

4. Estimation of breeding value. BLUP

4.1 Introduction

The selection index principle assumes that true means and variances are known. When this is the case, the *best linear prediction*, BLP, of the breeding value, I , is

$$I = \bar{I} + b_{AP}(P_i - \bar{P}) = \bar{I} + \frac{\sigma_{AP}}{\sigma_P^2}(P_i - \bar{P})$$

where $\bar{I}$ and $\bar{P}$ are the true means of breeding value and phenotypic trait, respectively. In practice, true means and variances are not known. In spite of that, selection indices have served their purposes. There are, however, some potential sources of error that could be overcome if fixed effects and breeding values were estimated simultaneously as is the case when using BLUP methodology (BLUP = *Best Linear Unbiased Prediction*):

1. Adjustment for fixed effects is often based on historical data. Therefore, adjustment factors used may not be quite in agreement with those effects that should be adjusted. This may change the ranking of potential breeding animals.
2. Adjustment for herd means, by using the record as a deviation from the herd mean, assumes that the animals in the groups that are compared are contemporary. This may be difficult to achieve in practice, and often it will result in the groups being so small that the mean will be estimated with large error which in turn will affect the phenotypic deviations. This is not accounted for in the selection index.
3. Fixed effects are not adjusted for differences in genetic levels of the groups.
4. The selection index does not account for selection going on, nor does it account for assortative mating.
5. The selection index does not account for different genetic levels of the groups from which the deviations are computed, e.g. herds. Two animals from different herds having the same deviation from the mean, will be ranked equal, even if the two herds have different genetic levels.

When using the BLUP method, where all the effects are estimated simultaneously, these difficulties have been overcome. The breeding value may be written as

$$u_i = \mu + g_i + \frac{\sigma_{AP}}{\sigma_P^2}(P_i - f(a,b,...,u,...))$$

where u_i	=	BLUP of true breeding value (or half the breeding value in some cases)
+ g_i	=	BLUE (Best Linear Unbiased Estimate) of genetic level
P_i	=	phenotypic observation
$f(a,b,...,u,...)$	=	mean of an estimated value of comparison for each phenotypic observation based on BLUE of relevant fixed effects $a,b,...$ and BLUP of breeding value u for individuals in the comparison group.

In practice, BLUP of breeding values are obtained as solutions to Henderson's *Mixed Model Equations* (MME). MME are normal equations of a generalised least squares type. They are generated from phenotypic observations by means of a statistical model that describes the observations. Solving such a system of equations results in "partial" effects in the same way as the regression coefficients in a multiple regression. In this way, the effects are estimated by simultaneously taking other factors into consideration. The fixed effects in the model are BLUE and the random effects are BLUP.

4.2 Animal model

A typical mixed model might look as follows:

$$P_{ijkl} = \mu + a_i + h_j + \dots + u_k + e_{ijkl}$$

where

P_{ijkl} is a phenotypic observation

μ is the overall mean

a_i, h_j are fixed effects

u_k is a random effect, e.g. the genotypic value of individual k

e_{ijkl} is a random effect specific for each observation

In matrix form, this can be written

$$\begin{bmatrix} Y_1 \\ Y_2 \\ \vdots \\ Y_n \end{bmatrix} = \begin{bmatrix} X_{11} & X_{12} & \cdot & \cdot & \cdot \\ X_{21} & X_{22} & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ X_{n1} & X_{n2} & \cdot & \cdot & \cdot \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \\ \cdot \\ \cdot \\ \cdot \end{bmatrix} + \begin{bmatrix} Z_{11} & Z_{12} & \cdot & \cdot & \cdot \\ Z_{21} & Z_{22} & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ Z_{n1} & Z_{n2} & \cdot & \cdot & \cdot \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \\ \cdot \\ \cdot \\ \cdot \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ \cdot \\ \cdot \\ e_n \end{bmatrix}$$

or

$$y = Xb + Zu + e \quad (33)$$

It is assumed that the expectations are $E(y) = Xb$, $E(u) = 0$ and $E(e) = 0$. Further it is assumed that the residuals are independently distributed with variance σ_e^2 . Therefore $V(e) = I \sigma_e^2 = R$, $V(u) = A \sigma_A^2 = G$ and $COV(u, e) = COV(e, u) = 0$. Hence

$$V \begin{bmatrix} u \\ e \end{bmatrix} = \begin{bmatrix} G & 0 \\ 0 & R \end{bmatrix}$$

X and Z are incidence matrices. This is the usual way of writing a BLUP model. In general, b represents fixed effects and u represents random effects, e.g. breeding values. Note that X and Z are very large when the number of observations is large.

In general matrix terms, Henderson's Mixed Model Equations are :

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z \\ Z'R^{-1}X & Z'R^{-1}Z + A^{-1} \frac{1}{\sigma_A^2} \end{bmatrix} \begin{bmatrix} b \\ u \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Z'R^{-1}y \end{bmatrix} \quad (34)$$

Note that $\mathbf{R}$ is diagonal with σ_e^2 on the diagonal, $\mathbf{X}$ and $\mathbf{Z}$ are incidence matrices and $\mathbf{A}$ is the additive relationship matrix. If the animals are unrelated, the variance of $\mathbf{A}$ is diagonal with σ_A^2 on the diagonal, i.e. $\mathbf{I}\sigma_A^2$. The MME equations can therefore be written as

$$\begin{bmatrix} \mathbf{X}'\mathbf{X}\frac{1}{\sigma_e^2} & \mathbf{X}'\mathbf{Z}\frac{1}{\sigma_e^2} \\ \mathbf{Z}'\mathbf{X}\frac{1}{\sigma_e^2} & \mathbf{Z}'\mathbf{Z}\frac{1}{\sigma_e^2} + \mathbf{I}\frac{1}{\sigma_A^2} \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{u} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{y}\frac{1}{\sigma_e^2} \\ \mathbf{Z}'\mathbf{y}\frac{1}{\sigma_e^2} \end{bmatrix} \quad (35)$$

Multiplying through with σ_e^2 gives

$$\begin{bmatrix} \mathbf{X}'\mathbf{X} & \mathbf{X}'\mathbf{Z} \\ \mathbf{Z}'\mathbf{X} & \mathbf{Z}'\mathbf{Z} + \mathbf{I}\frac{\sigma_e^2}{\sigma_A^2} \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{u} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{y} \\ \mathbf{Z}'\mathbf{y} \end{bmatrix} \quad (36)$$

The term $\frac{\sigma_e^2}{\sigma_A^2}$ is usually called λ . Since $\sigma_A^2 + \sigma_e^2 = \sigma_P^2$ and $h^2 = \frac{\sigma_A^2}{\sigma_P^2}$, $\sigma_A^2 = h^2\sigma_P^2$ and $\sigma_e^2 = \sigma_P^2 - \sigma_A^2 = (1 - h^2)\sigma_P^2$. Therefore, $\lambda = \frac{\sigma_e^2}{\sigma_A^2}$ can be written as $\frac{1 - h^2}{h^2}$

Example 4.2.1

In the following example, milk yield is recorded for three unrelated cows:

Cow	Yield
1	3000
2	4000
3	5000

Spelled out in detail, the model can be written as

$$P_i = \mu + u_1 + u_2 + u_3 + e_i$$

The incidence matrix is most easily set up by listing each animal below the model, writing the record (Y) to the left and the incidence matrix to the right of the equal sign in the model by writing a 1 if the effect is present and 0 otherwise (omitting the e's):

Y_i		u_1	u_2	u_3
3000	1	1	0	0
4000	1	0	1	0
5000	1	0	0	1

$$\text{Then } \mathbf{P} = \begin{bmatrix} 3000 \\ 4000 \\ 5000 \end{bmatrix}, \quad \mathbf{X} = \begin{bmatrix} 1 \\ 1 \\ 1 \end{bmatrix} \quad \text{and} \quad \mathbf{Z} = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix}.$$

$$\begin{bmatrix} \mathbf{X}'\mathbf{X} & \mathbf{X}'\mathbf{Z} \\ \mathbf{Z}'\mathbf{X} & \mathbf{Z}'\mathbf{Z} \end{bmatrix} \text{ is therefore } \begin{bmatrix} 3 & 1 & 1 & 1 \\ 1 & 1 & 0 & 0 \\ 1 & 0 & 1 & 0 \\ 1 & 0 & 0 & 1 \end{bmatrix}$$

Assuming a heritability of 0.5, becomes 1. Hence $\mathbf{A}^{-1}$ is a 3x3 diagonal matrix with 1's on the diagonal. The equation system then becomes:

$$\begin{bmatrix} 3 & 1 & 1 & 1 \\ 1 & 2 & 0 & 0 \\ 1 & 0 & 2 & 0 \\ 1 & 0 & 0 & 2 \end{bmatrix} \begin{bmatrix} \mu \\ u_1 \\ u_2 \\ u_3 \end{bmatrix} = \begin{bmatrix} 12000 \\ 3000 \\ 4000 \\ 5000 \end{bmatrix}$$

The solution is

$$\begin{bmatrix} \frac{2}{3} & -\frac{1}{3} & -\frac{1}{3} & -\frac{1}{3} \\ -\frac{1}{3} & \frac{2}{3} & \frac{1}{6} & \frac{1}{6} \\ -\frac{1}{3} & \frac{1}{6} & \frac{2}{3} & \frac{1}{6} \\ -\frac{1}{3} & \frac{1}{6} & \frac{1}{6} & \frac{2}{3} \end{bmatrix} \begin{bmatrix} 12000 \\ 3000 \\ 4000 \\ 5000 \end{bmatrix} = \begin{bmatrix} 4000 \\ -500 \\ 0 \\ 500 \end{bmatrix}$$

For the three unrelated animals, the system of equations is the following:

$$\begin{bmatrix} 3 & 1 & 1 & 1 \\ 1 & 1 + \frac{\sigma_e^2}{\sigma_A^2} & 0 & 0 \\ 1 & 0 & 1 + \frac{\sigma_e^2}{\sigma_A^2} & 0 \\ 1 & 0 & 0 & 1 + \frac{\sigma_e^2}{\sigma_A^2} \end{bmatrix} \begin{bmatrix} \mu \\ u_1 \\ u_2 \\ u_3 \end{bmatrix} = \begin{bmatrix} \Sigma Y_i \\ Y_1 \\ Y_2 \\ Y_3 \end{bmatrix}$$

For one animal, the equation is

$$\begin{aligned}\mu + \left(1 + \frac{\sigma_e^2}{\sigma_A^2}\right)u_i &= Y_i \\ \left(1 + \frac{\sigma_e^2}{\sigma_A^2}\right)u_i &= Y_i - \mu \\ \frac{\sigma_A^2 + \sigma_e^2}{\sigma_A^2}u_i &= Y_i - \mu \\ u_i &= \frac{\sigma_A^2}{\sigma_e^2 + \sigma_A^2} (Y_i - \mu) \\ u_i &= h^2(Y_i - \mu)\end{aligned}$$

This is the same equation as is obtained by the selection index equations, the only difference being that in BLUP, u_i is estimated from the data simultaneously with the breeding values.

4.2.1 Use of the relationship matrix

If the animals are related, then the variance of $\mathbf{u}$, $\mathbf{A}^{-1}_{A^2}$, is no longer diagonal. Use of the relationship matrix is shown in example 4.2.1.1.

Example 4.2.1.1

The following data are available:

Animal	Sire	Dam	Trait
1	?	?	10
2	?	?	9
3	?	?	8
4	?	?	7
5	1	2	9
6	1	2	10
7	3	4	8
8	5	6	11

The animals 1, 2, 3 and 4 are assumed to be unrelated and not inbred. Then the relationship matrix is:

					1.2	1.2	3.4	5.6
	1	2	3	4	5	6	7	8
1	1	0	0	0	0.5	0.5	0	0.5
2	0	1	0	0	0.5	0.5	0	0.5
3	0	0	1	0	0	0	0.5	0
4	0	0	0	1	0	0	0.5	0
5	0.5	0.5	0	0	1	0.5	0	0.75
6	0.5	0.5	0	0	0.5	1	0	0.75
7	0	0	0.5	0.5	0	0	1	0
8	0.5	0.5	0	0	0.75	0.75	0	1.25

The animal model equations are

$$\begin{bmatrix} n & \mathbf{1}' \\ \mathbf{1} & \mathbf{I} + \mathbf{A}^{-1}\lambda \end{bmatrix} \begin{bmatrix} \mu \\ u \end{bmatrix} = \begin{bmatrix} \mathbf{1}'\mathbf{Y} \\ \mathbf{Y} \end{bmatrix}$$

where $\mathbf{Y}$ is the vector of observations on the 8 animals and $\mathbf{1}$ is a vector of ones of dimension 8.

Let h^2 be 0.5, then $\sigma_e^2 = \sigma_A^2$ and $\lambda = 1$. The inverse relationship matrix $\mathbf{A}^{-1}$, is

$$\begin{bmatrix} 2 & 1 & 0 & 0 & -1 & -1 & 0 & 0 \\ 1 & 2 & 0 & 0 & -1 & -1 & 0 & 0 \\ 0 & 0 & 1.5 & 0.5 & 0 & 0 & -1 & 0 \\ 0 & 0 & 0.5 & 1.5 & 0 & 0 & -1 & 0 \\ -1 & -1 & 0 & 0 & 2.5 & 0.5 & 0 & -1 \\ -1 & -1 & 0 & 0 & 0.5 & 2.5 & 0 & -1 \\ 0 & 0 & -1 & -1 & 0 & 0 & 2 & 0 \\ 0 & 0 & 0 & 0 & -1 & -1 & 0 & 2 \end{bmatrix}$$

With $\lambda = 1$, the equations are

$$\begin{bmatrix} 8 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\ 1 & 3 & 1 & 0 & 0 & -1 & -1 & 0 & 0 \\ 1 & 1 & 3 & 0 & 0 & -1 & -1 & 0 & 0 \\ 1 & 0 & 0 & 2.5 & 0.5 & 0 & 0 & -1 & 0 \\ 1 & 0 & 0 & 0.5 & 2.5 & 0 & 0 & -1 & 0 \\ 1 & -1 & -1 & 0 & 0 & 3.5 & 0.5 & 0 & -1 \\ 1 & -1 & -1 & 0 & 0 & 0.5 & 3.5 & 0 & -1 \\ 1 & 0 & 0 & -1 & -1 & 0 & 0 & 3 & 0 \\ 1 & 0 & 0 & 0 & 0 & -1 & -1 & 0 & 3 \end{bmatrix} \begin{bmatrix} \mu \\ u_1 \\ u_2 \\ u_3 \\ u_4 \\ u_5 \\ u_6 \\ u_7 \\ u_8 \end{bmatrix} = \begin{bmatrix} 72 \\ 10 \\ 9 \\ 8 \\ 7 \\ 9 \\ 10 \\ 8 \\ 11 \end{bmatrix}$$

Consider the equation for animal 1:

$$+ 3u_1 + u_2 - u_5 - u_6 = 10$$

Isolating u_1 gives

$$u_1 = 1/3(10 - u_2 + u_5 + u_6)$$

which can be written as

$$u_1 = 1/3[(10 - \mu) + (u_5 - 1/2 u_2) + (u_6 - 1/2 u_2)]$$

$$= h_w^2 [(y - \bar{y}) + \sum_{i=1}^2 (u_{o_i} - 1/2 u_m)]$$

The contribution of each progeny to the breeding value of animal 1 is adjusted for half the breeding value of the mate, i.e. animal 2. This is an adjustment for assortative mating. It can also be seen that the record is adjusted for fixed effects, in this example the mean. For animal 8 the equation is

$$- u_5 - u_6 + 3 u_8 = 11$$

Rearranging gives $3u_8 = 11 - \mu + u_5 + u_6$

$$\begin{aligned} u_8 &= 1/3 (11 - \mu) + 1/3 (u_5 + u_6) \\ &= 1/3 (11 - \mu) + 1/2 (u_5 + u_6) - 1/6 (u_5 + u_6) \\ &= 1/2 (u_5 + u_6) + 1/3 [11 - \mu] - 1/2 (u_5 + u_6) \\ &= 1/2 (u_s + u_d) + h_w^2 [(y - \mu) - 1/2 (u_s + u_d)] \end{aligned}$$

The first term is the predicted breeding value of animal 8 based on the breeding value of u_5 and u_6 , the parents of animal 8. The second term is the phenotypic observation adjusted for fixed effects and the parents breeding value, weighted by the within family heritability. This is an estimate of the contribution of Mendelian sampling to the breeding value of animal 8. The within family heritability is

$$h_w^2 = \frac{\frac{1}{2} h^2 (1 - \bar{F})}{\frac{1}{2} h^2 (1 - \bar{F}) + (1 - h^2)} \quad (37)$$

where $\bar{F}$ is the average inbreeding of the parents.

$$\text{For this example, } h_w^2 = \frac{(0.5)(0.5)}{(0.5)(0.5) + 0.5} = 0.33$$

The transposed solution vector is

$$\begin{bmatrix} \mu & u_1 & u_2 & u_3 & u_4 & u_5 & u_6 & u_7 & u_8 \end{bmatrix} \\ = \begin{bmatrix} 8.7059 & 0.8676 & 0.3676 & -0.3676 & -0.8676 & .6716 & 1.0049 & -0.6471 & 1.3235 \end{bmatrix}$$

The breeding value of animals in the base population sum to zero. The base population in this example is the animals 1, 2, 3 and 4. The average of their breeding values is

$$1/4(0.8675 + 0.3676 - 0.3676 - 0.8676) = 0$$

The averages of expected breeding values of animals in subsequent generations are not zero. Generation 2 in this example is made up of animals 5, 6 and 7. The average of their breeding values is

$$1/3(0.6716 + 1.0049 - 0.6471) = 0.343$$

This figure represents selection and random drift. Animals 1 and 2, who had the highest breeding values in the base population, produced two progeny and animals 3 and 4, having the lowest breeding values in the base population, produced one progeny. This will explain why the average breeding value of animals in the first generation is greater than zero. Because of this property with the animal model, it can be used to estimate response to selection.

Example 4.2.1.2

In this example, both μ and year are included as fixed effects. The following data are available:

Animal	Sire	Dam	Y	Year
5	1	3	250	2
6	1	3	198	2
7	2	4	245	2
8	2	4	260	2
9	2	4	235	2
4	-	-	255	1
3	-	-	200	1
2	-	-	225	1

We may set up the following model:

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{u} + \mathbf{e}$$

where $\mathbf{y}$ = vector of observations

$\mathbf{b}$ = vector effect of μ and of year effects

$\mathbf{u}$ = vector of breeding values

$\mathbf{X}, \mathbf{Z}$ = incidence matrices

$\mathbf{e}$ = vector of random residual elements

Let $\mathbf{W} = [\mathbf{X} \ \mathbf{Z}]$. Then

$$\mathbf{W}'\mathbf{W} = \begin{bmatrix} \mathbf{X}' \\ \mathbf{Z}' \end{bmatrix} [\mathbf{X} \ \mathbf{Z}] = \begin{bmatrix} \mathbf{X}'\mathbf{X} & \mathbf{X}'\mathbf{Z} \\ \mathbf{Z}'\mathbf{X} & \mathbf{Z}'\mathbf{Z} \end{bmatrix}$$

Then the $\mathbf{y}$ vector and the $\mathbf{W}$ matrix can be set up by writing out the model in detail, omitting $\mathbf{e}$, and below write y-value or 0 or 1 depending on whether the effect is present or not:

$$\begin{bmatrix} y \\ 250 \\ 198 \\ 245 \\ 260 \\ 235 \\ 255 \\ 200 \\ 225 \end{bmatrix} = \begin{bmatrix} \mu & b_1 & b_2 & u_1 & u_2 & u_3 & u_4 & u_5 & u_6 & u_7 & u_8 & u_9 \\ 1 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ 1 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 1 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 1 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$

Transposing $\mathbf{W}$ and multiplying by $\mathbf{W}$ gives

$$\mathbf{W}'\mathbf{W} = \begin{bmatrix} 8 & 3 & 5 & 0 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\ 3 & 3 & 0 & 0 & 1 & 1 & 1 & 0 & 0 & 0 & 0 & 0 \\ 5 & 0 & 5 & 0 & 0 & 0 & 0 & 1 & 1 & 1 & 1 & 1 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 1 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

The inverse of the relationship matrix can be set up directly, using the method described in chapter 3. λ_i is 1 for the animals 1-4 and 2 for the animals 5-9:

$$A^{-1} = \begin{bmatrix} 2 & 0 & 1 & 0 & -1 & -1 & 0 & 0 & 0 \\ 0 & 2\frac{1}{2} & 0 & 1\frac{1}{2} & 0 & 0 & -1 & -1 & -1 \\ 1 & 0 & 2 & 0 & -1 & -1 & 0 & 0 & 0 \\ 0 & 1\frac{1}{2} & 0 & 2\frac{1}{2} & 0 & 0 & -1 & -1 & -1 \\ -1 & 0 & -1 & 0 & 2 & 0 & 0 & 0 & 0 \\ -1 & 0 & -1 & 0 & 0 & 2 & 0 & 0 & 0 \\ 0 & -1 & 0 & -1 & 0 & 0 & 2 & 0 & 0 \\ 0 & -1 & 0 & -1 & 0 & 0 & 0 & 2 & 0 \\ 0 & -1 & 0 & -1 & 0 & 0 & 0 & 0 & 2 \end{bmatrix}$$

The system of equations then becomes

$$\begin{bmatrix} X'X & X'Z \\ Z'X & Z'Z + A^{-1}\lambda \end{bmatrix} \begin{bmatrix} b \\ u \end{bmatrix} = \begin{bmatrix} X'y \\ Z'y \end{bmatrix} \quad (38)$$

Let $h^2 = 0.33$ and $\lambda = 2$. Then the system of equations is:

$$\begin{bmatrix} 8 & 3 & 5 & 0 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\ 3 & 3 & 0 & 0 & 1 & 1 & 1 & 0 & 0 & 0 & 0 & 0 \\ 5 & 0 & 5 & 0 & 0 & 0 & 0 & 1 & 1 & 1 & 1 & 1 \\ 0 & 0 & 0 & 4 & 0 & 2 & 0 & -2 & -2 & 0 & 0 & 0 \\ 1 & 1 & 0 & 0 & 6 & 0 & 3 & 0 & 0 & -2 & -2 & -2 \\ 1 & 1 & 0 & 2 & 0 & 5 & 0 & -2 & -2 & 0 & 0 & 0 \\ 1 & 1 & 0 & 0 & 3 & 0 & 6 & 0 & 0 & -2 & -2 & -2 \\ 1 & 0 & 1 & -2 & 0 & -2 & 0 & 5 & 0 & 0 & 0 & 0 \\ 1 & 0 & 1 & -2 & 0 & -2 & 0 & 0 & 5 & 0 & 0 & 0 \\ 1 & 0 & 1 & 0 & -2 & 0 & -2 & 0 & 0 & 5 & 0 & 0 \\ 1 & 0 & 1 & 0 & -2 & 0 & -2 & 0 & 0 & 0 & 5 & 0 \\ 1 & 0 & 1 & 0 & -2 & 0 & -2 & 0 & 0 & 0 & 0 & 5 \end{bmatrix} \begin{bmatrix} \mu \\ b_1 \\ b_2 \\ u_1 \\ u_2 \\ u_3 \\ u_4 \\ u_5 \\ u_6 \\ u_7 \\ u_8 \\ u_9 \end{bmatrix} = \begin{bmatrix} 1868 \\ 680 \\ 1188 \\ 0 \\ 225 \\ 200 \\ 255 \\ 250 \\ 198 \\ 245 \\ 260 \\ 235 \end{bmatrix}$$

The equation for μ gives the average adjusted for year effects and breeding values:

$$8 \mu + 3 b_1 + 5 b_2 + u_2 + u_3 + u_4 + u_5 + u_6 + u_7 + u_8 + u_9 = 1868$$

$$\mu = 1/8 (1868) - 3/8 b_1 - 5/8 b_2 - 1/8 (u_2 + u_3 + u_4 + u_5 + u_6 + u_7 + u_8 + u_9)$$

The equations for herd effects:

$$b_1 = 1/3 (680) - \mu - 1/3 (u_2 + u_3 + u_4)$$

$$b_2 = 1/5 (1188) - \mu - 1/5 (u_5 + u_6 + u_7 + u_8 + u_9)$$

These are herd effects adjusted for mean and breeding values. Equation for u_1 (parent without own record):

$$2 u_1 + u_3 - u_5 - u_6 = 0$$

After rearranging this can be written as

$$u_1 = 1/2(u_5 - 1/2 u_3) + 1/2(u_6 - 1/2 u_3) = 1/2 \sum(u_o - 1/2 u_m)$$

The breeding value of a parent without record is based on breeding values of the progeny adjusted for breeding value of the mates. Equation for u_2 (parent with own record):

$$+ b_1 + 6u_2 + 3 u_4 - 2 u_7 - 2 u_8 - 2 u_9 = 225$$

Rearranging gives:

$$u_2 = 1/6 (225 - \mu - b_1) + 1/3 [(u_7 - 1/2 u_4) + (u_8 - 1/2 u_4) + (u_9 - 1/2 u_4)]$$

$$u_2 = 1/6 (y - \mu - b_1) + 1/3 \sum(u_o - 1/2 u_m)$$

This is the record of the parent adjusted for mean and fixed effects. In addition there is a contribution from each progeny adjusted for breeding value of the mate.

Equation for u_7 (animal with record):

$$\mu + b_2 - 2 u_2 - 2u_4 + 5 u_7 = 245$$

$$u_7 = 1/2 (u_2 + u_4) + 1/5 (245 - \mu - b_2 - 1/2 (u_2 + u_4))$$

The first expression is the average breeding value of the parents. The second is the yields adjusted for fixed effects expressed as a deviation from the parental mean and weighted by the within family heritability. Solution to the equations is:

$$\mu = 235.07$$

$$\mathbf{b}' = \begin{bmatrix} -9.21 & 1.26 \end{bmatrix}$$

$$\mathbf{u}' = \begin{bmatrix} -2.41 & 1.32 & -10.23 & 11.32 & -2.32 & -12.72 & 6.79 & 9.79 & 4.79 \end{bmatrix}$$

4.2.2 Prediction error variance

Henderson has shown that prediction error variance is a function of the diagonal elements of the inverse of the coefficient matrix and the residual variance. Let

$$\begin{bmatrix} C_{11} & C_{12} \\ c_{21} & C_{22} \end{bmatrix}^{-1} = \begin{bmatrix} C^{11} & C^{12} \\ C^{21} & C^{22} \end{bmatrix}$$

Then

$$PEV = V(\mathbf{u} - \hat{\mathbf{u}}) = \mathbf{C}^{22}\sigma_e^2$$

PEV is the fraction of the additive variance not accounted for by the prediction.

What is the proportion of the additive variance not accounted for by the prediction?

$r_{\hat{u}}^2$ (r_{IA}^2) is the squared correlation between true and predicted breeding value. It is the *coefficient of determination*, i.e. it is a measure of the proportion of the variation in true breeding value that is accounted for by the variation in estimated breeding value. Then

$$\sigma_A^2 - r^2\sigma_A^2 = (1 - r^2)\sigma_A^2$$

is the proportion not accounted for. Then for animal i

$$c^{ii}\sigma_e^2 = (1 - r^2)\sigma_A^2$$

$$c^{ii}\frac{\sigma_e^2}{\sigma_A^2} = 1 - r^2 = c^{ii}\lambda$$

Therefore

$$PEV = c^{ii} \lambda \sigma_A^2$$

and standard error of prediction

$$SEP = \sqrt{c^{ii} \lambda \sigma_A^2}$$

4.3 Reduced animal model

The breeding value of an animal can be expressed as the sum of the additive genetic contributions of gametes from its parents, g_s from the sire and g_d from the dam:

$$u_i = g_s + g_d$$

If there is no selection or linkage, and if the gametes unite randomly, the variance of the breeding value is

$$V(u_i) = V(g_s) + V(g_d) = \frac{1}{2} \sigma_A^2 + \frac{1}{2} \sigma_A^2 = \sigma_A^2$$

Each gametic value can be expressed in terms of the breeding value of the parent (p) from which it was obtained plus a Mendelian sampling term:

$$g_p = \frac{1}{2} u_p + m_p,$$

where u_p is the breeding value of the parent and m_p is the contribution from sampling genes from the parents to the progeny. The variance of g_p is then

$$V(g_p) = 0.25 V(u_p) + V(m_p)$$

and if there is no selection

$$V(g_p) = 0.25 \sigma_A^2 + 0.25(1 - F)\sigma_A^2 = 0.5(1 - 0.5F_p)\sigma_A^2$$

Quaas and Pollak developed in 1980 a gametic or reduced animal model. Such a model can reduce computational requirements because it reduces the number of equations. The model is

$$u_i = g_s + g_d = \frac{1}{2} u_s + \frac{1}{2} u_d + m_i$$

where $m_i = m_s + m_d$

The variance of $\mathbf{m}$ is (see page 37)

$$V(\mathbf{m}) = \mathbf{D}\sigma_A^2$$

Equations for an animals breeding value are expressed in terms of the breeding value of its parents and a Mendelian sampling term combining both sire and dam contributions. The breeding values for all progeny with identified parents are

$$\mathbf{u} = \mathbf{Z}\mathbf{u}_p + \mathbf{m}$$

$\mathbf{Z}$ has one row for each progeny and one column for each parent. All elements of $\mathbf{Z}$ are zero except for the elements corresponding to the elements of the parents. These elements are $\frac{1}{2}$. Under the reduced animal model, the variance of breeding values is

$$V(\mathbf{u}) = \mathbf{Z}\mathbf{A}_p\mathbf{Z}'\sigma_A^2 + \mathbf{D}\sigma_A^2$$

where $\mathbf{A}_p$ is the additive genetic relationship matrix for the parents and $\mathbf{D}$ is a diagonal matrix with diagonal elements $d_i = (1 - \frac{1}{4} n_p)$, where n_p is the number of known parents., i. e. the coefficient $(1 - \frac{1}{4} n_p)$ becomes 1, $\frac{3}{4}$ or $\frac{1}{2}$ if 0, 1 or 2 parents are known (see chapter 3).

Consider the following animal model

$$y_i = \mu + u_i + e_i,$$

where u_i is the additive genetic value and e_i is the environmental value of the i^{th} animal. In matrix notation, the model is

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{u} + \mathbf{e}$$

and if there is only one record per animal, $\mathbf{Z} = \mathbf{I}$ and

$$V(y) = A\sigma_A^2 + I\sigma_e^2$$

We can express the genetic value of an individual in terms of gametic contributions of its parents plus a Mendelian sampling term:

$$u_i = \frac{1}{2} u_s + \frac{1}{2} u_d + m_i$$

where u_s and u_d are the breeding values of the sire and dam of animal i and m_i is the Mendelian sampling. The gametic model is therefore

$$y_i = \mu + \frac{1}{2} u_s + \frac{1}{2} u_d + m_i + e_i$$

The term m_i and e_i can be combined into a single residual term

$$e_i^* = m_i + e_i$$

with variance

$$V(e_i^*) = d_{ii} (1 - \bar{F}) \sigma_A^2 + \sigma_e^2$$

where $d_{ii} = \frac{1}{2}$ or $\frac{3}{4}$ if both or one parent is known. $\bar{F}$ is the average inbreeding of the sire and the dam. In matrix notation, the gametic model can be written as

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu}_p + \mathbf{e}^*$$

where $\mathbf{u}_p$ is a vector of breeding values of parents and $\mathbf{Z}$ is an incidence matrix of 0 and $\frac{1}{2}$, where $\frac{1}{2}$ identifies the parents of each animal with record.

We now assume that $V(\mathbf{u}_p) = \mathbf{A}_p \sigma_A^2$ and $V(\mathbf{e}^*) = \mathbf{I} \sigma_e^2$ where $\mathbf{A}_p$ is the additive genetic relationship matrix among parents and $\sigma_e^2 = d_{ii} \sigma_A^2 + \sigma_e^2$. We can therefore partition $\mathbf{y}$ into parental records and offspring records, $\mathbf{y}_p$ and $\mathbf{y}_o$:

$$\mathbf{y} = \begin{bmatrix} \mathbf{y}_p \\ \mathbf{y}_o \end{bmatrix} = \mathbf{Xb} + \begin{bmatrix} \mathbf{I}_1 \\ \mathbf{Z} \end{bmatrix} \mathbf{u}_p + \begin{bmatrix} \mathbf{e} \\ \mathbf{e}^* \end{bmatrix} = \mathbf{Xb} + \mathbf{S}\mathbf{u}_p + \boldsymbol{\epsilon}$$

Then

$$V(\mathbf{y}) = \mathbf{S}\mathbf{A}_p\mathbf{S}'\sigma_A^2 + \mathbf{R}, \text{ where } \mathbf{R} = \begin{bmatrix} I_1\sigma_e^2 & \mathbf{0} \\ \mathbf{0} & I_2\sigma_e^2 \end{bmatrix}$$

$\mathbf{R}$ is unaffected by selection, $\mathbf{A}_p$ accounts for all relationship among parents, and $\mathbf{Z}$ traces the flow of genes from parents to offspring.

The breeding values of the offspring can be obtained by back solving:

$$u_o = \frac{1}{2}(u_s + u_d) + c_i(Y - \mathbf{Xb} - \frac{1}{2}(u_s + u_d))$$

where

$$c_i = \frac{1}{1 + \frac{\sigma_e^2}{d_{ii} \sigma_A^2}} = \frac{1}{1 + \frac{\lambda}{d_{ii}}}$$

d_{ii} is diagonal element i of the $\mathbf{D}$ -matrix.

Example 4.3.1

The following data have been collected:

Animal	Sire	Dam	Herd	Yield
1	-	-	-	-
2	-	-	1	11
3	-	-	-	-
4	-	-	2	7
5	1	2	1	10
6	1	2	2	9
7	3	4	2	8

Assume $\sigma_A^2 = \sigma_e^2 = 1$. This gives a heritability of $h^2 = 1/(1 + 1) = 0.5$. We can set up the following model:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Su}_p + \mathbf{e}$$

The equations are:

$$\begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{S} \\ \mathbf{S}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{S}'\mathbf{R}^{-1}\mathbf{S} + \frac{\mathbf{A}_p^{-1}}{\sigma_A^2} \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{u}_p \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{S}'\mathbf{R}^{-1}\mathbf{y} \end{bmatrix} \quad (39)$$

$\mathbf{X}$ is the incidence matrix for fixed effects. Animals 1 and 3 have no record, animals 2 and 5 are in herd 1 and animals 4, 6 and 7 in herd 2. Hence

$$\mathbf{X}' = \begin{bmatrix} 1 & 0 & 1 & 0 & 0 \\ 0 & 1 & 0 & 1 & 1 \end{bmatrix}$$

Parents, i.e. animals 1, 2, 3 and 4 are unrelated. Therefore

$$\mathbf{A}_p = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix}$$

$\mathbf{R}$ is diagonal with σ_e^2 on the diagonal elements corresponding to the parents having record and elsewhere $d_{ii} (1 + \bar{F}) \sigma_A^2 + \sigma_e^2 = 0.5 (1) + 1 = 1.5$, because parents are not inbred. $\mathbf{R}$ is therefore

$$\mathbf{R} = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & \frac{3}{2} & 0 & 0 \\ 0 & 0 & 0 & \frac{3}{2} & 0 \\ 0 & 0 & 0 & 0 & \frac{3}{2} \end{bmatrix} \quad \text{and} \quad \mathbf{R}^{-1} = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & \frac{2}{3} & 0 & 0 \\ 0 & 0 & 0 & \frac{2}{3} & 0 \\ 0 & 0 & 0 & 0 & \frac{2}{3} \end{bmatrix}$$

$\mathbf{S}$ is a partitioned matrix composed of a matrix with number of rows corresponding to the number of parents with records and number of columns corresponding to total number of parents. This matrix contains a 1 for the elements corresponding to parents with record. In addition $\mathbf{S}$ contains an incidence matrix with zeroes in all places except those elements identifying parents, which are $\frac{1}{2}$. $\mathbf{S}$ is therefore

$$\mathbf{S} = \begin{bmatrix} 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 \\ \frac{1}{2} & \frac{1}{2} & 0 & 0 \\ \frac{1}{2} & \frac{1}{2} & 0 & 0 \\ 0 & 0 & \frac{1}{2} & \frac{1}{2} \end{bmatrix}$$

Then

$$\mathbf{X}'\mathbf{R}^{-1}\mathbf{X} = \begin{bmatrix} 1 & 0 & 1 & 0 & 0 \\ 0 & 1 & 0 & 1 & 1 \end{bmatrix} \begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & \frac{2}{3} & 0 & 0 \\ 0 & 0 & 0 & \frac{2}{3} & 0 \\ 0 & 0 & 0 & 0 & \frac{2}{3} \end{bmatrix} \begin{bmatrix} 1 & 0 \\ 0 & 1 \\ 1 & 0 \\ 0 & 1 \\ 0 & 1 \end{bmatrix} = \begin{bmatrix} 1\frac{2}{3} & 0 \\ 0 & 2\frac{1}{3} \end{bmatrix}$$

$$\mathbf{X}'\mathbf{R}^{-1}\mathbf{S} = \begin{bmatrix} 1 & 0 & 1 & 0 & 0 \\ 0 & 1 & 0 & 1 & 1 \end{bmatrix} \begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & \frac{2}{3} & 0 & 0 \\ 0 & 0 & 0 & \frac{2}{3} & 0 \\ 0 & 0 & 0 & 0 & \frac{2}{3} \end{bmatrix} \begin{bmatrix} 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 \\ \frac{1}{2} & \frac{1}{2} & 0 & 0 \\ \frac{1}{2} & \frac{1}{2} & 0 & 0 \\ 0 & 0 & \frac{1}{2} & \frac{1}{2} \end{bmatrix}$$

$$= \begin{bmatrix} \frac{1}{3} & 1\frac{1}{3} & 0 & 0 \\ \frac{1}{3} & \frac{1}{3} & \frac{1}{3} & 1\frac{1}{3} \end{bmatrix}$$

Similarly we can compute $\mathbf{S}'\mathbf{R}^{-1}\mathbf{S}$ as

$$\mathbf{S}'\mathbf{R}^{-1}\mathbf{S} = \begin{bmatrix} 0 & 0 & \frac{1}{2} & \frac{1}{2} & 0 \\ 1 & 0 & \frac{1}{2} & \frac{1}{2} & 0 \\ 0 & 0 & 0 & 0 & \frac{1}{2} \\ 0 & 1 & 0 & 0 & \frac{1}{2} \end{bmatrix} \begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & \frac{2}{3} & 0 & 0 \\ 0 & 0 & 0 & \frac{2}{3} & 0 \\ 0 & 0 & 0 & 0 & \frac{2}{3} \end{bmatrix} \begin{bmatrix} 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 \\ \frac{1}{2} & \frac{1}{2} & 0 & 0 \\ \frac{1}{2} & \frac{1}{2} & 0 & 0 \\ 0 & 0 & \frac{1}{2} & \frac{1}{2} \end{bmatrix}$$

$$= \begin{bmatrix} \frac{1}{3} & \frac{1}{3} & 0 & 0 \\ \frac{1}{3} & 1\frac{1}{3} & 0 & 0 \\ 0 & 0 & \frac{1}{6} & \frac{1}{6} \\ 0 & 0 & \frac{1}{6} & 1\frac{1}{6} \end{bmatrix}$$

Finally, $\mathbf{A}_p$ a 4x4 identity matrix, and the additive genetic variance = 1, so $\mathbf{A}_p^{-1} \frac{1}{\sigma_A^2}$ is also a 4x4 identity matrix. The full equation system is then

$$\begin{bmatrix} 1\frac{2}{3} & 0 & \frac{1}{3} & 1\frac{1}{3} & 0 & 0 \\ 0 & 2\frac{1}{3} & \frac{1}{3} & \frac{1}{3} & \frac{1}{3} & 1\frac{1}{3} \\ \frac{1}{3} & \frac{1}{3} & 1\frac{1}{3} & \frac{1}{3} & 0 & 0 \\ 1\frac{1}{3} & \frac{1}{3} & \frac{1}{3} & 2\frac{1}{3} & 0 & 0 \\ 0 & \frac{1}{3} & 0 & 0 & 1\frac{1}{6} & \frac{1}{6} \\ 0 & 1\frac{1}{3} & 0 & 0 & \frac{1}{6} & 2\frac{1}{6} \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \\ u_1 \\ u_2 \\ u_3 \\ u_4 \end{bmatrix} = \begin{bmatrix} 17\frac{2}{3} \\ 18\frac{1}{3} \\ 6\frac{1}{3} \\ 17\frac{1}{3} \\ 2\frac{2}{3} \\ 9\frac{2}{3} \end{bmatrix}$$

The following solution is obtained:

$$\mathbf{b} = \begin{bmatrix} 10.269 & 8.077 \end{bmatrix}; \quad \mathbf{u} = \begin{bmatrix} 0.064 & 0.397 & 0.051 & -0.513 \end{bmatrix}$$

The breeding values of the progeny may now be obtained by back solving. Both parents are known for all offspring and $\sigma_A^2 = \sigma_e^2 = 1$. Hence, $c = 1/3$.

$$u_5 = \frac{1}{2}(u_1 + u_2) + \frac{1}{3}(y - b_1 - \frac{1}{2}(u_1 + u_2))$$

$$= \frac{1}{2}(0.064 + 0.397) + \frac{1}{3}(10 - 10.269 - \frac{1}{2}(0.064 + 0.397)) = 0.064$$

$$u_6 = \frac{1}{2}(0.064 + 0.397) + \frac{1}{3}(9 - 8.077 - \frac{1}{2}(0.064 + 0.397)) = 0.461$$

$$u_7 = \frac{1}{2}(0.051 + (-0.513)) + \frac{1}{3}(8 - 8.077 - \frac{1}{2}(0.051 + (-0.513))) = -0.179$$

4.4 Repeatability model

When there are more observations per animal, the animal model should be modified to a *repeatability* model. A repeatability model might have the following form:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{Zp} + \mathbf{e}$$

where $\mathbf{y}$ = vector of observations

$\mathbf{b}$ = vector of fixed effects

$\mathbf{u}$ = vector of breeding values

$\mathbf{e}$ = vector of residuals

$\mathbf{p}$ = vector of permanent environmental effects

$\mathbf{X}$ and $\mathbf{Z}$ = incidence matrices

It is assumed that $E(\mathbf{y}) = \mathbf{Xb}$ and $V \begin{bmatrix} \mathbf{u} \\ \mathbf{p} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} A\sigma_A^2 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & I\sigma_p^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & I\sigma_e^2 \end{bmatrix}$.

The MME are

$$\begin{bmatrix} \mathbf{X}'\mathbf{X} & \mathbf{X}'\mathbf{Z} & \mathbf{X}'\mathbf{Z} \\ \mathbf{Z}'\mathbf{X} & \mathbf{Z}'\mathbf{Z} + \mathbf{A}^{-1}\lambda & \mathbf{Z}'\mathbf{Z} \\ \mathbf{Z}'\mathbf{X} & \mathbf{Z}'\mathbf{Z} & \mathbf{Z}'\mathbf{Z} + \mathbf{I}_Y \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{u} \\ \mathbf{p} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{y} \\ \mathbf{Z}'\mathbf{y} \\ \mathbf{Z}'\mathbf{y} \end{bmatrix} \quad (40)$$

Since the phenotypic variance, $\sigma_p^2 = \sigma_A^2 + \sigma_p^2 + \sigma_e^2$ and $r = \frac{\sigma_A^2 + \sigma_p^2}{\sigma_p^2}$

$$\text{then } \lambda = \frac{\sigma_e^2}{\sigma_A^2} = \frac{1 - r}{h^2} \text{ and } \gamma = \frac{\sigma_e^2}{\sigma_p^2} = \frac{1 - r}{r - h^2}$$

Consider the following data for feed intake on dairy cows from parturition to 4 weeks in the lactation for first lactation cows:

Cow	Sire	Dam	Feed intake
5	10	1	2.1, 2.5
6	10	2	1.8, 1.9, 2.3
7	20	3	3.0
8	20	4	2.8, 2.7
9	20	4	2.6

The following model applies:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{Zp} + \mathbf{e}$$

where $\mathbf{b}$, $\mathbf{y}$, $\mathbf{u}$, $\mathbf{e}$, $\mathbf{X}$ and $\mathbf{Z}$ are as defined above.

The animals 1 through 4, 10 and 20 do not themselves have records. We can partition the vector of breeding values, $\mathbf{u}$, into $\mathbf{u}_1$ and $\mathbf{u}_2$, where $\mathbf{u}_1$ contains the breeding values of animals without records and $\mathbf{u}_2$ contains breeding values of animals with records. Then $\mathbf{Z}$ can be partitioned correspondingly into $\mathbf{Z}_1$ and $\mathbf{Z}_2$, where $\mathbf{Z}_1$ is $\mathbf{0}$. Further, if we let

$$\mathbf{A}^{-1} = \begin{bmatrix} \mathbf{A}_{11}^{-1} & \mathbf{A}_{12}^{-1} \\ \mathbf{A}_{21}^{-1} & \mathbf{A}_{22}^{-1} \end{bmatrix} \quad (41)$$

then the equations become

$$\begin{bmatrix} \mathbf{1}'\mathbf{1} & \mathbf{0} & \mathbf{1}'\mathbf{Z}_2 & \mathbf{1}'\mathbf{Z}_2 \\ \mathbf{0} & \mathbf{A}_{11}^{-1}\lambda & \mathbf{A}_{12}^{-1}\lambda & \mathbf{0} \\ \mathbf{Z}_2'\mathbf{1} & \mathbf{A}_{21}^{-1}\lambda & \mathbf{Z}_2'\mathbf{Z}_2 + \mathbf{A}_{22}^{-1}\lambda & \mathbf{Z}_1'\mathbf{Z}_2 \\ \mathbf{Z}_2'\mathbf{1} & \mathbf{0} & \mathbf{Z}_2'\mathbf{Z}_2 & \mathbf{Z}_2'\mathbf{Z}_2 + \mathbf{I}_Y \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{u}_1 \\ \mathbf{u}_2 \\ \mathbf{p} \end{bmatrix} = \begin{bmatrix} \mathbf{1}'\mathbf{y} \\ \mathbf{0} \\ \mathbf{Z}_2'\mathbf{y} \\ \mathbf{Z}_2'\mathbf{y} \end{bmatrix} \quad (42)$$

Let

$$h^2 = \frac{\sigma_A^2}{\sigma_A^2 + \sigma_p^2 + \sigma_e^2} = 0.1$$

$$r = \frac{\sigma_A^2 + \sigma_p^2}{\sigma_A^2 + \sigma_p^2 + \sigma_e^2} = 0.7$$

$$\frac{\sigma_e^2}{\sigma_A^2} = \frac{1 - r}{h^2} = 3$$

$$\frac{\sigma_e^2}{\sigma_p^2} = \frac{1 - r}{r - h^2} = 0.5$$

To set up the equations, write out the following

$$\begin{bmatrix} y_i \\ 2.1 \\ 2.5 \\ 1.8 \\ 1.9 \\ 2.3 \\ 3.0 \\ 2.8 \\ 2.7 \\ 2.6 \end{bmatrix} \begin{bmatrix} \mu & u_{10} & u_{20} & u_1 & u_2 & u_3 & u_4 & u_5 & u_6 & u_7 & u_8 & u_9 & p_5 & p_6 & p_7 & p_8 & p_9 \end{bmatrix}$$

Call the entire design matrix $\mathbf{W}$ and calculate $\mathbf{W}'\mathbf{W}$ and $\mathbf{W}'\mathbf{y}$. Add $\mathbf{A}^{-1}$ and $\mathbf{I}$ starting at the proper elements of $\mathbf{W}'\mathbf{W}$ to obtain

$$\begin{bmatrix}
 9 & 0 & 0 & 0 & 0 & 0 & 0 & 2 & 3 & 1 & 2 & 1 & 2 & 3 & 1 & 2 & 1 \\
 0 & 6 & 0 & 1.5 & 1.5 & 0 & 0 & -3 & -3 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 7.5 & 0 & 0 & 1.5 & 3 & 0 & 0 & -3 & -3 & -3 & 0 & 0 & 0 & 0 & 0 \\
 0 & 1.5 & 0 & 4.5 & 0 & 0 & 0 & -3 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 1.5 & 0 & 0 & 4.5 & 0 & 0 & 0 & -3 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 1.5 & 0 & 0 & 4.5 & 0 & 0 & 0 & -3 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 3 & 0 & 0 & 0 & 6 & 0 & 0 & 0 & -3 & -3 & 0 & 0 & 0 & 0 & 0 \\
 2 & -3 & 0 & -3 & 0 & 0 & 0 & 8 & 0 & 0 & 0 & 0 & 2 & 0 & 0 & 0 & 0 \\
 3 & -3 & 0 & 0 & -3 & 0 & 0 & 0 & 9 & 0 & 0 & 0 & 0 & 3 & 0 & 0 & 0 \\
 1 & 0 & -3 & 0 & 0 & -3 & 0 & 0 & 0 & 7 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\
 2 & 0 & -3 & 0 & 0 & 0 & -3 & 0 & 0 & 0 & 8 & 0 & 0 & 0 & 0 & 2 & 0 \\
 1 & 0 & -3 & 0 & 0 & 0 & -3 & 0 & 0 & 0 & 0 & 7 & 0 & 0 & 0 & 0 & 1 \\
 2 & 0 & 0 & 0 & 0 & 0 & 0 & 2 & 0 & 0 & 0 & 0 & 2.5 & 0 & 0 & 0 & 0 \\
 3 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 3 & 0 & 0 & 0 & 0 & 3.5 & 0 & 0 & 0 \\
 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 1.5 & 0 & 0 \\
 2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 2 & 0 & 0 & 0 & 0 & 2.5 & 0 \\
 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 1.5
 \end{bmatrix}
 \begin{bmatrix}
 b \\
 u_{10} \\
 u_{20} \\
 u_1 \\
 u_2 \\
 u_3 \\
 u_4 \\
 u_5 \\
 u_6 \\
 u_7 \\
 u_8 \\
 u_9 \\
 p_5 \\
 p_6 \\
 p_7 \\
 p_8 \\
 p_9
 \end{bmatrix}
 =
 \begin{bmatrix}
 21.7 \\
 0 \\
 0 \\
 0 \\
 0 \\
 0 \\
 0 \\
 4.6 \\
 6.0 \\
 3.0 \\
 5.5 \\
 2.6 \\
 4.6 \\
 6.0 \\
 3.0 \\
 5.5 \\
 2.6
 \end{bmatrix}$$

The solutions are $\mathbf{b} = \begin{bmatrix} 2.5010 \end{bmatrix}$

$$\begin{bmatrix}
 u_5 \\
 u_6 \\
 u_7 \\
 u_8 \\
 u_9
 \end{bmatrix}
 =
 \begin{bmatrix}
 -.0373 \\
 -.0674 \\
 0.0577 \\
 0.0433 \\
 0.0333
 \end{bmatrix};
 \begin{bmatrix}
 u_{10} \\
 u_{20} \\
 u_1 \\
 u_2 \\
 u_3 \\
 u_4
 \end{bmatrix}
 =
 \begin{bmatrix}
 -.0419 \\
 0.0419 \\
 -.0109 \\
 -.0310 \\
 0.0245 \\
 0.0174
 \end{bmatrix};
 \begin{bmatrix}
 p_5 \\
 p_6 \\
 p_7 \\
 p_8 \\
 p_9
 \end{bmatrix}
 =
 \begin{bmatrix}
 -.1309 \\
 -.3716 \\
 0.2942 \\
 0.1645 \\
 0.0438
 \end{bmatrix}$$

The equation for cow no. 6 is:

$$3 + 9 u_6 - 3 u_{10} - 3 u_2 + 3 p_6 = 6.0, \text{ or}$$

$$n_i + (n_i + 2) u_i - u_s - u_d + n_i p_i = \sum_{j=1}^{n_i} Y_i,$$

where n_i is the number of records of the i^{th} individual

u_s is breeding value of sire

u_d is breeding value of dam

This equation can be rearranged to give

$$u_i = \frac{1}{n_i} \sum Y_i - \mu - \frac{2\lambda}{n_i} (u_i - \frac{1}{2}(u_s + u_d)) - p_i$$

The breeding value of animal i is composed of the average of the observations, $\frac{1}{n_i} \sum_{j=1}^{n_i} Y_i$, an adjustment for μ , an adjustment for permanent environmental effects, p_i , and an adjustment for the deviation of the breeding value from an index based on the average breeding values of the parents, u_s and u_d . The genetic merit of the animal is thus compared with the predicted genetic merit based on the genetic merit of the sire and dam of the animal and adjusted for fixed effects and permanent environmental effects. If the cow also had progeny with records, then the general form of u_i would be

$$u_i = \frac{1}{n_i} \sum Y_i - \mu - p_i - \frac{2\lambda}{n_i} (u_i - \frac{1}{2}(u_s + u_d)) + \frac{\lambda}{n_i} \sum_{j=1}^l (u_j - \frac{1}{2}(u_i + u_{mj}))$$

where u_j is the breeding value of progeny of cow _{i} ,

u_{mj} is the breeding value of the mate of cow _{i} , and

l is the number of progeny of cow _{i} ,

i.e. each progeny is compared to its pedigree value. If there is random mating, then as l goes to infinity, the sum of these differences goes to zero. The animal's own difference from the pedigree value will not change by much, but the influence of that difference will decrease as the number of records, n_i , increases. With the exception of males used for AI, most animals will have less than 20 records or progeny. Therefore, A^{-1} may have a substantial influence on the evaluation of the individuals.

4.5 Animal model with grouping

When using the relationship matrix in animal model BLUP estimation of breeding values, it is assumed that all animals with unknown parents are sampled from a single population with average breeding value of zero and common variance σ_A^2 . Breeding values of animals in subsequent generations are expressed relative to breeding values of animals in the base population. However, there will often be animals in a population with unknown parents and derived from a population with a genetic mean different from the one in the population, in which they are active. An obvious example is bulls or boars imported from other countries. Although being of the same breed, the base population in Denmark may date back several decades while imported breeding stock may constitute a base population of a much newer date. If this is not accounted for in the model, the imported stock will be part of the common base population and affect the genetic mean, i.e. it will introduce a bias in the breeding values.

A procedure for grouping animals derived from different base populations has been developed by Westell and Van Vleck (Westell & Van Vleck, 1987. J. Dairy Science 70, 1006). If, for instance, sires have been imported over a period of time, these sires could be assigned to groups according to their year of birth or country of origin. Each sire with one or both parents unknown is assigned phantom parents in such a way that each phantom parent only has one progeny. The phantom parents are then grouped according to the chosen criteria (e.g. year of birth, country of origin, sex of progeny). The following model will apply:

$$y_{ij} = b_j + u_i + \sum_{k=1}^n a_{ik} g_k + e_{ij}$$

where

y_{ij} = observation on animal i in systematic effect j

b_j = systematic effect j, e.g. herd j

u_i = effect of animal i

a_{ik} = additive genetic relationship between the i^{th} and the k^{th} animal, summation being over all n ancestors of animal i

g_k = group effect containing the k^{th} ancestor

e_{ij} = random environmental effect

Note that the term $\sum_{k=1}^n a_{ik} g_k$ weighs the contribution of the group to the observation with the proportion of the genes passed on to the animal with record by the ancestors in the group.

Let $\mathbf{G}$ be a matrix that assigns ancestors to groups and $\mathbf{T}$ a lower triangular matrix expressing the flow of genes through generations (obtained from $\mathbf{A} = \mathbf{TDT}'$). Then the matrix $\mathbf{Q} = \mathbf{TG}$ is a matrix expressing the proportion of genes contributed by ancestors of the groups. The model can then be written

$$\mathbf{y} = \mathbf{Xb} + \mathbf{ZQg} + \mathbf{Zu} + \mathbf{e}$$

The Mixed Model Equations are

$$\begin{bmatrix} X'X & X'Z & X'ZQ \\ Z'X & Z'Z + A^{-1}\lambda & Z'ZQ \\ Q'Z'X & Q'Z'Z & Q'Z'ZQ \end{bmatrix} \begin{bmatrix} b \\ u \\ g \end{bmatrix} = \begin{bmatrix} X'y \\ Z'y \\ Q'Z'y \end{bmatrix}$$

The breeding value used for ranking the animals is then $u^* = Qg + u$, i.e. the group effect weighted by the proportion of genes contributed by the group is added to the breeding value. In other words, the breeding value, u^* , is estimated relative to a mixture of two base populations, depending on the proportion of genes originating from the two base populations.

The MME can, however, be modified in such a way that u^* is obtained directly (Westell et al., 1988. J. Dairy Sci. 71, 1310):

$$\begin{bmatrix} X'X & X'Z & 0 \\ Z'X & Z'Z + A_{nn}^{-1}\lambda & A_{np}^{-1}\lambda \\ 0 & A_{pn}^{-1}\lambda & A_{pp}^{-1}\lambda \end{bmatrix} \begin{bmatrix} b \\ u + Qg \\ g \end{bmatrix} = \begin{bmatrix} X'y \\ Z'y \\ 0 \end{bmatrix}$$

where n is the number of animals and p is the number of groups. The relationship matrix is extended so as to comprise the groups, and the inverse is obtained using the usual rules (see p. 38), i.e.

If parents unknown, $\lambda_i = 1$
 if one parent is known, $\lambda_i = 4/3$
 if both parents are known $\lambda_i = 2$,

or $\lambda_i = 4/(2 + \text{number of phantom parents of animal } i \text{ assigned to groups})$.

Then add

- λ_i to element (i,i) of A^{-1}
- $-\lambda_i/2$ to the elements (i,s), (s,i), i,d) and (d,i)
- $\lambda_i/4$ to elements (s,s), (d,d), (s,d) and (d,s)

Example 4.5.1

Given the following data of lean content measured on pigs:

Table 4.1. Lean content based on ultrasonic measurements

Pig no.	Sex	Sire	Dam	Per cent lean
4	1	1	-	62.0
5	2	1	3	59.0
6	2	2	4	61.7
7	1	2	5	61.0
8	1	1	6	62.8

If these data are analysed using an ordinary animal model, we set up the model

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e}$$

where

- $\mathbf{y}$ = vector of observations
- $\mathbf{b}$ = vector of fixed effects
- $\mathbf{u}$ = vector of breeding values
- $\mathbf{X}, \mathbf{Z}$ = incidence matrices

The heritability of lean content is estimated to 0.5. The MME before adding A^{-1} are

$$\begin{bmatrix} 5 & 3 & 2 & 0 & 0 & 0 & 1 & 1 & 1 & 1 & 1 \\ 3 & 3 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 1 & 1 \\ 2 & 0 & 2 & 0 & 0 & 0 & 0 & 1 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 1 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} \mu \\ b_1 \\ b_2 \\ u_1 \\ u_2 \\ u_3 \\ u_4 \\ u_5 \\ u_6 \\ u_7 \\ u_8 \end{bmatrix} = \begin{bmatrix} 306.5 \\ 185.8 \\ 120.7 \\ 0 \\ 0 \\ 0 \\ 62.0 \\ 59.0 \\ 61.7 \\ 61.0 \\ 62.8 \end{bmatrix}$$

The inverse relationship matrix is

$$A^{-1} = \begin{bmatrix} 2.3333 & 0 & 0.5 & -.6667 & -1 & 0.5 & 0 & -1 \\ 0 & 2 & 0 & 0.5 & 0.5 & -1 & -1 & 0 \\ 0.5 & 0 & 1.5 & 0 & -1 & 0 & 0 & 0 \\ -.6667 & 0.5 & 0 & 1.8333 & 0 & -1 & 0 & 0 \\ -1 & 0.5 & -1 & 0 & 2.5 & 0 & -1 & 0 \\ 0.5 & -1 & 0 & -1 & 0 & 2.5 & 0 & -1 \\ 0 & -1 & 0 & 0 & -1 & 0 & 2 & 0 \\ -1 & 0 & 0 & 0 & 0 & -1 & 0 & 2 \end{bmatrix}$$

Since the heritability is 0.5, and $\lambda = \frac{1 - 0.5}{0.5} = 1.0$, $A^{-1} = A^{-1}$. Adding this to the coefficient

matrix gives the following MME:

$$\begin{bmatrix} 5 & 3 & 2 & 0 & 0 & 0 & 1 & 1 & 1 & 1 & 1 \\ 3 & 3 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 1 & 1 \\ 2 & 0 & 2 & 0 & 0 & 0 & 0 & 1 & 1 & 0 & 0 \\ 0 & 0 & 0 & 2.3333 & 0 & 0.5 & -.6667 & -1 & 0.5 & 0 & -1 \\ 0 & 0 & 0 & 0 & 2 & 0 & 0.5 & 0.5 & -1 & -1 & 0 \\ 0 & 0 & 0 & 0.5 & 0 & 1.5 & 0 & -1 & 0 & 0 & 0 \\ 1 & 1 & 0 & -.6667 & 0.5 & 0 & 2.8333 & 0 & -1 & 0 & 0 \\ 1 & 0 & 1 & -1 & 0.5 & -1 & 0 & 3.5 & 0 & -1 & 0 \\ 1 & 0 & 1 & 0.5 & -1 & 0 & -1 & 0 & 3.5 & 0 & -1 \\ 1 & 1 & 0 & 0 & -1 & 0 & 0 & -1 & 0 & 3 & 0 \\ 1 & 1 & 0 & -1 & 0 & 0 & 0 & 0 & -1 & 0 & 3 \end{bmatrix} \begin{bmatrix} \mu \\ b_1 \\ b_2 \\ u_1 \\ u_2 \\ u_3 \\ u_4 \\ u_5 \\ u_6 \\ u_7 \\ u_8 \end{bmatrix} = \begin{bmatrix} 306.5 \\ 185.8 \\ 120.7 \\ 0 \\ 0 \\ 0 \\ 62.0 \\ 59.0 \\ 61.7 \\ 61.0 \\ 62.8 \end{bmatrix}$$

and the solution is $\mu = 60.43$, $\mathbf{b}' = [1.35 \ -0.11]$ and

$$\mathbf{u}' = [-0.014 \ 0.252 \ -0.430 \ 0.281 \ -0.653 \ 0.712 \ -0.393 \ 0.573]$$

Assuming that the unknown sires and dams have different genetic origin, we may assign these to two different groups. We can assign phantom parents to the animals with unknown parents. Each animal has different phantom parents:

Animal	Sire	Dam
1	P ₁	P ₂
2	P ₃	P ₄
3	P ₅	P ₆
4	1	P ₇
5	1	3
6	2	4
7	2	5
8	1	6

The T-matrix is

$$T = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ .5 & .5 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & .5 & .5 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & .5 & .5 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ .25 & .25 & 0 & 0 & 0 & 0 & .5 & .5 & 0 & 0 & 1 & 0 & 0 & 0 \\ .25 & .25 & 0 & 0 & .25 & .25 & 0 & .5 & 0 & .5 & 0 & 1 & 0 & 0 \\ .125 & .125 & .25 & .25 & 0 & 0 & .25 & .25 & .5 & 0 & .5 & 0 & 1 & 0 \\ .125 & .125 & .25 & .25 & .125 & .125 & 0 & .25 & .5 & .25 & 0 & .5 & 0 & 1 \\ .3125 & .3125 & .125 & .125 & 0 & 0 & .125 & .625 & .25 & 0 & .25 & 0 & .5 & 0 & 1 \end{bmatrix}$$

We can now assign the phantom parents to groups by setting up the following matrix (**G**). The matrix will assign the unknown sires of animals 1, 2 and 3 (phantom parents P₁, P₃ and P₅) to one group and the unknown dams of animals 1, 2, 3 and 4 (phantom parents P₂, P₄, P₆ and P₇) to another group. Column 1 identifies group 1 and column 2 identifies group 2:

$$G = \begin{bmatrix} 1 & 0 \\ 0 & 1 \\ 1 & 0 \\ 0 & 1 \\ 1 & 0 \\ 0 & 1 \\ 0 & 1 \\ 0 & 0 \\ 0 & 0 \\ 0 & 0 \\ 0 & 0 \\ 0 & 0 \\ 0 & 0 \\ 0 & 0 \\ 0 & 0 \end{bmatrix} \quad \text{and the product } Q = TG = \begin{bmatrix} 1 & 0 \\ 0 & 1 \\ 1 & 0 \\ 0 & 1 \\ 1 & 0 \\ 0 & 1 \\ 0 & 1 \\ 0.5 & 0.5 \\ 0.5 & 0.5 \\ 0.5 & 0.5 \\ 0.25 & 0.75 \\ 0.5 & 0.5 \\ 0.375 & 0.625 \\ 0.5 & 0.5 \\ 0.4375 & 0.5625 \end{bmatrix}$$

The product, Q, shows how each animal is related to the phantom parents in group 1, respectively group 2. The MME are now

$$\begin{bmatrix} X'X & X'Z & X'ZQ \\ Z'X & Z'Z + A^{-1}\lambda & Z'ZQ \\ Q'Z'X & Q'Z'Z & Q'Z'ZQ \end{bmatrix} \begin{bmatrix} b \\ u \\ g \end{bmatrix} = \begin{bmatrix} X'Y \\ Z'Y \\ Q'Z'Y \end{bmatrix}$$

Inserting the figures from the example gives the following set of equations:

$$\begin{bmatrix}
5 & 3 & 2 & 0 & 0 & 0 & 1 & 1 & 1 & 1 & 1 & 2.0625 & 2.9375 \\
3 & 3 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 1 & 1 & 1.1875 & 1.8125 \\
2 & 0 & 2 & 0 & 0 & 0 & 0 & 1 & 1 & 0 & 0 & 0.8750 & 1.1250 \\
0 & 0 & 0 & 2.3333 & 0 & .5 & -.6667 & -1 & .5 & 0 & -1 & 0 & 0 \\
0 & 0 & 0 & 0 & 2 & 0 & .5 & .5 & -1 & -1 & 0 & 0 & 0 \\
0 & 0 & 0 & .5 & 0 & 1.5 & 0 & -1 & 0 & 0 & 0 & 0 & 0 \\
1 & 1 & 0 & -.6667 & .5 & 0 & 2.8333 & 0 & -1 & 0 & 0 & .25 & .75 \\
1 & 0 & 1 & -1 & .5 & -1 & 0 & 3.5 & 0 & -1 & 0 & .5 & .5 \\
1 & 0 & 1 & .5 & -1 & 0 & -1 & 0 & 3.5 & 0 & -1 & .375 & .625 \\
1 & 1 & 0 & 0 & -1 & 0 & 0 & -1 & 0 & 3 & 0 & .5 & .5 \\
1 & 1 & 0 & -1 & 0 & 0 & 0 & 0 & -1 & 0 & 3 & .4375 & .5625 \\
2.0625 & 1.1875 & .875 & 0 & 0 & 0 & .25 & .5 & .375 & .5 & .4375 & .8945 & 1.168 \\
2.9375 & 1.8125 & 1.125 & 0 & 0 & 0 & .75 & .5 & .625 & .5 & .5625 & 1.168 & 1.7695
\end{bmatrix}
\begin{bmatrix}
\mu \\
b_1 \\
b_2 \\
u_1 \\
u_2 \\
u_3 \\
u_4 \\
u_5 \\
u_6 \\
u_7 \\
u_8 \\
g_1 \\
g_2
\end{bmatrix}
=
\begin{bmatrix}
306.5 \\
185.8 \\
120.7 \\
0 \\
0 \\
0 \\
62.0 \\
59.0 \\
61.7 \\
61.0 \\
62.8 \\
126.1125 \\
180.3875
\end{bmatrix}$$

and the solution is $\mu = 62.05$, $\mathbf{b}' = [1.48 \quad 0.16]$,

$\mathbf{u}' = [-0.016 \quad 0.333 \quad -.317 \quad -.009 \quad -.483 \quad 0.585 \quad -.164 \quad 0.585]$ and $\mathbf{g} = [-4.350 \quad 0.000]$. The group effects influence both fixed effects and breeding values. These estimates differ therefore from those obtained using the model without grouping.

The breeding values taking groups into consideration are now $\mathbf{u}^* = \mathbf{u} + \mathbf{Qg}$:

$$\begin{bmatrix}
-0.016 \\
0.333 \\
-.317 \\
-.009 \\
-.483 \\
0.585 \\
-.164 \\
0.585
\end{bmatrix}
+
\begin{bmatrix}
.5 & .5 \\
.5 & .5 \\
.5 & .5 \\
.25 & .75 \\
.5 & .5 \\
.375 & .625 \\
.5 & .5 \\
.4375 & .5625
\end{bmatrix}
\begin{bmatrix}
-4.350 \\
0
\end{bmatrix}
=
\begin{bmatrix}
-2.191 \\
-1.842 \\
-2.492 \\
-1.097 \\
-2.658 \\
-1.046 \\
-2.339 \\
-1.318
\end{bmatrix}$$

A solution for the breeding values directly can be obtained using the MME

$$\begin{bmatrix}
\mathbf{X}'\mathbf{X} & \mathbf{X}'\mathbf{Z} & 0 \\
\mathbf{Z}'\mathbf{X} & \mathbf{Z}'\mathbf{Z} + \mathbf{A}_{mn}^{-1}\lambda & \mathbf{A}_{mn}^{-1}\lambda \\
0 & \mathbf{A}_{mn}^{-1}\lambda & \mathbf{A}_{mm}^{-1}\lambda
\end{bmatrix}
\begin{bmatrix}
\mathbf{b} \\
\mathbf{a} + \mathbf{Qg} \\
\mathbf{g}
\end{bmatrix}
=
\begin{bmatrix}
\mathbf{X}'\mathbf{y} \\
\mathbf{Z}'\mathbf{y} \\
0
\end{bmatrix}$$

These equations look as follows:

$$\begin{bmatrix}
 5 & 3 & 2 & 0 & 0 & 0 & 1 & 1 & 1 & 1 & 1 & 0 & 0 \\
 3 & 3 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 1 & 1 & 0 & 0 \\
 2 & 0 & 2 & 0 & 0 & 0 & 0 & 1 & 1 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 2.3333 & 0 & .5 & -.6667 & -1 & .5 & 0 & -1 & -.5 & -.6667 \\
 0 & 0 & 0 & 0 & 2 & 0 & .5 & .5 & -1 & -1 & 0 & -.5 & -.5 \\
 0 & 0 & 0 & .5 & 0 & 1.5 & 0 & -1 & 0 & 0 & 0 & -.5 & -.5 \\
 1 & 1 & 0 & -.6667 & .5 & 0 & 2.8333 & 0 & -1 & 0 & 0 & 0 & -.6667 \\
 1 & 0 & 1 & -1 & .5 & -1 & 0 & 3.5 & 0 & -1 & 0 & 0 & .0 \\
 1 & 0 & 1 & .5 & -1 & 0 & -1 & 0 & 3.5 & 0 & -1 & 0 & 0 \\
 1 & 1 & 0 & 0 & -1 & 0 & 0 & -1 & 0 & 3 & 0 & 0 & 0 \\
 1 & 1 & 0 & -1 & 0 & 0 & 0 & 0 & -1 & 0 & 3 & 0 & 0 \\
 0 & 0 & 0 & -.5 & -.5 & -.5 & 0 & 0 & 0 & 0 & 0 & 0.75 & 0.75 \\
 0 & 0 & 0 & -.1667 & -.5 & -.5 & -.6667 & 0 & 0 & 0 & 0 & 0.75 & 1.0833
 \end{bmatrix}
 \begin{bmatrix}
 \mu \\
 b_1 \\
 b_2 \\
 u_1 \\
 u_2 \\
 u_3 \\
 u_4 \\
 u_5 \\
 u_6 \\
 u_7 \\
 u_8 \\
 g_1 \\
 g_2
 \end{bmatrix}
 =
 \begin{bmatrix}
 306.5 \\
 185.8 \\
 120.7 \\
 0 \\
 0 \\
 0 \\
 62.0 \\
 59.0 \\
 61.7 \\
 61.0 \\
 62.8 \\
 0 \\
 0
 \end{bmatrix}$$

The solution is $\mu = 62.20$, $\mathbf{b}' = [1.32 \quad 0.00]$,

$\mathbf{u}' = [-2.192 \quad -1.842 \quad -2.492 \quad -1.096 \quad -2.658 \quad -1.047 \quad -2.340 \quad -1.319]$ and $\mathbf{g} = [-4.350 \quad 0.000]$.

These estimates are similar to those obtained above.

4.6 Sire model

Traditionally, sire models have been used in the estimation of breeding value in cattle. The reason for this is partly that bulls normally have a large number of progeny because of the use of AI, so that the main part of the genetic progress comes from selection of bulls, partly that these models are easier to handle computationally. The model is

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zs} + \mathbf{e},$$

where $\mathbf{y}$ is a vector of observations

$\mathbf{b}$ is a vector of fixed effects

$\mathbf{s}$ is a vector of transmitting abilities (half the breeding values)

$\mathbf{X}$ and $\mathbf{Z}$ are incidence matrices.

The expectation of $\mathbf{y}$ is $E(\mathbf{Y}) = \mathbf{Xb}$ and
$$V \begin{bmatrix} \mathbf{s} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_s^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{I}\sigma_e^2 \end{bmatrix} = \begin{bmatrix} \mathbf{A}\frac{1}{4}\sigma_A^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{I}\sigma_e^2 \end{bmatrix}$$

Only bulls are evaluated and the additive relationship matrix includes only relationships between bulls. Further, since $\sigma_s^2 = \frac{1}{4}h^2\sigma_p^2$ and $\sigma_e^2 = \frac{4-h^2}{4}\sigma_p^2$, then

$$\frac{\sigma_e^2}{\sigma_s^2} = \frac{4-h^2}{h^2} = \lambda$$

Example 4.6.1

The following example is from Nicolas (1987). Milk yields has been recorded on 14 cows:

Herd-year-season	Sire	Cow	Yield
1	1	111	3677
1	1	112	4161
1	1	113	3505
1	1	114	3904
1	3	131	3957
1	3	132	3447
2	1	211	3534
2	2	221	2941
2	2	222	3366
2	2	223	3755
2	3	231	2318
2	3	232	2730
2	3	233	3629
2	3	234	3158

The model is

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{s} + \mathbf{e}$$

where $\mathbf{y}$ = vector of yields for the cows
 $\mathbf{b}$ = herd-year-season fixed effects
 $\mathbf{s}$ = transmitting ability of the sires
 $\mathbf{e}$ = vector of residuals
 $\mathbf{X}, \mathbf{Z}$ = incidence matrices

It is assumed that the sires are unrelated and that the heritability is 0.25, giving $\lambda = (4 - 0.25)/0.25 = 15$.

To set up the equations, write out the model except the residuals and make $\mathbf{W} = [\mathbf{X} \ \mathbf{Z}]$:

$$\begin{bmatrix} Y \\ 3677 \\ 4161 \\ 3506 \\ 3904 \\ 3957 \\ 3447 \\ 3534 \\ 2941 \\ 3366 \\ 3755 \\ 2318 \\ 2730 \\ 3629 \\ 3158 \end{bmatrix} \begin{bmatrix} \mu & b_1 & b_2 & s_1 & s_2 & s_3 \\ 1 & 1 & 0 & 1 & 0 & 0 \\ 1 & 1 & 0 & 1 & 0 & 0 \\ 1 & 1 & 0 & 1 & 0 & 0 \\ 1 & 1 & 0 & 1 & 0 & 0 \\ 1 & 1 & 0 & 0 & 0 & 1 \\ 1 & 1 & 0 & 0 & 0 & 1 \\ 1 & 0 & 1 & 1 & 0 & 0 \\ 1 & 0 & 1 & 0 & 1 & 0 \\ 1 & 0 & 1 & 0 & 1 & 0 \\ 1 & 0 & 1 & 0 & 1 & 0 \\ 1 & 0 & 1 & 0 & 0 & 1 \\ 1 & 0 & 1 & 0 & 0 & 1 \\ 1 & 0 & 1 & 0 & 0 & 1 \\ 1 & 0 & 1 & 0 & 0 & 1 \end{bmatrix}$$

Now calculate

$$W'W + \begin{bmatrix} 0 & 0 \\ 0 & A^{-1}\lambda \end{bmatrix} = \begin{bmatrix} X'X & X'Z \\ Z'X & Z'Z + A^{-1}\lambda \end{bmatrix} \text{ and } W'y = \begin{bmatrix} X'y \\ Z'y \end{bmatrix}$$

Since the sires are unrelated, $A^{-1} = I$. The equations therefore become

$$\begin{bmatrix} 14 & 6 & 8 & 5 & 3 & 6 \\ 6 & 6 & 0 & 4 & 0 & 2 \\ 8 & 0 & 8 & 1 & 3 & 4 \\ 5 & 4 & 1 & (5 + 15) & 0 & 0 \\ 3 & 0 & 3 & 0 & (3 + 15) & 0 \\ 6 & 2 & 4 & 0 & 0 & (6 + 15) \end{bmatrix} \begin{bmatrix} \mu \\ b_1 \\ b_2 \\ s_1 \\ s_2 \\ s_3 \end{bmatrix} = \begin{bmatrix} 48083 \\ 22652 \\ 25431 \\ 18782 \\ 10062 \\ 19239 \end{bmatrix}$$

The solution is $\bar{y} = 3172.0$; $\mathbf{b} = \begin{bmatrix} 604.3 \\ 19.4 \end{bmatrix}$; $\mathbf{s} = \begin{bmatrix} 24.3 \\ 27.1 \\ -51.4 \end{bmatrix}$;

The $\mathbf{s}$ vector contains the transmitting ability of the sires. Their breeding values are therefore 48.6 for sire 1, 54.2 for sire 2 and -102.8 for sire 3.

What is the relation between breeding values obtained by the sire model and by the selection index method? In the selection index method, the first step is to adjust the data for fixed effects (herd-year-season, HYS). The following means can be obtained from the data:

Overall mean	Herd-year-season means	Sire means
34344	(1) 3775.2	(1) 3756.9
	(2) 3178.9	(2) 3354.2
		(3) 3206.5

Now compute the average HYS effect for progeny of each of the three sires. Sire₁ has 4 progeny in HYS₁ and 1 progeny in HYS₂, sire₂ has 3 progeny in HYS₂ and sire₃ has 2 progeny in HYS₁ and 4 progeny in HYS₂.

HYS for sire = (no. of progeny in HYS₁(HYSmean₁) +
no. of progeny in HYS₂(HYSmean₂)/no. of progeny

HYS for sire₁ : $(4(3775) + 3178.9)/5 = 3655.9$

HYS for sire₂ : 3178.9

HYS for sire₃ : $(2(3775.2) + 4(3178.9))/6 = 3377.7$

Next, compute sire means adjusted for HYS-effects:

sire mean - (HYS for sire - overall mean)

Mean for sire₁ : $3756.2 - (3655.9 - 3434.4) = 3534.7$

Mean for sire₂ : 3354.2 - (3178.9 - 3434.4) = 3609.7

Mean for sire₃ : 3206.5 - (3377.7 - 3434.4) = 3263.2

Now the breeding values may be calculated as

$$BV = b_{AIP_n}(\bar{P}_n - \bar{P}) = \frac{a'h^2n}{1 + (n-1)a''h^2}(\bar{P}_n - \bar{P})$$

$$\text{Sire}_1: BV_1 = \frac{0.5(0.25)(5)}{1 + 4(0.25)(0.25)}(3534.7 - 3434.4) = 50.2$$

$$\text{Sire}_2: BV_2 = \frac{0.5(0.25)(3)}{1 + 2(0.25)(0.25)}(3609.7 - 3434.4) = 58.4$$

$$\text{Sire}_3: BV_3 = \frac{0.5(0.25)(6)}{1 + 5(0.25)(0.25)}(3263.2 - 3434.4) = -97.8$$

The breeding values found using the sire model are $\mathbf{u}' = [48.6 \quad 54.2 \quad -102.8]$. In the selection index approach, the data are adjusted for fixed effects before calculating the breeding values. When using BLUP, fixed effects and breeding values are estimated simultaneously. The result of this is that fixed effects are also adjusted for breeding values. If the herd-year-season effects and the overall mean used in the selection index case are adjusted for breeding values, identical breeding values are obtained for the two methods.

Herd-year-season effects are adjusted for breeding values using the following expression:

$\text{HYS}_i = \text{unadjusted mean of HYS}_i - ((\text{no. Of sires in HYS}_i)(\text{transmitting ability for sire}_j))/\text{no. of sires} - \text{adjusted overall mean}$:

$$\text{HYS}_1 = 3775.2 - (4(24.3) + 2(-51.4))/6 - 3172 = 604.1$$

$$\text{HYS}_2 = 3178.9 - (24.3 + 3(27.1) + 4(-51.4))/8 - 3172 = 19.4$$

The overall mean adjusted for HYS-effects and for breeding values then becomes

$$\text{mean} = 3434.4 - [6(604.1) + 8(19.4) + 5(24.3) + 3(27.1) + 6(-51.4)]/14 = 3172$$

Using these estimates, HYS for sires can now be obtained as:

$$\text{HYS for sire}_1 : (4(604.1) + 19.4)/5 = 487.2$$

$$\text{HYS for sire}_2 : 19.4$$

$$\text{HYS for sire}_3 : (2(604.1) + 4(19.4))/6 = 214.3$$

The sire means are adjusted for adjusted HYS using the following expression:

$$\text{Adjusted sire mean} = \text{unadjusted sire mean} - \text{adjusted HYS for sire}$$

$$\text{Sire}_1 : 3756.2 - 487.2 = 3269.0$$

$$\text{Sire}_2 : 3354.2 - 19.4 = 3334.8$$

$$\text{Sire}_3 : 3206.5 - 214.3 = 2992.2$$

The breeding values can now be calculated:

$$\text{Sire}_1: BV_1 = \frac{0.5(0.25)(5)}{1 + 4(0.25)(0.25)}(3269.0 - 3172) = 48.5$$

$$\text{Sire}_2: BV_2 = \frac{0.5(0.25)(3)}{1 + 2(0.25)(0.25)}(3334.8 - 3172) = 54.2$$

$$\text{Sire}_3: BV_3 = \frac{0.5(0.25)(6)}{1 + 5(0.25)(0.25)}(2992.2 - 3172) = -102.7$$

These breeding values are identical to those obtained using the sire model.

4.7 Multiple trait BLUP

The value of an animal is usually not restricted to a single trait. As a general rule, several traits are included in the breeding goal. Using the single trait animal model to estimate breeding values implies that in combining the breeding values into an index comprising more than one trait, no attention is paid to the phenotypic and genetic correlations between the traits.

A multiple trait animal model takes into consideration associations between the traits, because both environmental and genetic variances and covariances are included in the estimation. Therefore, provided reliable covariances can be obtained, the multiple trait animal model gives better estimates of breeding values.

The increase in accuracy of estimation depends on the difference in genetic and environmental correlations between the traits. The more different these correlations are, the more the accuracy is increased. If the heritability and the genetic and environmental correlations between two traits are equal, breeding values obtained with a single trait model and with a multiple trait model is expected to be equal.

The chief disadvantages of the multiple trait animal model are that a multiple trait analysis requires reliable estimates of genetic and phenotypic covariances. These are not always easy to obtain. Further, multiple trait analyses increases computing requirements substantially. An n-trait multiple animal model analysis requires more computing power than n single trait animal model analyses.

In the following, an example of a multiple trait animal model is presented assuming a situation where all animals with records have all traits recorded. The example is a two trait analysis. We may set up a model for each trait.

Model for trait 1:

$$\mathbf{y}_1 = \mathbf{X}\mathbf{b}_1 + \mathbf{Z}\mathbf{u}_1 + \mathbf{e}_1$$

and for trait 2:

$$\mathbf{y}_2 = \mathbf{X}\mathbf{b}_2 + \mathbf{Z}\mathbf{u}_2 + \mathbf{e}_2$$

where $\mathbf{y}_i$ is a vector of observations for trait i
 $\mathbf{X}$ is a design matrix for fixed effects
 $\mathbf{Z}$ is a design matrix for breeding values
 $\mathbf{b}_i$ is a vector of fixed effects for trait i
 $\mathbf{u}_i$ is a vector of breeding values for trait i and
 $\mathbf{e}_i$ is a vector of residual effects for trait i

These models can be combined into the following:

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{X}_2 \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_2 \end{bmatrix} \begin{bmatrix} \mathbf{u}_1 \\ \mathbf{u}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix}$$

Let $\mathbf{G} = \begin{bmatrix} \mathbf{g}_{11} & \mathbf{g}_{12} \\ \mathbf{g}_{21} & \mathbf{g}_{22} \end{bmatrix}$ be the additive genetic variance-covariance matrix, i.e. $\mathbf{g}_{11}$ is the genetic

variance of trait 1, $\mathbf{g}_{12} = \mathbf{g}_{21}$ = genetic covariance between the two traits and $\mathbf{g}_{22}$ is the genetic

covariance of trait 2 and $\mathbf{R} = \begin{bmatrix} \mathbf{r}_{11} & \mathbf{r}_{12} \\ \mathbf{r}_{21} & \mathbf{r}_{22} \end{bmatrix}$ be the variance-covariance matrix of residual effects, then

the variances of breeding values and residual effects are assumed to be

$$\text{var} \begin{bmatrix} \mathbf{u}_1 \\ \mathbf{u}_2 \\ \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{g}_{11}\mathbf{A} & \mathbf{g}_{12}\mathbf{A} & 0 & 0 \\ \mathbf{g}_{21}\mathbf{A} & \mathbf{g}_{22}\mathbf{A} & 0 & 0 \\ 0 & 0 & \mathbf{r}_{11} & \mathbf{r}_{12} \\ 0 & 0 & \mathbf{r}_{21} & \mathbf{r}_{22} \end{bmatrix}$$

where $\mathbf{A}$ is the matrix of additive genetic relationships.

The MME are as shown in equation (34) on page 42:

$$\begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{Z} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{Z}'\mathbf{R}^{-1}\mathbf{Z} + \mathbf{A}^{-1} \end{bmatrix} \frac{1}{\sigma_A^2} \begin{bmatrix} \mathbf{b} \\ \mathbf{u} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{y} \end{bmatrix}$$

It is assumed that animals with observations always have both traits recorded. The above MME equations can then be constructed by assuming $\mathbf{X} = [\mathbf{X}_1 \ \mathbf{X}_2]$ and $\mathbf{Z} = [\mathbf{Z}_1 \ \mathbf{Z}_2]$.

$\mathbf{R}^{-1} = \begin{bmatrix} r^{11} & r^{12} \\ r^{21} & r^{22} \end{bmatrix}$ is the inverted residual variance-covariance matrix and $1/\sigma_A^2$ is replaced by

$\mathbf{G}^{-1} = \begin{bmatrix} g^{11} & g^{12} \\ g^{21} & g^{22} \end{bmatrix}$, which is the inverted matrix of additive genetic variances and covariances.

Written in details, the MME become

$$\begin{bmatrix} \mathbf{X}'_1\mathbf{r}^{11}\mathbf{X}_1 & \mathbf{X}'_1\mathbf{r}^{12}\mathbf{X}_2 & \mathbf{X}'_1\mathbf{r}^{11}\mathbf{Z}_1 & \mathbf{X}'_1\mathbf{r}^{12}\mathbf{Z}_2 \\ \mathbf{X}'_2\mathbf{r}^{21}\mathbf{X}_1 & \mathbf{X}'_2\mathbf{r}^{22}\mathbf{X}_2 & \mathbf{X}'_2\mathbf{r}^{21}\mathbf{Z}_1 & \mathbf{X}'_2\mathbf{r}^{22}\mathbf{Z}_2 \\ \mathbf{Z}'_1\mathbf{r}^{11}\mathbf{X}_1 & \mathbf{Z}'_1\mathbf{r}^{12}\mathbf{X}_2 & \mathbf{Z}'_1\mathbf{r}^{11}\mathbf{Z}_1 + \mathbf{A}^{-1}\mathbf{g}^{11} & \mathbf{Z}'_1\mathbf{r}^{12}\mathbf{Z}_2 + \mathbf{A}^{-1}\mathbf{g}^{12} \\ \mathbf{Z}'_2\mathbf{r}^{21}\mathbf{X}_1 & \mathbf{Z}'_2\mathbf{r}^{22}\mathbf{X}_2 & \mathbf{Z}'_2\mathbf{r}^{21}\mathbf{Z}_1 + \mathbf{A}^{-1}\mathbf{g}^{21} & \mathbf{Z}'_2\mathbf{r}^{22}\mathbf{Z}_2 + \mathbf{A}^{-1}\mathbf{g}^{22} \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \\ \mathbf{u}_1 \\ \mathbf{u}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{X}'_1\mathbf{r}^{11}\mathbf{y}_1 + \mathbf{X}'_1\mathbf{r}^{12}\mathbf{y}_2 \\ \mathbf{X}'_2\mathbf{r}^{21}\mathbf{y}_1 + \mathbf{X}'_2\mathbf{r}^{22}\mathbf{y}_2 \\ \mathbf{Z}'_1\mathbf{r}^{11}\mathbf{y}_1 + \mathbf{Z}'_1\mathbf{r}^{12}\mathbf{y}_2 \\ \mathbf{Z}'_2\mathbf{r}^{21}\mathbf{y}_1 + \mathbf{Z}'_2\mathbf{r}^{22}\mathbf{y}_2 \end{bmatrix}$$

Numerical example

Given the following data:

Animal	Sex	Sire	Dam	Y ₁	Y ₂
4	1	-	-	9	7
5	2	2	3	6	5
6	2	2	1	8	7
7	1	5	4	7	6
8	1	6	3	10	8

Genetic variances and covariances ($\mathbf{G}$) and residual variances and covariances ($\mathbf{R}$) are as follows:

$$\mathbf{G} = \begin{bmatrix} 2.0 & 1.3 \\ 1.3 & 1.5 \end{bmatrix} \quad \mathbf{G}^{-1} = \begin{bmatrix} \mathbf{g}^{11} & \mathbf{g}^{12} \\ \mathbf{g}^{21} & \mathbf{g}^{22} \end{bmatrix} = \begin{bmatrix} 11450 & -0.9924 \\ -0.9924 & 15267 \end{bmatrix}$$

$$\mathbf{R} = \begin{bmatrix} 4.0 & 1.0 \\ 1.0 & 4.5 \end{bmatrix} \quad \mathbf{R}^{-1} = \begin{bmatrix} \mathbf{r}^{11} & \mathbf{r}^{12} \\ \mathbf{r}^{21} & \mathbf{r}^{22} \end{bmatrix} = \begin{bmatrix} 0.2647 & -0.0588 \\ -0.0588 & 0.2353 \end{bmatrix}$$

Heritabilities and correlations are the following:

$$h_1^2 = \frac{2}{2+4} = 0.33; \quad h_2^2 = \frac{1.5}{1.5+4.5} = 0.25; \quad r_p = \frac{1.3+10}{\sqrt{(2.0+4.0)(1.5+4.5)}} = \frac{2.3}{\sqrt{(6.0)(6.0)}} = 0.38;$$

$$r_e = \frac{10}{\sqrt{(4.0)(4.5)}} = 0.24; \quad r_A = \frac{1.3}{\sqrt{(2.0)(1.5)}} = 0.75;$$

Since it is assumed that the two traits are always measured on the same animal, $\mathbf{X}_1 = \mathbf{X}_2$ and $\mathbf{Z}_1 = \mathbf{Z}_2$.

The following sub matrices can now be constructed:

$$\mathbf{Y}_1 = \begin{bmatrix} 9 \\ 6 \\ 8 \\ 7 \\ 10 \end{bmatrix} \quad \mathbf{Y}_2 = \begin{bmatrix} 7 \\ 5 \\ 7 \\ 6 \\ 8 \end{bmatrix} \quad \mathbf{X} = [\mathbf{X}_1 \quad \mathbf{X}_2] = \begin{bmatrix} 1 & 0 & 1 & 0 \\ 0 & 1 & 0 & 1 \\ 0 & 1 & 0 & 1 \\ 1 & 0 & 1 & 0 \\ 1 & 0 & 1 & 0 \end{bmatrix}$$

$$\mathbf{Z} = [\mathbf{Z}_1 \quad \mathbf{Z}_2] = \begin{bmatrix} 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

$$\mathbf{X}'\mathbf{X} = \begin{bmatrix} 3 & 0 & 3 & 0 \\ 0 & 2 & 0 & 2 \\ 3 & 0 & 3 & 0 \\ 0 & 2 & 0 & 2 \end{bmatrix}$$

The matrix $\mathbf{X}'\mathbf{X}$ consists of four identical sub matrices $\begin{bmatrix} 3 & 0 \\ 0 & 2 \end{bmatrix}$. Each of these sub matrices is multiplied by the respective elements in $\mathbf{R}^{-1}$ to obtain

$$\begin{bmatrix} \mathbf{X}_1' \mathbf{r}^{11} \mathbf{X}_1 & \mathbf{X}_1' \mathbf{r}^{12} \mathbf{X}_2 \\ \mathbf{X}_2' \mathbf{r}^{21} \mathbf{X}_1 & \mathbf{X}_2' \mathbf{r}^{22} \mathbf{X}_2 \end{bmatrix} = \begin{bmatrix} 0.7941 & 0 & -0.1764 & 0 \\ 0 & 0.5294 & 0 & -0.1176 \\ -0.1764 & 0 & 0.7059 & 0 \\ 0 & -0.1176 & 0 & 0.4706 \end{bmatrix}$$

$\mathbf{Z}'\mathbf{Z}$ is found as

$$\begin{bmatrix} \mathbf{Z}_1 \\ \mathbf{Z}_2 \end{bmatrix} [\mathbf{Z}_1 \quad \mathbf{Z}_2] = \begin{bmatrix} \mathbf{Z}_1' \mathbf{Z}_1 & \mathbf{Z}_1' \mathbf{Z}_2 \\ \mathbf{Z}_2' \mathbf{Z}_1 & \mathbf{Z}_2' \mathbf{Z}_2 \end{bmatrix} = \begin{bmatrix} \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix} & \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix} \end{bmatrix}$$

As indicated, also $\mathbf{Z}'\mathbf{Z}$ consists of four identical sub matrices. Again each of these four sub matrices is multiplied by the respective elements of $\mathbf{R}^{-1}$ to obtain

$$\begin{bmatrix} \mathbf{z}_1' \mathbf{r}^{11} \mathbf{z}_1 & \mathbf{z}_1' \mathbf{r}^{12} \mathbf{z}_2 \\ \mathbf{z}_2' \mathbf{r}^{21} \mathbf{z}_1 & \mathbf{z}_2' \mathbf{r}^{22} \mathbf{z}_2 \end{bmatrix} =$$

$$\begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.2647 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & -0.0588 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.2647 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & -0.0588 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.2647 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & -0.0588 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0.2647 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & -0.0588 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.2647 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & -0.0588 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.2647 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.2647 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.2647 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.2647 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.2647 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.2647 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.2647 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.2647 \end{bmatrix}$$

Now the product of the inverted relationship matrix and the inverted genetic variance- covariance matrix should be included by adding $\mathbf{A}^{-1}\mathbf{G}^{\text{ii}}$ to the above matrix. The additive relationship matrix is

$$\mathbf{A} = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0.5 & 0 & 0.25 \\ 0 & 1 & 0 & 0 & 0.5 & 0.5 & 0.25 & 0.25 \\ 0 & 0 & 1 & 0 & 0.5 & 0 & 0.25 & 0.5 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0.5 & 0 \\ 0 & 0.5 & 0.5 & 0 & 1 & 0.25 & 0.5 & 0.375 \\ 0.5 & 0.5 & 0 & 0 & 0.25 & 1 & 0.125 & 0.5 \\ 0 & 0.25 & 0.25 & 0.5 & 0.5 & 0.125 & 1 & 0.1875 \\ 0.25 & 0.25 & 0.5 & 0 & 0.375 & 0.5 & 0.1875 & 1 \end{bmatrix}$$

and the inverse

$$\mathbf{A}^{-1} = \begin{bmatrix} 1.5 & 0.5 & 0 & 0 & 0 & -1 & 0 & 0 \\ 0.5 & 2 & 0.5 & 0 & -1 & -1 & 0 & 0 \\ 0 & 0.5 & 2 & 0 & -1 & 0.5 & 0 & -1 \\ 0 & 0 & 0 & 1.5 & 0.5 & 0 & -1 & 0 \\ 0 & -1 & -1 & 0.5 & 2.5 & 0 & -1 & 0 \\ -1 & -1 & 0.5 & 0 & 0 & 2.5 & 0 & -1 \\ 0 & 0 & 0 & -1 & -1 & 0 & 2 & 0 \\ 0 & 0 & -1 & 0 & 0 & -1 & 0 & 2 \end{bmatrix}$$

This inverted relationship matrix is added to each of the four sub matrices in the matrix shown above after multiplication with the proper element of the inverted genetic variance- covariance matrix. Thus,

$$\mathbf{Z}'\mathbf{R}^{-1}\mathbf{Z} + \mathbf{A}^{-1}\mathbf{G} = \begin{bmatrix} \mathbf{Z}_1'\mathbf{r}^{11}\mathbf{Z}_1 + \mathbf{A}^{-1}\mathbf{g}^{11} & \mathbf{Z}_1'\mathbf{r}^{12}\mathbf{Z}_2 + \mathbf{A}^{-1}\mathbf{g}^{12} \\ \mathbf{Z}_2'\mathbf{r}^{21}\mathbf{Z}_1 + \mathbf{A}^{-1}\mathbf{g}^{21} & \mathbf{Z}_2'\mathbf{r}^{22}\mathbf{Z}_2 + \mathbf{A}^{-1}\mathbf{g}^{22} \end{bmatrix} =$$

1.7175	0.5725	0	0	0	-11450	0	0	-1.4886	-.4962	0	0	0	0.9924	0	0
0.5725	2.2900	0.5725	0	-11450	-11450	0	0	-.4962	-1.9848	-.4862	0	0.9924	0.9924	0	0
0	0.5725	2.2900	0	-11450	0.5725	0	-11450	0	-.4962	-1.9848	0	0.9924	-.4962	0	0.9924
0	0	0	1.9955	0.5725	0	-11450	0	0	0	0	-1.5474	-.4962	0	0.9924	0
0	-11450	-11450	0.5725	31405	0	-11450	0	0	0.9924	0.9924	-.4962	-2.5398	0	0.9924	0
-11450	-11450	0.5725	0	0	31405	0	-11450	0.9924	0.9924	-.4962	0	0	-2.5398	0	0.9924
0	0	0	-11450	-11450	0	2.5680	0	0	0	0	0.9924	0.9924	0	-2.0436	0
0	0	-11450	0	0	-11450	0	2.5680	0	0	0.9924	0	0	0.9924	0	-2.0436
-1.4886	-.4962	0	0	0	0.9924	0	0	2.2901	0.7634	0	0	0	-1.5267	0	0
-.4962	-1.9848	-.4962	0	0.9924	0.9924	0	0	0.7634	3.0534	0.7634	0	-1.5267	-1.5267	0	0
0	-.4962	-1.9848	0	0.9924	-.4962	0	0.9924	0	0.7634	3.0534	0	-1.5267	0.7634	0	-1.5267
0	0	0	-1.5474	-.4962	0	0.9924	0	0	0	0	2.5254	0.7634	0	-1.5267	0
0	0.9924	0.9924	-.4962	-2.5398	0	0.9924	0	0	-1.5267	-1.5267	0.7634	4.0521	0	-1.5267	0
0.9924	0.9924	-.4962	0	0	-2.5398	0	0.9924	-1.5267	-1.5267	0.7634	0	0	4.0521	0	-1.5267
0	0	0	0.9924	0.9924	0	-2.0436	0	0	0	0	-1.5267	-1.5267	0	3.2887	0
0	0	0.9924	0	0	0.9924	0	-2.0436	0	0	-1.5267	0	0	-1.5267	0	3.2887

The product $\mathbf{X}'\mathbf{Z}$ becomes $\mathbf{X}'\mathbf{Z} = \begin{bmatrix} \mathbf{X}'_1\mathbf{Z}_1 & \mathbf{X}'_1\mathbf{Z}_2 \\ \mathbf{X}'_2\mathbf{Z}_1 & \mathbf{X}'_2\mathbf{Z}_2 \end{bmatrix} =$

$$\begin{bmatrix} \begin{bmatrix} 0 & 0 & 0 & 1 & 0 & 0 & 1 & 1 \end{bmatrix} \\ \begin{bmatrix} 0 & 0 & 0 & 0 & 1 & 1 & 0 & 0 \end{bmatrix} \\ \begin{bmatrix} 0 & 0 & 0 & 1 & 0 & 0 & 1 & 1 \end{bmatrix} \\ \begin{bmatrix} 0 & 0 & 0 & 0 & 1 & 1 & 0 & 0 \end{bmatrix} \end{bmatrix} \begin{bmatrix} \begin{bmatrix} 0 & 0 & 0 & 1 & 0 & 0 & 1 & 1 \end{bmatrix} \\ \begin{bmatrix} 0 & 0 & 0 & 0 & 1 & 1 & 0 & 0 \end{bmatrix} \\ \begin{bmatrix} 0 & 0 & 0 & 1 & 0 & 0 & 1 & 1 \end{bmatrix} \\ \begin{bmatrix} 0 & 0 & 0 & 0 & 1 & 1 & 0 & 0 \end{bmatrix} \end{bmatrix}$$

Again, each sub matrix is multiplied by the proper element of $\mathbf{R}^{-1}$ to obtain

$\mathbf{X}'\mathbf{R}^{-1}\mathbf{Z} =$

$$\begin{bmatrix} 0 & 0 & 0 & 0.2647 & 0 & 0 & 0.2647 & 0.2647 & 0 & 0 & 0 & -0.0588 & 0 & 0 & -0.0588 & -0.0588 \\ 0 & 0 & 0 & 0 & 0.2647 & 0.2647 & 0 & 0 & 0 & 0 & 0 & 0 & -0.0588 & -0.0588 & 0 & 0 \\ 0 & 0 & 0 & -0.0588 & 0 & 0 & -0.0588 & -0.0588 & 0 & 0 & 0 & 0.2353 & 0 & 0 & 0.2353 & 0.2353 \\ 0 & 0 & 0 & 0 & -0.0588 & -0.0588 & 0 & 0 & 0 & 0 & 0 & 0 & 0.2353 & 0.2353 & 0 & 0 \end{bmatrix}$$

The left hand side (apart from the parameter vector) can now be constructed as

$$\begin{bmatrix} \mathbf{X}'_1\mathbf{R}^{11}\mathbf{X}_1 & \mathbf{X}'_1\mathbf{R}^{12}\mathbf{X}_2 & \mathbf{X}'_1\mathbf{R}^{11}\mathbf{Z}_1 & \mathbf{X}'_1\mathbf{R}^{12}\mathbf{Z}_2 \\ \mathbf{X}'_2\mathbf{R}^{21}\mathbf{X}_1 & \mathbf{X}'_2\mathbf{R}^{22}\mathbf{X}_2 & \mathbf{X}'_2\mathbf{R}^{21}\mathbf{Z}_1 & \mathbf{X}'_2\mathbf{R}^{22}\mathbf{Z}_2 \\ \mathbf{Z}'_1\mathbf{R}^{11}\mathbf{X}_1 & \mathbf{Z}'_1\mathbf{R}^{12}\mathbf{X}_2 & \mathbf{Z}'_1\mathbf{R}^{11}\mathbf{Z}_1 + \mathbf{A}^{-1}\mathbf{G}^{11} & \mathbf{Z}'_1\mathbf{R}^{12}\mathbf{Z}_2 + \mathbf{A}^{-1}\mathbf{G}^{12} \\ \mathbf{Z}'_2\mathbf{R}^{21}\mathbf{X}_1 & \mathbf{Z}'_2\mathbf{R}^{22}\mathbf{X}_2 & \mathbf{Z}'_2\mathbf{R}^{21}\mathbf{Z}_1 + \mathbf{A}^{-1}\mathbf{G}^{21} & \mathbf{Z}'_2\mathbf{R}^{22}\mathbf{Z}_2 + \mathbf{A}^{-1}\mathbf{G}^{22} \end{bmatrix} =$$

0.79	0	-18	0	0	0	0	0.26	0	0	0.26	0.26	0	0	0	0	-06	0	0	-06	-06
0	0.53	0	-12	0	0	0	0	0.26	0.26	0	0	0	0	0	0	0	-06	-06	0	0
-18	0	0.71	0	0	0	0	-06	0	0	-06	-06	0	0	0	0.24	0	0	0.24	0.24	
0	-12	0	0.47	0	0	0	0	-06	-06	0	0	0	0	0	0	0.24	0.24	0	0	
0	0	0	0	1.72	0.57	0	0	0	-1.15	0	0	-1.49	-50	0	0	0	0.99	0	0	
0	0	0	0	0.57	2.29	0.57	0	-1.15	-1.15	0	0	-50	-198	-50	0	0.99	0.99	0	0	
0	0	0	0	0	0.57	2.29	0	-1.15	0.57	0	-1.15	0	-50	-198	0	0.99	-50	0	0.99	
0.26	0	-06	0	0	0	0	2.00	0.57	0	-1.15	0	0	0	0	-1.55	-50	0	0.99	0	
0	0.26	0	-06	0	-1.15	-1.15	0.57	3.14	0	-1.15	0	0	0.99	0.99	-50	-2.54	0	0.99	0	
0	0.26	0	-06	-1.15	-1.15	0.57	0	0	3.14	0	-1.15	0.99	0.99	-50	0	0	-2.54	0	0.99	
0.26	0	-06	0	0	0	0	-1.15	-1.15	0	2.57	0	0	0	0	0.99	0.99	0	-2.04	0	
0.26	0	-06	0	0	0	-1.15	0	0	-1.15	0	2.57	0	0	0.99	0	0	0.99	0	-2.04	
0	0	0	0	-1.49	-50	0	0	0	0.99	0	0	2.29	0.76	0	0	0	-1.53	0	0	
0	0	0	0	-50	-198	-50	0	0.99	0.99	0	0	0.76	3.05	0.76	0	-1.53	-1.53	0	0	
0	0	0	0	0	-50	-198	0	0.99	-50	0	0.99	0	0.76	3.05	0	-1.53	0.76	0	-1.53	
-06	0	0.24	0	0	0	0	-1.55	-50	0	0.99	0	0	0	0	2.53	0.76	0	-1.53	0	
0	-06	0	0.24	0	0.99	0.99	-50	-2.54	0	0.99	0	0	-1.53	-1.53	0.76	4.05	0	-1.53	0	
0	-06	0	0.24	0.99	0.99	-50	0	0	-2.54	0	0.99	-1.53	-1.53	0.76	0	0	4.05	0	-1.53	
-06	0	0.24	0	0	0	0	0.99	0.99	0	-2.04	0	0	0	0	-1.53	-1.53	0	3.29	0	
-06	0	0.24	0	0	0	0.99	0	0	0.99	0	-2.04	0	0	-1.53	0	0	-1.53	0	3.29	

The right hand side is composed of eight sub vectors:

$$\mathbf{X}'_1 \mathbf{r}^{11} \mathbf{y}_1 = \begin{bmatrix} 6.8822 \\ 3.7058 \end{bmatrix}, \mathbf{X}'_1 \mathbf{r}^{12} \mathbf{y}_2 = \begin{bmatrix} -1.2348 \\ -0.7056 \end{bmatrix}, \mathbf{X}'_2 \mathbf{r}^{21} \mathbf{y}_1 = \begin{bmatrix} -1.5288 \\ -0.8232 \end{bmatrix}, \mathbf{X}'_2 \mathbf{r}^{22} \mathbf{y}_2 = \begin{bmatrix} 4.4913 \\ 2.8236 \end{bmatrix}$$

$$\mathbf{Z}'_1 \mathbf{r}^{11} \mathbf{y}_1 = \begin{bmatrix} 0.0000 \\ 0.0000 \\ 0.0000 \\ 2.3823 \\ 1.5882 \\ 2.1176 \\ 1.8529 \\ 2.6470 \end{bmatrix}, \mathbf{Z}'_1 \mathbf{r}^{12} \mathbf{y}_2 = \begin{bmatrix} 0.0000 \\ 0.0000 \\ 0.0000 \\ -0.4116 \\ -0.2940 \\ -0.4116 \\ -0.3528 \\ -0.4704 \end{bmatrix}, \mathbf{Z}'_2 \mathbf{r}^{21} \mathbf{y}_1 = \begin{bmatrix} 0.0000 \\ 0.0000 \\ 0.0000 \\ -0.5292 \\ -0.3528 \\ -0.4704 \\ -0.4116 \\ -0.5880 \end{bmatrix}, \mathbf{Z}'_2 \mathbf{r}^{22} \mathbf{y}_2 = \begin{bmatrix} 0.0000 \\ 0.0000 \\ 0.0000 \\ 2.6471 \\ 1.1765 \\ 1.6476 \\ 1.4118 \\ 1.8824 \end{bmatrix}$$

Now, the right hand side can be constructed as:

$$\begin{bmatrix} X_1' r^{11} y_1 + X_1' r^{12} y_2 \\ X_2' r^{21} y_1 + X_2' r^{22} y_2 \\ Z_1' r^{11} y_1 + Z_1' r^{12} y_2 \\ Z_2' r^{21} y_1 + Z_2' r^{22} y_2 \end{bmatrix} = \begin{bmatrix} 5.6474 \\ 3.0002 \\ 3.4125 \\ 2.0004 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 1.9707 \\ 1.2942 \\ 1.7060 \\ 1.5001 \\ 2.1766 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 2.1179 \\ 0.8237 \\ 1.1772 \\ 1.0002 \\ 1.2944 \end{bmatrix}$$

The parameter vector may now be found from the following:

$$\begin{bmatrix} \mathbf{X}_1'\mathbf{r}^{11}\mathbf{X}_1 & \mathbf{X}_1'\mathbf{r}^{12}\mathbf{X}_2 & \mathbf{X}_1'\mathbf{r}^{11}\mathbf{Z}_1 & \mathbf{X}_1'\mathbf{r}^{12}\mathbf{Z}_2 \\ \mathbf{X}_2'\mathbf{r}^{21}\mathbf{X}_1 & \mathbf{X}_2'\mathbf{r}^{22}\mathbf{X}_2 & \mathbf{X}_2'\mathbf{r}^{21}\mathbf{Z}_1 & \mathbf{X}_2'\mathbf{r}^{22}\mathbf{Z}_2 \\ \mathbf{Z}_1'\mathbf{r}^{11}\mathbf{X}_1 & \mathbf{Z}_1'\mathbf{r}^{12}\mathbf{X}_2 & \mathbf{Z}_1'\mathbf{r}^{11}\mathbf{Z}_1 + \mathbf{A}^{-1}\mathbf{g}^{11} & \mathbf{Z}_1'\mathbf{r}^{12}\mathbf{Z}_2 + \mathbf{A}^{-1}\mathbf{g}^{12} \\ \mathbf{Z}_2'\mathbf{r}^{21}\mathbf{X}_1 & \mathbf{Z}_2'\mathbf{r}^{22}\mathbf{X}_2 & \mathbf{Z}_2'\mathbf{r}^{21}\mathbf{Z}_1 + \mathbf{A}^{-1}\mathbf{g}^{21} & \mathbf{Z}_2'\mathbf{r}^{22}\mathbf{Z}_2 + \mathbf{A}^{-1}\mathbf{g}^{22} \end{bmatrix}^{-1} \begin{bmatrix} \mathbf{X}_1'\mathbf{r}^{11}\mathbf{y}_1 + \mathbf{X}_1'\mathbf{r}^{12}\mathbf{y}_2 \\ \mathbf{X}_2'\mathbf{r}^{21}\mathbf{y}_1 + \mathbf{X}_2'\mathbf{r}^{22}\mathbf{y}_2 \\ \mathbf{Z}_1'\mathbf{r}^{11}\mathbf{y}_1 + \mathbf{Z}_1'\mathbf{r}^{12}\mathbf{y}_2 \\ \mathbf{Z}_2'\mathbf{r}^{21}\mathbf{y}_1 + \mathbf{Z}_2'\mathbf{r}^{22}\mathbf{y}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \\ \mathbf{u}_1 \\ \mathbf{u}_2 \end{bmatrix}$$

$$\begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \\ \mathbf{u}_1 \\ \mathbf{u}_2 \end{bmatrix} = \begin{bmatrix} 8.7819 \\ 6.9926 \\ 7.0907 \\ 5.9850 \\ 0.3035 \\ -0.0413 \\ -0.1088 \\ -0.1439 \\ -0.4198 \\ 0.4346 \\ -0.6005 \\ 0.3988 \\ 0.2514 \\ -0.0246 \\ -0.0929 \\ -0.1274 \\ -0.3347 \\ 0.3648 \\ -0.4638 \\ 0.3190 \end{bmatrix}$$

i.e.

$$\mathbf{b}_1' = [8.7819 \ 6.9926]; \quad \mathbf{b}_2' = [7.0907 \ 5.9850]$$

$$\mathbf{u}_1' = [0.3035 \ -0.0413 \ -0.1088 \ -0.1439 \ -0.4198 \quad 0.4346 \quad -0.6005 \quad 0.3988]$$

$$\mathbf{u}_2' = [0.2514 \ -0.0246 \ -0.0929 \ -0.1274 \ -0.3347 \quad 0.3648 \quad -0.4638 \quad 0.3190]$$

The corresponding estimates using a single trait animal model are shown in table 4.1. The ranking of the animals is the same in both cases, but the variation in breeding value is slightly smaller when using the single trait model.

Table 4.2. Comparison of estimates of fixed effects and breeding values obtained in multiple trait and single trait analyses

Effect	Trait 1		Trait 2	
	Multiple trait	Single trait	Multiple trait	Single trait
b_1	8.78	8.78	7.09	7.06
b_2	6.99	7.00	5.99	5.98
u_1	0.3	0.26	0.25	0.18
u_2	-0.04	-0.04	-0.02	-0.004
u_3	-0.11	-0.09	-0.09	-0.07
u_4	-0.14	-0.13	-0.13	-0.11
u_5	-0.42	-0.38	-0.33	-0.22
u_6	0.43	0.37	0.36	0.27
u_7	-0.6	-0.55	-0.46	-0.3
u_8	0.4	0.36	0.32	0.22