} * (\text{Breed}_A^\circ - \text{Breed}_B^\circ) + \sum_{j=1}^{j=4} W_{\text{ma } j \text{ Anim } i} * \hat{m}_j + \hat{a}_{ai}$$

where

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

Breed_A° = generalized least squares solution for breed A,

Breed_B° = generalized least squares solution for breed B,

$W_{\text{ma } j \text{ Anim } i}$ = number of “second” alleles in marker locus j of animal i,

\hat{m}_j = BLUP of m_{aj} , and

\hat{a}_{ai} = BLUP of a_{ai} .

The matrix of variances of errors of prediction (VEP) for the vector of predicted genetic values (\hat{u}_a)

is:

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

where

K_a = $n_{anim} \times n_{eq}$ matrix specifying multipliers for breed differences, **allele difference in marker locus j , $j = 1, 2, 3, 4$** , and random animal deviations, 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.

The standard errors of prediction (SEP) of the \hat{u}_{ai} are computed as the square roots of the diagonal elements of the $VEP(\hat{u}_{ai})$ matrix.

Matrix K_a for the Example is:

ka															
0.00	1.00	-1.00	0.00	0.00	0.00	2.00	1.00	1.00	2.00	1.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	2.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
0.00	0.50	-0.50	0.00	0.00	0.00	1.00	2.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
0.00	0.50	-0.50	0.00	0.00	0.00	1.00	2.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
0.00	0.50	-0.50	0.00	0.00	0.00	1.00	2.00	0.00	1.00	0.00	0.00	0.00	0.00	1.00	0.00
0.00	0.75	-0.75	0.00	0.00	0.00	2.00	1.00	2.00	2.00	0.00	0.00	0.00	0.00	0.00	1.00

Remarks: Marker effects were **not** confounded with other effects in the model when treated as random effects. Verified by multiplying matrix $K_a * ginvlhs * lhs$. Multipliers for marker loci j , $j = 1, 2, 3, 4$ in matrix K_a were recreated exactly in matrix $(K_a * ginvlhs * lhs)$, thus they were predicted unbiasedly.

Matrix $K_a * ginvlhs * lhs$ was:

kagl															
-0.00	1.00	-1.00	-0.00	0.00	-0.00	2.00	1.00	1.00	2.00	1.00	-0.00	0.00	-0.00	-0.00	-0.00
-0.00	-0.00	0.00	-0.00	-0.00	-0.00	0.00	1.00	2.00	0.00	-0.00	1.00	0.00	0.00	-0.00	-0.00
-0.00	0.50	-0.50	-0.00	0.00	-0.00	1.00	2.00	0.00	-0.00	-0.00	-0.00	1.00	-0.00	-0.00	-0.00
-0.00	0.50	-0.50	-0.00	0.00	-0.00	1.00	2.00	0.00	0.00	-0.00	0.00	-0.00	1.00	0.00	-0.00
-0.00	0.50	-0.50	-0.00	0.00	-0.00	1.00	2.00	0.00	1.00	-0.00	-0.00	0.00	-0.00	1.00	0.00
-0.00	0.75	-0.75	-0.00	-0.00	-0.00	2.00	1.00	2.00	2.00	-0.00	-0.00	0.00	-0.00	-0.00	1.00

Matrix $K_a * \text{ginvlhs} * \text{lhs} = K_a$, thus, polygenic-genomic predictions for all animals were unbiased.

The \hat{u}_{ai} and their SEP for the animals in the Example are:

Anim	Prob _A	Br _A ^o - Br _B ^o	w _{ma1}	w _{ma2}	w _{ma3}	w _{ma4}	\widehat{ma}_1	\widehat{ma}_2	\widehat{ma}_3	\widehat{ma}_4	\hat{a}_{add}	\hat{u}_a	SEP (\hat{u}_a)
1	1	9.32	2	1	1	2	-0.03	0.03	-0.09	0.03	0.85	10.00	15.01
2	0	9.32	0	1	2	0	-0.03	0.03	-0.09	0.03	-0.66	-0.81	7.02
3	0.5	9.32	1	2	0	0	-0.03	0.03	-0.09	0.03	-1.71	2.99	9.71
4	0.5	9.32	1	2	0	0	-0.03	0.03	-0.09	0.03	1.35	6.05	8.69
5	0.5	9.32	1	2	0	1	-0.03	0.03	-0.09	0.03	0.45	5.11	11.59
6	0.75	9.32	2	1	2	2	-0.03	0.03	-0.09	0.03	-1.29	5.43	12.85

Polygenic-Genomic Marker Model with a large number of random marker locus effects

Example

Prediction of the polygenic-genomic values of animals for weaning weight using the following phenotypic and genomic information for 60 marker loci on 6 calves.

Anim	Breed Compsn	loc 1 ¹	loc 2 ¹	loc 3 ¹	loc 4 ¹	...	loc 60 ¹	Sex	WWt (kg)	Sire	Breed Comp	Dam	Breed Compsn
1	A	2	1	1	2	...	2	M	289	0	A	0	A
2	B	0	1	2	0	...	1	F	245	0	B	0	B
3	½ A ½ B	1	2	0	0	...	2	F	256	0	A	2	B
4	½ A ½ B	1	2	0	0	...	1	F	261	1	A	0	B
5	½ A ½ B	1	2	0	1	...	1	M	292	1	A	2	B
6	¾ A ¼ B	2	1	2	2	...	1	M	286	1	A	3	½ A ½ B

¹Number of “second” alleles (VanRaden, 2008).

Additive Genetic and Residual Variances

Variance	Additive Genetic	Residual
Intrabreed AA	36 kg ²	49 kg ²
Intrabreed BB	44 kg ²	16 kg ²
Interbreed AB	22 kg ²	25 kg ²

Polygenic-Genomic Marker Model

$$\text{Wean wt} = \text{overall mean} + \text{breed regression} + \text{heterosis regression} + \text{sex} + \text{sum regression markers 1 to 60} + \text{residual}$$

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

$$\begin{aligned}
\text{Var}(\text{Wean wt}) &= \text{sum} [\text{var}(\text{ma } j \text{ regression}), j = 1 \text{ to } 60] + \text{var}(\text{residual}) \\
\text{cov}(\text{Wean wt}_{ik}, \text{Wean wt}_{i'k'}) &= \text{sum} [\text{cov}(\text{ma } j \text{ regression}, \text{ma } j' \text{ regression}), j, j' = 1 \text{ to } 60 \\
&\quad + \text{cov}(\text{residual}_{ik}, \text{residual}_{i'k'}) \\
&= 0 + \text{cov}(\text{residual}_{ik}, \text{residual}_{i'k'}) \\
&= \text{cov}(\text{residual}_{ik}, \text{residual}_{i'k'})
\end{aligned}$$

The polygenic-genomic marker model, in matrix notation, is:

$$y = Xb + Z_a Q_a g_a + Z_n Q_n g_n + Z_{ma} m_a + \varepsilon$$

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

$$\text{var} \begin{bmatrix} m_a \\ \varepsilon \end{bmatrix} = \begin{bmatrix} G_{ma} & 0 \\ 0 & R \end{bmatrix}$$

$$\text{var}(y) = Z_{ma} G_{ma} Z_{ma}' + R$$

where

y = vector of animal records,

b = vector of unknown fixed effects (mean, sex of calf),

g_a = vector of unknown additive group genetic effects (breed),

g_n = vector of unknown nonadditive group genetic effects (heterosis at 1 locus),

m_a = vector of unknown random marker locus additive genomic effects,

ε = 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 random polygenic nonadditive genetic effects in vector a_n (a_n is assumed to be part of the residual),

- Z_{ma} = known incidence matrix relating records to elements of vector m_a ; elements of Z_{ma} will be 0, 1, 2 depending on the number of “second” alleles in marker locus j , $j = 1, \dots, 60$. Values [0,1, 2] are called gene content. Other parameterizations are: 1) [-1, 0, 1] obtained by subtracting 1 from [0, 1, 2]; and 2) deviate [-1, 0, 1] from $2(p_j - 0.5)$, which yields $[-2p_j, 1 - 2p_j, 2 - 2p_j]$, where 0.5 is the allele frequency used to center matrix Z_{ma} . Other frequencies used to center matrix Z_{ma} are the base population mean computed using a linear regression on gene content (Gengler et al., 2007) and the current population mean (Aguilar et al., 2009).
- Q_a = known incidence matrix relating random polygenic additive genetic effects to additive genetic groups in vector g_a ,
- Q_n = known incidence matrix relating random polygenic nonadditive genetic effects to nonadditive genetic groups in vector g_n ,
- G_{ma} = $n_{ma} \times n_{ma}$ diagonal matrix of marker locus additive genomic variances (assumed to be equal for all markers associated with a trait),
- = $I * \sigma_a^2$
- = $I * \{ \sigma_a^2 / 2 \sum_{j=1}^{j=n_{ma}} p_j (1 - p_j) \}$, where σ_a^2 = polygenic additive genetic variance, n_{ma} = number of marker loci (in linkage disequilibrium with QTL), and p_j = frequency of the “second” allele in marker j ,
- R = matrix of residual variances for purebred and crossbred animals (sums of nonadditive genetic and environmental variances).

The mixed model with the information of the 6 calves can be written as follows:

$$\begin{bmatrix} 289 \\ 245 \\ 256 \\ 261 \\ 292 \\ 286 \end{bmatrix} = \begin{bmatrix} 1 & 1 & 0 & 0 & 1 & 0 \\ 1 & 0 & 1 & 0 & 0 & 1 \\ 1 & 1/2 & 1/2 & 1 & 0 & 1 \\ 1 & 1/2 & 1/2 & 1 & 0 & 1 \\ 1 & 1/2 & 1/2 & 1 & 1 & 0 \\ 1 & 3/4 & 1/4 & 1/2 & 1 & 0 \end{bmatrix} \begin{bmatrix} mean \\ breed_A \\ breed_B \\ heterosis_{AB} \\ sex_M \\ sex_F \end{bmatrix} + \begin{bmatrix} 2 & 1 & 1 & 2 & \dots & 2 \\ 0 & 1 & 2 & 0 & \dots & 1 \\ 1 & 2 & 0 & 0 & \dots & 2 \\ 1 & 2 & 0 & 0 & \dots & 1 \\ 1 & 2 & 0 & 1 & \dots & 1 \\ 2 & 1 & 2 & 2 & \dots & 1 \end{bmatrix} \begin{bmatrix} ma_1 \\ ma_2 \\ ma_3 \\ ma_4 \\ \vdots \\ ma_{60} \end{bmatrix} + \begin{bmatrix} residual_{anim\ 1} \\ residual_{anim\ 2} \\ residual_{anim\ 3} \\ residual_{anim\ 4} \\ residual_{anim\ 5} \\ residual_{anim\ 6} \end{bmatrix}$$

The mixed model equations (MME) are:

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z_aQ_a & X'R^{-1}Z_nQ_n & X'R^{-1}Z_{ma} \\ Q'_aZ'_aR^{-1}X & Q'_aZ'_aR^{-1}Z_aQ_a & Q'_aZ'_aR^{-1}Z_nQ_n & Q'_aZ'_aR^{-1}Z_{ma} \\ Q'_nZ'_nR^{-1}X & Q'_nZ'_nR^{-1}Z_aQ_a & Q'_nZ'_nR^{-1}Z_nQ_n & Q'_nZ'_nR^{-1}Z_{ma} \\ Z'_{ma}R^{-1}X & Z'_{ma}R^{-1}Z_aQ_a & Z'_{ma}R^{-1}Z_nQ_n & Z'_{ma}R^{-1}Z_{ma} + G_{ma}^{-1} \end{bmatrix} \begin{bmatrix} b \\ g_a \\ g_n \\ ma_a \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Q'_aZ'_aR^{-1}y \\ Q'_nZ'_nR^{-1}y \\ Z'_{ma}R^{-1}y \end{bmatrix}$$

Matrix $[X \ Z_aQ_a \ Z_nQ_n \ Z_{ma}]$ is:

$xf = [X \ Z_aQ_a \ Z_nQ_n \ Z_{ma}]$															
1	1	0	0	1	0	2	1	1	2	1	1	...	0	2	2
1	0	1	0	0	1	0	1	2	0	0	1	...	1	2	1
1	0.5	0.5	1	0	1	1	2	0	0	1	1	...	1	1	2
1	0.5	0.5	1	0	1	1	2	0	0	0	2	...	1	2	1
1	0.5	0.5	1	1	0	1	2	0	1	1	1	...	2	2	1
1	0.75	0.25	0.5	1	0	2	1	2	2	1	2	...	1	2	1

The inverse of the matrix of residual effects, R^{-1} , is:

invr = R ⁻¹					
0.0204082	0	0	0	0	0
0	0.0625	0	0	0	0
0	0	0.0307692	0	0	0
0	0	0	0.0307692	0	0
0	0	0	0	0.0307692	0
0	0	0	0	0	0.0212766

The diagonal matrix of marker locus additive genomic variances is equal to:

$$G_{ma} = I * \{ \sigma_a^2 / 2 \sum_{j=1}^{j=60} p_j (1 - p_j) \}$$

Where

$$\{ \sigma_a^2 / 2 \sum_{j=1}^{j=60} p_j (1 - p_j) \} = 36 / 20.974159 = 1.7163978$$

Thus, G_{ma}^{-1} is equal to:

$gmainv = G_{ma}^{-1}$									
0.5826155	0	0	0	0	0	...	0	0	0
0	0.5826155	0	0	0	0	...	0	0	0
0	0	0.5826155	0	0	0	...	0	0	0
0	0	0	0.5826155	0	0	...	0	0	0
0	0	0	0	0.5826155	0	...	0	0	0
0	0	0	0	0	0.5826155	...	0	0	0
...
0	0	0	0	0	0	...	0.5826155	0	0
0	0	0	0	0	0	...	0	0.5826155	0
0	0	0	0	0	0	...	0	0	0.5826155

The LHS matrix, the vector of effects, and the RHS vector of the mixed model equations are:

LHS																Effect	RHS
0.196	0.083	0.114	0.103	0.072	0.124	0.176	0.289	0.188	0.114	0.103	0.249	...	0.207	0.362	0.248	Mean	52.19
0.083	0.055	0.027	0.054	0.052	0.031	0.119	0.129	0.052	0.088	0.067	0.114	...	0.077	0.150	0.118	Breed _A	22.91
0.114	0.027	0.087	0.049	0.021	0.093	0.057	0.160	0.136	0.026	0.036	0.135	...	0.129	0.213	0.129	Breed _B	29.28
0.103	0.054	0.049	0.098	0.041	0.062	0.114	0.195	0.021	0.052	0.072	0.144	...	0.134	0.175	0.134	Heterosis _{SAB}	27.93
0.072	0.052	0.021	0.041	0.072	0.000	0.114	0.103	0.063	0.114	0.072	0.094	...	0.083	0.145	0.093	Sex _M	20.97
0.124	0.031	0.093	0.062	0.000	0.124	0.062	0.186	0.125	0.000	0.031	0.155	...	0.124	0.217	0.155	Sex _F	31.22
0.176	0.119	0.057	0.114	0.114	0.062	0.842	0.268	0.126	0.198	0.145	0.249	...	0.166	0.321	0.247	ma ₁	48.86
0.289	0.129	0.160	0.195	0.103	0.186	0.268	1.056	0.188	0.145	0.165	0.372	...	0.330	0.516	0.371	ma ₂	77.08
0.188	0.052	0.136	0.021	0.063	0.125	0.126	0.188	0.938	0.126	0.063	0.231	...	0.168	0.376	0.208	ma ₃	48.69
0.114	0.088	0.026	0.052	0.114	0.000	0.198	0.145	0.126	0.780	0.114	0.157	...	0.104	0.228	0.155	ma ₄	32.95
0.103	0.067	0.036	0.072	0.072	0.031	0.145	0.165	0.063	0.114	0.686	0.124	...	0.114	0.176	0.154	ma ₅	28.84
0.249	0.114	0.135	0.144	0.094	0.155	0.249	0.372	0.231	0.157	0.124	0.935	...	0.259	0.466	0.300	ma ₆	66.30
...
0.207	0.077	0.129	0.134	0.083	0.124	0.166	0.33	0.168	0.104	0.114	0.259	...	0.851	0.383	0.238	ma ₅₈	55.27
0.362	0.150	0.213	0.175	0.145	0.217	0.321	0.516	0.376	0.228	0.176	0.466	...	0.383	1.276	0.434	ma ₅₉	96.50
0.248	0.118	0.129	0.134	0.093	0.155	0.247	0.371	0.208	0.155	0.154	0.300	...	0.238	0.434	0.933	ma ₆₀	65.96

The vector of solutions and their standard errors are:

Effect	SOL	SESOL	Effect	SOL	SESOL	Effect	SOL	SESOL
Mean ^o	133.32	6.47	\widehat{ma}_{17}	0	1.31	\widehat{ma}_{39}	0.13	1.29
Breed _A ^o	72.17	8.61	\widehat{ma}_{18}	0	1.29	\widehat{ma}_{40}	0	1.31
Breed _B ^o	61.16	9.07	\widehat{ma}_{19}	0.06	1.27	\widehat{ma}_{41}	0.06	1.3
Heterosis _{SAB} ^o	8.24	7.43	\widehat{ma}_{20}	-0.07	1.27	\widehat{ma}_{42}	0	1.31
Sex _M ^o	82.59	6.11	\widehat{ma}_{21}	0	1.31	\widehat{ma}_{43}	0.09	1.3
Sex _F ^o	50.73	5.68	\widehat{ma}_{22}	0	1.29	\widehat{ma}_{44}	0.03	1.31

$\widehat{m}a_1$	-0.03	1.31	$\widehat{m}a_{23}$	-0.09	1.3	$\widehat{m}a_{45}$	0.06	1.3
$\widehat{m}a_2$	0.03	1.31	$\widehat{m}a_{24}$	-0.03	1.28	$\widehat{m}a_{46}$	-0.09	1.3
$\widehat{m}a_3$	-0.09	1.29	$\widehat{m}a_{25}$	0.03	1.31	$\widehat{m}a_{47}$	0	1.31
$\widehat{m}a_4$	-0.03	1.31	$\widehat{m}a_{26}$	0	1.31	$\widehat{m}a_{48}$	0.03	1.31
$\widehat{m}a_5$	-0.06	1.3	$\widehat{m}a_{27}$	0.03	1.31	$\widehat{m}a_{49}$	0	1.31
$\widehat{m}a_6$	0	1.29	$\widehat{m}a_{28}$	-0.09	1.29	$\widehat{m}a_{50}$	-0.03	1.31
$\widehat{m}a_7$	0.03	1.3	$\widehat{m}a_{29}$	0.03	1.3	$\widehat{m}a_{51}$	0.07	1.27
$\widehat{m}a_8$	-0.1	1.28	$\widehat{m}a_{30}$	0	1.31	$\widehat{m}a_{52}$	0.03	1.31
$\widehat{m}a_9$	-0.16	1.28	$\widehat{m}a_{31}$	-0.06	1.3	$\widehat{m}a_{53}$	-0.06	1.3
$\widehat{m}a_{10}$	-0.03	1.31	$\widehat{m}a_{32}$	-0.09	1.3	$\widehat{m}a_{54}$	-0.03	1.31
$\widehat{m}a_{11}$	0.03	1.31	$\widehat{m}a_{33}$	-0.06	1.3	$\widehat{m}a_{55}$	0	1.31
$\widehat{m}a_{12}$	0.16	1.28	$\widehat{m}a_{34}$	0.03	1.3	$\widehat{m}a_{56}$	0.03	1.3
$\widehat{m}a_{13}$	-0.19	1.27	$\widehat{m}a_{35}$	0	1.29	$\widehat{m}a_{57}$	0	1.31
$\widehat{m}a_{14}$	0.13	1.29	$\widehat{m}a_{36}$	0.16	1.28	$\widehat{m}a_{58}$	0	1.31
$\widehat{m}a_{15}$	-0.09	1.3	$\widehat{m}a_{37}$	-0.09	1.3	$\widehat{m}a_{59}$	0.06	1.3
$\widehat{m}a_{16}$	0	1.29	$\widehat{m}a_{38}$	0.12	1.28	$\widehat{m}a_{60}$	-0.03	1.3

Prediction of polygenic-genomic values

Predictions of additive polygenic-genomic values (\hat{u}_{ai}) are computed as the sum of the breed effect, the sum of the weighted random effects of the 60 markers, and the animal genomic deviation from the breed effect, i.e.,

$$\hat{u}_{ai} = \text{Prob}_{A\text{anim } i} * (\text{Breed}_A^\circ - \text{Breed}_B^\circ) + \sum_{j=1}^{60} W_{ma\ j\ \text{Anim } i} * \hat{m}_j$$

where

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

Breed_A° = generalized least squares solution for breed A,

Breed_B° = generalized least squares solution for breed B,

$W_{ma\ j\ \text{Anim } i}$ = number of “second” alleles in marker locus j of animal i, and

\hat{m}_j = BLUP of m_j .

The matrix of variances of errors of prediction (VEP) for the vector of predicted genetic values (\hat{u}_a)

is:

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

where

K_a = $n_{\text{anim}} \times n_{\text{eq}}$ matrix specifying multipliers for breed differences and **allele differences in marker loci $j = 1, 2, 3, 4, \dots, 60$** , 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 the MME.

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

Matrix K_a for the Example is:

ka															
0.00	1.00	-1.00	0.00	0.00	0.00	2.00	1.00	1.00	2.00	1.00	1.00	...	0.00	2.00	2.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	2.00	0.00	0.00	1.00	...	1.00	2.00	1.00
0.00	0.50	-0.50	0.00	0.00	0.00	1.00	2.00	0.00	0.00	1.00	1.00	...	1.00	1.00	2.00
0.00	0.50	-0.50	0.00	0.00	0.00	1.00	2.00	0.00	0.00	0.00	2.00	...	1.00	2.00	1.00
0.00	0.50	-0.50	0.00	0.00	0.00	1.00	2.00	0.00	1.00	1.00	1.00	...	2.00	2.00	1.00
0.00	0.75	-0.75	0.00	0.00	0.00	2.00	1.00	2.00	2.00	1.00	2.00	...	1.00	2.00	1.00

We can verify that predictions for markers 1 to 60 are **not** confounded by computing matrix $K_a * \text{ginvlhs} * \text{lhs}$. If multipliers for marker loci $j, j = 1, \dots, 60$, in matrix K_a are recreated in matrix $(K_a * \text{ginvlhs} * \text{lhs})$ exactly, then they were predicted unbiasedly.

Matrix $K_a * \text{ginvlhs} * \text{lhs}$ was:

kagl															
0.00	1.00	-1.00	0.00	0.00	0.00	2.00	1.00	1.00	2.00	1.00	1.00	...	0.00	2.00	2.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	2.00	0.00	0.00	1.00	...	1.00	2.00	1.00
0.00	0.50	-0.50	0.00	0.00	0.00	1.00	2.00	0.00	0.00	1.00	1.00	...	1.00	1.00	2.00
0.00	0.50	-0.50	0.00	0.00	0.00	1.00	2.00	0.00	0.00	0.00	2.00	...	1.00	2.00	1.00
0.00	0.50	-0.50	0.00	0.00	0.00	1.00	2.00	0.00	1.00	1.00	1.00	...	2.00	2.00	1.00
0.00	0.75	-0.75	0.00	0.00	0.00	2.00	1.00	2.00	2.00	1.00	2.00	...	1.00	2.00	1.00

Thus, genomic predictions for all animals were unbiased.

The \hat{u}_{ai} and their SEP for the animals in the Example are:

Anim	Prob_A	Br_A^o - Br_B^o	W_{ma1}	W_{ma2}	W_{ma3}	...	W_{ma60}	\widehat{ma}_1	\widehat{ma}_2	\widehat{ma}_3	...	\widehat{ma}_{60}	\hat{u}_a	SEP (\hat{u}_a)
1	1	11.01	2	1	1	...	2	-0.03	0.03	-0.09	...	-0.03	11.05	19.97
2	0	11.01	0	1	2	...	1	-0.03	0.03	-0.09	...	-0.03	-0.21	14.03
3	0.5	11.01	1	2	0	...	2	-0.03	0.03	-0.09	...	-0.03	3.76	14.88
4	0.5	11.01	1	2	0	...	1	-0.03	0.03	-0.09	...	-0.03	6.35	14.94
5	0.5	11.01	1	2	0	...	1	-0.03	0.03	-0.09	...	-0.03	6.11	17.51
6	0.75	11.01	2	1	2	...	1	-0.03	0.03	-0.09	...	-0.03	6.49	18.38

Polygenic-Genomic Animal Model with a large number of random marker locus effects

Example

Prediction of the polygenic-genomic values of animals for weaning weight using the following phenotypic and genomic information for 60 marker loci on 6 calves.

Anim	Breed Compsn	loc 1 ¹	loc 2 ¹	loc 3 ¹	loc 4 ¹	...	loc 60 ¹	Sex	WWt (kg)	Sire	Breed Comp	Dam	Breed Compsn
1	A	2	1	1	2	...	2	M	289	0	A	0	A
2	B	0	1	2	0	...	1	F	245	0	B	0	B
3	½ A ½ B	1	2	0	0	...	2	F	256	0	A	2	B
4	½ A ½ B	1	2	0	0	...	1	F	261	1	A	0	B
5	½ A ½ B	1	2	0	1	...	1	M	292	1	A	2	B
6	¾ A ¼ B	2	1	2	2	...	1	M	286	1	A	3	½ A ½ B

¹Number of “second” alleles (VanRaden, 2008).

Additive Genetic and Residual Variances

Variance	Additive Genetic	Residual
Intrabreed AA	36 kg ²	49 kg ²
Intrabreed BB	44 kg ²	16 kg ²
Interbreed AB	22 kg ²	25 kg ²

Polygenic-Genomic Animal Model

$$\text{Wean wt} = \text{overall mean} + \text{breed regression} + \text{heterosis regression} + \text{sex} + \text{animal genomic} + \text{residual}$$

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

$$\begin{aligned}\text{Var}(\text{Wean wt}) &= \text{var}(\text{animal genomic}) + \text{var}(\text{residual}) \\ \text{cov}(\text{Wean wt}_{ik}, \text{Wean wt}_{i'k'}) &= \text{cov}(\text{animal genomic } j, \text{animal genomic } j') \\ &\quad + \text{cov}(\text{residual}_{ik}, \text{residual}_{i'k'})\end{aligned}$$

The polygenic-genomic animal model, in matrix notation, is:

$$y = Xb + Z_a Q_a g_a + Z_n Q_n g_n + Z_a Z_{ma} m_a + \varepsilon$$

Letting $a_a = Z_{ma} m_a$, the animal genomic model becomes:

$$y = Xb + Z_a Q_a g_a + Z_n Q_n g_n + Z_a a_a + \varepsilon$$

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

$$\text{var} \begin{bmatrix} a_a \\ \varepsilon \end{bmatrix} = \begin{bmatrix} Z_{ma} G_{ma} Z_{ma}' & 0 \\ 0 & R \end{bmatrix}$$

$$\text{var}(y) = Z_a Q_a G_{ma} Z_{ma}' + R$$

Where

y = vector of animal records,

b = vector of unknown fixed effects (mean, sex of calf),

g_a = vector of unknown additive group genetic effects (breed),

g_n = vector of unknown nonadditive group genetic effects (heterosis at 1 locus),

a_a = vector of unknown random animal additive genomic effects,

ε = 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 random polygenic nonadditive genetic effects in vector a_n (a_n is assumed to be part of the residual),

Q_a = known incidence matrix relating random polygenic additive genetic effects to

additive genetic groups in vector g_a ,

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

Z_{ma} = known incidence matrix relating records to elements of vector ma ; elements of Z_{ma} will be 0, 1, 2 depending on the number of “second” alleles in marker locus j , $j = 1, \dots, 60$. Values [0,1, 2] are called gene content. Other parameterizations are: 1) [-1, 0, 1] obtained by subtracting 1 from [0, 1, 2]; and 2) deviate [-1, 0, 1] from $2(p_j - 0.5)$, which yields $[-2p_j, 1 - 2p_j, 2 - 2p_j]$, where 0.5 is the allele frequency used to center matrix Z_{ma} . Other frequencies used to center matrix Z_{ma} are the base population mean (computed using a linear regression on gene content; Gengler et al., 2007 and the current population mean (Aguilar et al., 2009).

G_{ma} = $nma \times nma$ diagonal matrix of marker locus additive genomic variances (assumed to be equal for all markers associated with a trait),

$$= I * \sigma_{ma}^2$$

$$= I * \{\sigma_a^2 / kma\}, \text{ where } kma = 2 \sum_{j=1}^{nma} p_j(1 - p_j), \text{ } nma = \text{number of marker loci (in linkage disequilibrium with QTL), } p_j = \text{frequency of the “second” allele in marker } j, \text{ and } \sigma_a^2 = \text{polygenic additive genetic variance,}$$

R = matrix of residual variances for purebred and crossbred animals (sums of nonadditive genetic and environmental variances).

Substituting $(I * (\sigma_a^2 / kma))$ for G_{ma} in $var \begin{bmatrix} u_a \\ \varepsilon \end{bmatrix}$ yields:

$$var \begin{bmatrix} u_a \\ \varepsilon \end{bmatrix} = \begin{bmatrix} Z_{ma}(I * (\sigma_a^2 / kma))Z_{ma}' & 0 \\ 0 & R \end{bmatrix}$$

$$\text{var} \begin{bmatrix} u_a \\ \varepsilon \end{bmatrix} = \begin{bmatrix} Z_{ma}Z'_{ma} \left(\frac{\sigma_a^2}{kma} \right) & 0 \\ 0 & R \end{bmatrix}$$

$$\text{var} \begin{bmatrix} u_a \\ \varepsilon \end{bmatrix} = \begin{bmatrix} \left(\frac{Z_{ma}Z'_{ma}}{2 \sum_{j=1}^{nma} p_j(1-p_j)} \right) * \sigma_a^2 & 0 \\ 0 & R \end{bmatrix}$$

$$\text{var} \begin{bmatrix} u_a \\ \varepsilon \end{bmatrix} = \begin{bmatrix} A_{gg} * \sigma_a^2 & 0 \\ 0 & R \end{bmatrix}$$

$$\text{var} \begin{bmatrix} u_a \\ \varepsilon \end{bmatrix} = \begin{bmatrix} G_{gg} & 0 \\ 0 & R \end{bmatrix}$$

Where

$$G_{gg} = \left(\frac{Z_{ma}Z'_{ma}}{2 \sum_{j=1}^{nma} p_j(1-p_j)} \right) * \sigma_a^2 \text{ is the genomic additive covariance matrix,}$$

$$A_{gg} = Z_{ma}Z'_{ma} / 2 \sum_{j=1}^{nma} p_j(1-p_j) \text{ is the genomic relationship matrix, and}$$

$$\sigma_a^2 = \text{polygenic additive genetic variance.}$$

The mixed model with the information of the 6 calves can be written as follows:

$$\begin{bmatrix} 289 \\ 245 \\ 256 \\ 261 \\ 292 \\ 286 \end{bmatrix} = \begin{bmatrix} 1 & 1 & 0 & 0 & 1 & 0 \\ 1 & 0 & 1 & 0 & 0 & 1 \\ 1 & 1/2 & 1/2 & 1 & 0 & 1 \\ 1 & 1/2 & 1/2 & 1 & 0 & 1 \\ 1 & 1/2 & 1/2 & 1 & 1 & 0 \\ 1 & 3/4 & 1/4 & 1/2 & 1 & 0 \end{bmatrix} \begin{bmatrix} \text{mean} \\ \text{breed}_A \\ \text{breed}_B \\ \text{heterosis}_{AB} \\ \text{sex}_M \\ \text{sex}_F \end{bmatrix} + \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} a_{a1} \\ a_{a2} \\ a_{a3} \\ a_{a4} \\ a_{a5} \\ a_{a6} \end{bmatrix}$$

$$+ \begin{bmatrix} \text{residual}_{anim 1} \\ \text{residual}_{anim 2} \\ \text{residual}_{anim 3} \\ \text{residual}_{anim 4} \\ \text{residual}_{anim 5} \\ \text{residual}_{anim 6} \end{bmatrix}$$

The mixed model equations (MME) are:

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z_aQ_a & X'R^{-1}Z_nQ_n & X'R^{-1}Z_a \\ Q'_aZ'_aR^{-1}X & Q'_aZ'_aR^{-1}Z_aQ_a & Q'_aZ'_aR^{-1}Z_nQ_n & Q'_aZ'_aR^{-1}Z_a \\ Q'_nZ'_nR^{-1}X & Q'_nZ'_nR^{-1}Z_aQ_a & Q'_nZ'_nR^{-1}Z_nQ_n & Q'_nZ'_nR^{-1}Z_a \\ Z'_aR^{-1}X & Z'_aR^{-1}Z_aQ_a & Z'_aR^{-1}Z_nQ_n & Z'_aR^{-1}Z_a + G_{gg}^{-1} \end{bmatrix} \begin{bmatrix} b \\ g_a \\ g_n \\ a_a \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Q'_aZ'_aR^{-1}y \\ Q'_nZ'_nR^{-1}y \\ Z'_aR^{-1}y \end{bmatrix}$$

Matrix $[X \ Z_aQ_a \ Z_nQ_n \ Z_a]$ is:

$xf = [X \ Z_aQ_a \ Z_nQ_n \ Z_a]$										
1	1	0	0	1	0	1	0	0	0	0
1	0	1	0	0	1	0	1	0	0	0
1	0.5	0.5	1	0	1	0	0	1	0	0
1	0.5	0.5	1	0	1	0	0	0	1	0
1	0.5	0.5	1	1	0	0	0	0	0	1
1	0.75	0.25	0.5	1	0	0	0	0	0	1

The inverse of the matrix of residual effects, R^{-1} , is:

$invr = R^{-1}$					
0.0204082	0	0	0	0	0
0	0.0625	0	0	0	0
0	0	0.0307692	0	0	0
0	0	0	0.0307692	0	0
0	0	0	0	0.0307692	0
0	0	0	0	0	0.0212766

Matrix Z_{ma} is equal to:

$zg = Z_{ma}$																							
2	1	1	2	1	1	2	2	0	1	1	1	0	1	2	1	2	0	2	2	...	0	2	2
0	1	2	0	0	1	2	2	1	2	2	0	1	2	1	1	2	1	0	2	...	1	2	1
1	2	0	0	1	1	1	2	2	2	1	0	1	0	2	1	2	1	2	2	...	1	1	2
1	2	0	0	0	2	2	0	0	2	1	2	0	1	1	0	2	2	1	0	...	1	2	1
1	2	0	1	1	1	1	1	1	2	2	2	0	1	1	1	2	0	2	2	...	2	2	1
2	1	2	2	1	2	2	1	1	2	1	1	2	0	2	0	2	1	0	1	...	1	2	1

Matrix $G_{gg} = \left(\frac{Z_{ma}Z'_{ma}}{2 \sum_{j=1}^{j=nma} p_j(1-p_j)} \right) * \sigma_a^2 = A_{gg} * \sigma_a^2$, where σ_a^2 was assumed to be equal to 36.

Matrix $Z_{ma}Z'_{ma}$ is equal to:

$zgtzg = Z_{ma}Z'_{ma}$					
98	73	76	65	84	79
73	115	79	80	86	84
76	79	98	72	79	79
65	80	72	92	73	76
84	86	79	73	108	80
79	84	79	76	80	105

and $2 \sum_{j=1}^{j=nma} p_j(1-p_j) = 20.974159$. Thus, matrix A_{gg} is equal to:

$agg = A_{gg}$					
4.6724161	3.4804733	3.6235064	3.0990515	4.0049281	3.7665395
3.4804733	5.4829373	3.7665395	3.8142173	4.1002836	4.0049281
3.6235064	3.7665395	4.6724161	3.4327955	3.7665395	3.7665395

<i>agg = A_{gg}</i>					
3.0990515	3.8142173	3.4327955	4.3863499	3.4804733	3.6235064
4.0049281	4.1002836	3.7665395	3.4804733	5.1491933	3.8142173
3.7665395	4.0049281	3.7665395	3.6235064	3.8142173	5.0061602

Matrix $G_{gg}^{-1} = A_{gg}^{-1} * \sigma_a^{-2}$, where A_{gg}^{-1} is equal to:

<i>ginvagg = A_{gg}⁻¹</i>					
0.8512058	0.060374	-0.215621	0.0313554	-0.382859	-0.257494
0.060374	0.6505867	-0.098489	-0.219139	-0.225089	-0.161681
-0.215621	-0.098489	0.7976226	-0.179542	-0.106107	-0.148298
0.0313554	-0.219139	-0.179542	0.7840894	-0.093191	-0.209725
-0.382859	-0.225089	-0.106107	-0.093191	0.8171375	-0.007168
-0.257494	-0.161681	-0.148298	-0.209725	-0.007168	0.7916714

Thus, $G_{gg}^{-1} = A_{gg}^{-1} * (36)^{-1}$, i.e.,

<i>ginvggg = G_{gg}⁻¹</i>					
0.0236446	0.0016771	-0.005989	0.000871	-0.010635	-0.007153
0.0016771	0.0180719	-0.002736	-0.006087	-0.006252	-0.004491
-0.005989	-0.002736	0.0221562	-0.004987	-0.002947	-0.004119
0.000871	-0.006087	-0.004987	0.0217803	-0.002589	-0.005826
-0.010635	-0.006252	-0.002947	-0.002589	0.0226983	-0.000199
-0.007153	-0.004491	-0.004119	-0.005826	-0.000199	0.0219909

The LHS matrix, the vector of effects, and the RHS vector of the mixed model equations are:

LHS												Effect	RHS
0.196	0.083	0.114	0.103	0.072	0.124	0.020	0.063	0.031	0.031	0.031	0.021	Mean	52.19
0.083	0.055	0.027	0.054	0.052	0.031	0.020	0.000	0.015	0.015	0.015	0.016	Breed _A	22.91
0.114	0.027	0.087	0.049	0.021	0.093	0.000	0.063	0.015	0.015	0.015	0.005	Breed _B	29.28
0.103	0.054	0.049	0.098	0.041	0.062	0.000	0.000	0.031	0.031	0.031	0.011	Heterosis _{AB}	27.93
0.072	0.052	0.021	0.041	0.072	0.000	0.020	0.000	0.000	0.000	0.031	0.021	Sex _M	20.97
0.124	0.031	0.093	0.062	0.000	0.124	0.000	0.063	0.031	0.031	0.000	0.000	Sex _F	31.22
0.020	0.020	0.000	0.000	0.020	0.000	0.044	0.002	-0.006	0.001	-0.011	-0.007	a _{a1}	5.90
0.063	0.000	0.063	0.000	0.000	0.063	0.002	0.081	-0.003	-0.006	-0.006	-0.004	a _{a2}	15.31
0.031	0.015	0.015	0.031	0.000	0.031	-0.006	-0.003	0.053	-0.005	-0.003	-0.004	a _{a3}	7.88
0.031	0.015	0.015	0.031	0.000	0.031	0.001	-0.006	-0.005	0.053	-0.003	-0.006	a _{a4}	8.03
0.031	0.015	0.015	0.031	0.031	0.000	-0.011	-0.006	-0.003	-0.003	0.053	-0.000	a _{a5}	8.98
0.021	0.016	0.005	0.011	0.021	0.000	-0.007	-0.004	-0.004	-0.006	-0.000	0.043	a _{a6}	6.09

The **vector of solutions and their standard errors** for the example are:

Effect	SOL	SESOL
Mean ^o	133.32	6.47
Breed _A ^o	72.17	8.61
Breed _B ^o	61.16	9.07
Heterosis _{AB} ^o	8.24	7.43
Sex _M ^o	82.59	6.11
Sex _F ^o	50.73	5.68
\hat{a}_{a1}	0.04	12.77
\hat{a}_{a2}	-0.21	14.03

\hat{a}_{a3}	-1.75	12.42
\hat{a}_{a4}	0.84	12.21
\hat{a}_{a5}	0.60	13.39
\hat{a}_{a6}	-1.76	12.87

Prediction of polygenic-genomic values

Predictions of additive polygenic-genomic values (\hat{u}_{ai}) are computed as the sum of the breed effect and the animal genomic deviation from the breed effect, i.e.,

$$\hat{u}_{ai} = \text{Prob}_{A_{\text{anim } i}} * (\text{Breed}_A^\circ - \text{Breed}_B^\circ) + \hat{a}_{ai}$$

where

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

Breed_A° = generalized least squares solution for breed A,

Breed_B° = generalized least squares solution for breed B, and

\hat{a}_{ai} = Genomic BLUP (GBLUP) of a_{ai} .

The matrix of variances of errors of prediction (VEP) for the vector of predicted genetic values (\hat{u}_a)

is:

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

where

K_a = $n_{\text{anim}} \times n_{\text{eq}}$ matrix specifying multipliers for breed differences and **random animal additive genomic deviations**, 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.

The standard errors of prediction (SEP) of the \hat{u}_{ai} are computed as the square roots of the diagonal elements of the $VEP(\hat{u}_{ai})$ matrix.

Matrix K_a for the Example is:

ka											
0.00	1.00	-1.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
0.00	0.50	-0.50	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
0.00	0.50	-0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
0.00	0.50	-0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
0.00	0.75	-0.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00

The \hat{u}_{ai} and their **SEP** for the animals in the Example are:

Animal	Prob _{Aanim}	Breed _A ^o - Breed _B ^o	\hat{a}_{add}	\hat{u}_a	SEP (\hat{u}_a)
1	1	11.01	0.04	11.05	19.97
2	0	11.01	-0.21	-0.21	14.03
3	0.5	11.01	-1.75	3.76	14.88
4	0.5	11.01	0.84	6.35	14.94
5	0.5	11.01	0.60	6.11	17.51
6	0.75	11.01	-1.76	6.49	18.38

Computation of marker BLUP from animal genomic BLUP

Marker BLUP can be predicted from the GBLUP of a_a by conditioning m_a on \hat{a}_a and assuming normality. Firstly, under normality,

$$m_a | a_a = Z_{ma} m_a \sim MVN \{E[m_a | a_a = Z_{ma} m_a], \text{var}(m_a | a_a = Z_{ma} m_a)\}$$

where,

$$E[m_a | a_a = Z_{ma} m_a] = E[m_a] + \text{cov}(m_a, m_a' Z_{ma}') \text{var}(Z_{ma} m_a)^{-1} (Z_{ma} m_a - E[Z_{ma} m_a])$$

$$\text{var}(m_a | a_a = Z_{ma} m_a) = \text{var}(m_a) - \text{cov}(m_a, m_a' Z_{ma}') \text{var}(Z_{ma} m_a)^{-1} \text{cov}(Z_{ma} m_a, m_a')$$

$$E[m_a] = 0$$

$$E[a_a = Z_{ma} m_a] = 0$$

$$\text{var}(m_a) = (I * (\sigma_a^2 / kma))$$

$$\text{cov}(m_a, m_a' Z_{ma}') = (I * (\sigma_a^2 / kma)) Z_{ma}'$$

$$\text{var}(Z_{ma} m_a)^{-1} = (Z_{ma} (I * (\sigma_a^2 / kma)) Z_{ma}')^{-1}$$

$$\text{cov}(Z_{ma} m_a, m_a') = Z_{ma} (I * (\sigma_a^2 / kma))$$

and,

$$kma = 2 \sum_{j=1}^{j=nma} p_j (1 - p_j)$$

Thus,

$$E[m_a | a_a] = (I * (\sigma_a^2 / kma)) Z_{ma}' (Z_{ma} (I * (\sigma_a^2 / kma)) Z_{ma}')^{-1} a_a$$

and,

$$\text{var}(m_a | a_a) = (I * (\sigma_a^2 / kma))$$

$$- (I * (\sigma_a^2 / kma)) Z_{ma}' (Z_{ma} (I * (\sigma_a^2 / kma)) Z_{ma}')^{-1} Z_{ma} (I * (\sigma_a^2 / kma))$$

But $E[a_a|\hat{a}_a] = \hat{a}_a$, the MLE of a_a and the BLUP of a_a under normality. By the invariance property of MLE, the MLE of m_a (and the BLUP of m_a under normality) can be predicted as

$\hat{m}_a = K\hat{a}_a$, where

$$K = \text{cov}(m_a, m_a' Z_{ma}') \text{var}(Z_{ma} m_a)^{-1}$$

$$K = (I * (\sigma_a^2/kma)) Z_{ma}' (Z_{ma} (I * (\sigma_a^2/kma)) Z_{ma}')^{-1}$$

Thus,

$$\hat{m}_a = (I * (\sigma_a^2/kma)) Z_{ma}' (Z_{ma} (I * (\sigma_a^2/kma)) Z_{ma}')^{-1} \hat{a}_a$$

In other words, by the invariance property of MLE,

$$\hat{m}_a = E[m_a|\hat{a}_a] = (I * (\sigma_a^2/kma)) Z_{ma}' (Z_{ma} (I * (\sigma_a^2/kma)) Z_{ma}')^{-1} \hat{a}_a$$

where $\hat{a}_a = \text{BLUP of } a_a = Z_{ma} m_a$ obtained by solving the MME for the animal genomic model.

The error variance of prediction of \hat{m}_a , i.e., $\text{var}(\hat{m}_a - m_a)$, can be computed as follows:

$$\text{var}(m_a) = E[\text{var}(m_a|\hat{a}_a)] + \text{var}(E[m_a|\hat{a}_a])$$

or,

$$\text{var}(m_a) = \text{var}(\hat{m}_a - m_a) + \text{var}(\hat{m}_a)$$

Thus,

$$\text{var}(\hat{m}_a - m_a) = \text{var}(m_a) - \text{var}(\hat{m}_a)$$

where

$$\text{var}(m_a) = (I * (\sigma_a^2/kma))$$

$$\text{var}(\hat{m}_a) = \text{cov}(m_a, m_a' Z_{ma}') \text{var}(Z_{ma} m_a)^{-1} \text{var}(\hat{a}_a) \text{var}(Z_{ma} m_a)^{-1} \text{cov}(Z_{ma} m_a, m_a')$$

$$\text{var}(\hat{m}_a) = (I * (\sigma_a^2/kma)) Z_{ma}' (Z_{ma} (I * (\sigma_a^2/kma)) Z_{ma}')^{-1} \text{var}(\hat{a}_a) (Z_{ma} (I * (\sigma_a^2/kma)) Z_{ma}')^{-1} Z_{ma} (I * (\sigma_a^2/kma))$$

where,

$$var(\hat{a}_a) = var(a_a) - B^{22}$$

$$var(\hat{a}_a) = var(Z_{ma}m_a) - B^{22}$$

$$var(\hat{a}_a) = Z_{ma}(I * (\sigma_a^2/kma))Z'_{ma} - B^{22}$$

and,

B^{22} = submatrix of the inverse of the LHS of the MME for the animal genomic model

corresponding to animal genomic effects a_a .

The standard errors of prediction (**SEP**) of the marker BLUP are computed as the square root of the diagonal elements of $var(\hat{m}_a)$, the matrix variances of prediction.

The MLE of m_a for the Example is $\hat{m}_a = K\hat{a}_a$, where $K = cov(m_a, m_a'Z_{ma}')var(Z_{ma}m_a)^{-1}$.

The $nma \times nanim$ $cov(m_a, m_a'Z_{ma}') = (I * (\sigma_a^2/kma))Z_{ma}'$ is equal to:

covtzgg = $cov(m_a, m_a'Z_{ma}')$					
3.433	0.000	1.716	1.716	1.716	3.433
1.716	1.716	3.433	3.433	3.433	1.716
1.716	3.433	0.000	0.000	0.000	3.433
3.433	0.000	0.000	0.000	1.716	3.433
1.716	0.000	1.716	0.000	1.716	1.716
1.716	1.716	1.716	3.433	1.716	3.433
3.433	3.433	1.716	3.433	1.716	3.433
3.433	3.433	3.433	0.000	1.716	1.716
...
0.000	1.716	1.716	1.716	3.433	1.716
3.433	3.433	1.716	3.433	3.433	3.433
3.433	1.716	3.433	1.716	1.716	1.716

The $\text{nanim} \times \text{nanim}$ $\text{var}(Z_{ma}m_a)^{-1} = (Z_{ma}(I * (\sigma_a^2/kma))Z_{ma}')^{-1} = G_{gg}^{-1}$ is equal to:

$g_{inv}g_{gg} = \text{var}(Z_{ma}m_a)^{-1} = G_{gg}^{-1}$					
0.0236446	0.0016771	-0.005989	0.000871	-0.010635	-0.007153
0.0016771	0.0180719	-0.002736	-0.006087	-0.006252	-0.004491
-0.005989	-0.002736	0.0221562	-0.004987	-0.002947	-0.004119
0.000871	-0.006087	-0.004987	0.0217803	-0.002589	-0.005826
-0.010635	-0.006252	-0.002947	-0.002589	0.0226983	-0.000199
-0.007153	-0.004491	-0.004119	-0.005826	-0.000199	0.0219909

Thus, matrix **K** is equal to:

$\text{cov}z_g = K = \text{cov}(m_a, m_a'Z_{ma}')\text{var}(Z_{ma}m_a)^{-1}$					
0.030	-0.036	-0.010	0.007	-0.008	0.034
-0.023	-0.026	0.027	0.030	0.030	-0.017
0.022	0.049	-0.034	-0.039	-0.040	0.048
0.038	-0.020	-0.040	-0.021	0.002	0.051
-0.000	-0.020	0.016	-0.022	0.015	0.018
-0.007	-0.018	-0.013	0.033	-0.005	0.028
0.037	0.016	-0.028	0.024	-0.034	0.008
0.036	0.040	0.034	-0.049	-0.029	-0.017
...
-0.055	-0.013	0.008	-0.001	0.057	0.012
0.019	0.005	-0.033	0.019	0.005	0.008
0.034	-0.002	0.030	-0.002	-0.023	-0.019

The $\text{nanim} \times 1$ vector \hat{a}_a is equal to:

$gebv = \hat{a}_a$
0.04
-0.21
-1.75
0.84
0.60
-1.76

The variance of prediction errors of \hat{m}_a is $var(\hat{m}_a - m_a) = var(m_a) - var(\hat{m}_a)$, where $var(m_a) = (I * (\sigma_a^2/kma)) = G_{ma}$, $var(\hat{m}_a) = Kvar(\hat{a}_a)K'$, $var(\hat{a}_a) = var(Z_{ma}m_a) - B^{22}$, and $var(Z_{ma}m_a) = Z_{ma}(I * (\sigma_a^2/kma))Z'_{ma} = G_{gg}$. Thus,

$$var(\hat{m}_a - m_a) = G_{ma} - K(G_{gg} - B^{22})K'$$

Matrix G_{ma} is equal to:

$covg = var(m_a) = (I * (\sigma_a^2/kma)) = G_{ma}$									
1.7163978	0	0	0	0	0	...	0	0	0
0	1.7163978	0	0	0	0	...	0	0	0
0	0	1.7163978	0	0	0	...	0	0	0
0	0	0	1.7163978	0	0	...	0	0	0
0	0	0	0	1.7163978	0	...	0	0	0
0	0	0	0	0	1.7163978	...	0	0	0
...
0	0	0	0	0	0	...	1.7163978	0	0
0	0	0	0	0	0	...	0	1.7163978	0
0	0	0	0	0	0	...	0	0	1.7163978

Matrix G_{gg} is equal to:

$covagg = var(Z_{ma}m_a) = Z_{ma}(I * (\sigma_a^2/kma))Z'_{ma} = G_{gg}$					
168.21	125.30	130.45	111.57	144.18	135.60
125.30	197.39	135.60	137.31	147.61	144.18
130.45	135.60	168.21	123.58	135.60	135.60
111.57	137.31	123.58	157.91	125.30	130.45
144.18	147.61	135.60	125.30	185.37	137.31
135.60	144.18	135.60	130.45	137.31	180.22

Matrix B^{22} (quadrant 22 of the inverse of the LHS) is equal to:

$gevp = B^{22}$					
162.95	126.62	125.38	117.47	138.97	141.27
126.62	196.93	135.82	136.35	149.25	141.74
125.38	135.82	154.15	133.82	133.50	132.20
117.47	136.35	133.82	149.01	129.70	128.47
138.97	149.25	133.50	129.70	179.30	145.72
141.27	141.74	132.20	128.47	145.72	165.58

The error variance of prediction matrix for \hat{m}_a , $var(\hat{m}_a - m_a) = G_{ma} - K(G_{gg} - B^{22})K'$, is equal to:

$evpm = var(\hat{m}_a - m_a) = G_{ma} - K(G_{gg} - B^{22})K'$									
1.71	0.01	-0.02	-0.01	0	-0.01	...	0	0	0
0.01	1.71	0.02	0.01	0	0.01	...	0	0	0
-0.02	0.02	1.67	-0.02	0	-0.03	...	0	0	0.01
-0.01	0.01	-0.02	1.71	0	-0.01	...	0	0	0

$$evpm = var(\hat{m}_a - m_a) = G_{ma} - K(G_{gg} - B^{22})K'$$

0	0	0	0	1.7	0.02	...	0	0.02	-0.02
-0.01	0.01	-0.03	-0.01	0.02	1.68	...	0	-0.02	0.03
...
0	0	0	0	0	0	...	1.72	0	0
0	0	0	0	0.02	-0.02	...	0	1.7	0.02
0	0	0.01	0	-0.02	0.03	...	0	0.02	1.69

Thus, the vector of **marker BLUP** and their **standard errors of prediction** for the Example are equal to:

Marker	SOL	SESOL	Marker	SOL	SESOL	Marker	SOL	SESOL
\hat{m}_{a1}	-0.03	1.31	\hat{m}_{a21}	0.00	1.31	\hat{m}_{a41}	0.06	1.30
\hat{m}_{a2}	0.03	1.31	\hat{m}_{a22}	-0.00	1.29	\hat{m}_{a42}	-0.00	1.31
\hat{m}_{a3}	-0.09	1.29	\hat{m}_{a23}	-0.09	1.30	\hat{m}_{a43}	0.09	1.30
\hat{m}_{a4}	-0.03	1.31	\hat{m}_{a24}	-0.03	1.28	\hat{m}_{a44}	0.03	1.31
\hat{m}_{a5}	-0.06	1.30	\hat{m}_{a25}	0.03	1.31	\hat{m}_{a45}	0.06	1.30
\hat{m}_{a6}	0.00	1.29	\hat{m}_{a26}	0.00	1.31	\hat{m}_{a46}	-0.09	1.30
\hat{m}_{a7}	0.03	1.30	\hat{m}_{a27}	0.03	1.31	\hat{m}_{a47}	-0.00	1.31
\hat{m}_{a8}	-0.10	1.28	\hat{m}_{a28}	-0.09	1.29	\hat{m}_{a48}	0.03	1.31
\hat{m}_{a9}	-0.16	1.28	\hat{m}_{a29}	0.03	1.30	\hat{m}_{a49}	-0.00	1.31
\hat{m}_{a10}	-0.03	1.31	\hat{m}_{a30}	0.00	1.31	\hat{m}_{a50}	-0.03	1.31
\hat{m}_{a11}	0.03	1.31	\hat{m}_{a31}	-0.06	1.30	\hat{m}_{a51}	0.07	1.27
\hat{m}_{a12}	0.16	1.28	\hat{m}_{a32}	-0.09	1.30	\hat{m}_{a52}	0.03	1.31

$\widehat{m}a_{13}$	-0.19	1.27	$\widehat{m}a_{33}$	-0.06	1.30	$\widehat{m}a_{53}$	-0.06	1.30
$\widehat{m}a_{14}$	0.13	1.29	$\widehat{m}a_{34}$	0.03	1.30	$\widehat{m}a_{54}$	-0.03	1.31
$\widehat{m}a_{15}$	-0.09	1.30	$\widehat{m}a_{35}$	0.00	1.29	$\widehat{m}a_{55}$	0.00	1.31
$\widehat{m}a_{16}$	-0.00	1.29	$\widehat{m}a_{36}$	0.16	1.28	$\widehat{m}a_{56}$	0.03	1.30
$\widehat{m}a_{17}$	-0.00	1.31	$\widehat{m}a_{37}$	-0.09	1.30	$\widehat{m}a_{57}$	0.00	1.31
$\widehat{m}a_{18}$	0.00	1.29	$\widehat{m}a_{38}$	0.12	1.28	$\widehat{m}a_{58}$	0.00	1.31
$\widehat{m}a_{19}$	0.06	1.27	$\widehat{m}a_{39}$	0.13	1.29	$\widehat{m}a_{59}$	0.06	1.30
$\widehat{m}a_{20}$	-0.07	1.27	$\widehat{m}a_{40}$	0.00	1.31	$\widehat{m}a_{60}$	-0.03	1.30

Summary of predictions by genomic-polygenic models

Animal	Polygenic		Polygenic-Genomic with 1 Fixed Marker		Polygenic-Genomic with 4 Fixed Markers		Polygenic-Genomic with 4 Random Markers		Marker Polygenic-Genomic with 60 Random Markers		Animal Polygenic-Genomic with 60 Random Markers	
	\hat{u}_a	SEP (\hat{u}_a)	\hat{u}_a	SEP (\hat{u}_a)	\hat{u}_a	SEP (\hat{u}_a)	\hat{u}_a	SEP (\hat{u}_a)	\hat{u}_a	SEP (\hat{u}_a)	\hat{u}_a	SEP (\hat{u}_a)
1	10.25	14.66	9.70	14.74	146.12	11.72	10.00	15.01	11.05	19.97	11.05	19.97
2	-0.65	6.37	-0.75	6.38	105.45	8.80	-0.81	7.02	-0.21	14.03	-0.21	14.03
3	2.94	9.32	3.14	9.33	154.69	6.42	2.99	9.71	3.76	14.88	3.76	14.88
4	6.04	8.25	5.91	8.26	157.47	5.40	6.05	8.69	6.35	14.94	6.35	14.94
5	5.19	11.34	4.47	11.50	186.25	7.61	5.11	11.59	6.11	17.51	6.11	17.51
6	5.70	12.30	2.58	14.83	161.69	11.78	5.43	12.85	6.49	18.38	6.49	18.38

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