BLUP
How it works

- A joint evaluation of all animals,
  - uses all additive genetic relationships
  - uses all data on all animal jointly

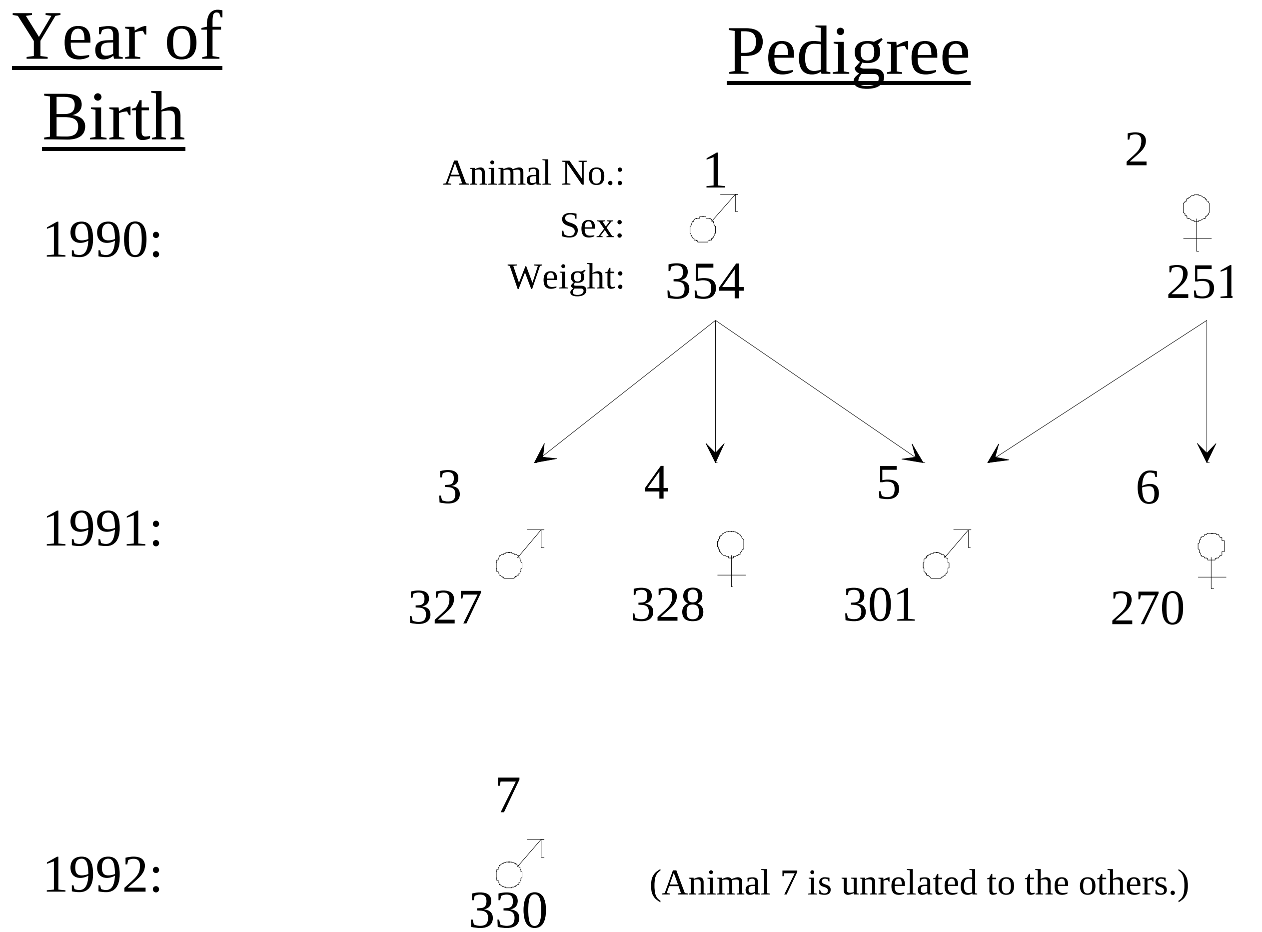
- It works as a linear model
  - correcting different effects for each other
  - jointly estimates animal effects and fixed effects (herds)

- ……..but has Selection Index properties

  (Regression with "heritability")

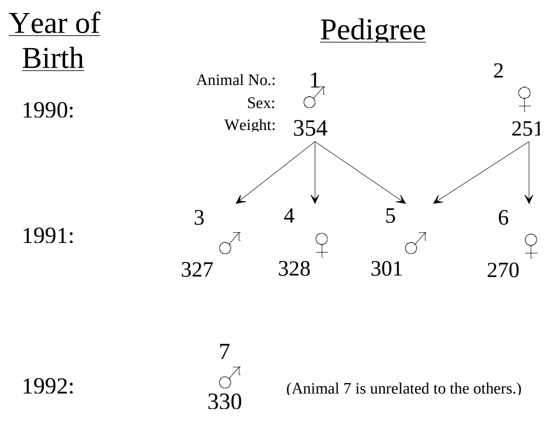
Estimating EBV's with linear models

example:



Putting the data

into a linear model



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

$$\begin{pmatrix} 354 \\ 251 \\ 327 \\ 328 \\ 301 \\ 270 \\ 330 \end{pmatrix} = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix} \begin{pmatrix} u_1 \\ u_2 \\ u_3 \\ u_4 \\ u_5 \\ u_6 \\ u_7 \end{pmatrix} + \begin{pmatrix} e_1 \\ e_2 \\ e_3 \\ e_4 \\ e_5 \\ e_6 \\ e_7 \end{pmatrix}$$

HERE: animal effects only

A breeding value is not treated as a fixed, but as a random effect

Estimating animal's effects as EBV's

If treated as fixed effect

$$\hat{u} = (Z'Z)^{-1} Z' y$$

Basically means per animal

This is wrong because we want:

- **Deviations from a mean:**

$$\hat{u} = (Z'Z)^{-1} Z' (y - \bar{y})$$

Basically mean deviations per animal

- **Shrink the breeding values**

We need to pre-multiply these deviations with 'heritability'

- see next

The need to shrink!

In a fixed effect model: $\hat{u} = y - \bar{y}$

We are used to regressing this toward the mean:

$$\hat{\mathbf{u}} = \mathbf{h}^2(\mathbf{y} - \bar{\mathbf{y}}) = \frac{\mathbf{V_A}}{\mathbf{V_A} + \mathbf{V_E}}(\mathbf{y} - \bar{\mathbf{y}}) = \frac{\mathbf{1}}{\mathbf{1} + \frac{\mathbf{V_E}}{\mathbf{V_A}}}(\mathbf{y} - \bar{\mathbf{y}}) = \frac{\mathbf{1}}{\mathbf{1} + \boldsymbol{\lambda}}(\mathbf{y} - \bar{\mathbf{y}})$$

And in linear model language this looks like

$$\hat{u} = (Z'Z + \lambda)^{-1}(y - \bar{y})$$

Where $\lambda = \dfrac{V_E}{V_A}$

In BLUP we can also take relationships among animals into account

$$\hat{u} = (Z'Z + \lambda)^{-1}(y - \bar{y})$$

Is expanded to

$$\hat{u} = (Z'Z + \lambda A^{-1})^{-1}(y - \bar{y})$$

This A is a matrix with all relationships among all animals in the vector u

The relationships matrix A -NRM

We need:

$$\hat{u} = (Z'Z + \lambda A^{-1})^{-1}(y - \bar{y})$$

$$\begin{pmatrix} 1 & 0 & .5 & .5 & .5 & 0 & 0 \\ 0 & 1 & 0 & 0 & .5 & .5 & 0 \\ .5 & 0 & 1 & .25 & .25 & 0 & 0 \\ .5 & 0 & .25 & 1 & .25 & 0 & 0 \\ .5 & .5 & .25 & .25 & 1 & .25 & 0 \\ 0 & .5 & 0 & 0 & .25 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix}$$

Elements are straightforward

But we need inverse

Direct inverse is easier for complex pedigree

Building the relationships matrix –

We need the inverse

which can be done directly with simple rules

For each animal which is to have an estimate of u, add to A^{-1}:

	Both parents known	One parent known	Neither parent known
Own diagonal	2	4/3	1
parent x animal	-1	-2/3	
parents' diagonals	1/2	1/3	
parent x parent	1/2		

Now solve the EBV's from the linear model

$$\hat{u} = [\; z'z \quad + \quad A^{-1}\lambda \;]^{-1} \; Z'(y-\hat{y})$$

$\lambda = 1$ if $h^2 = 0.5$

$$\begin{bmatrix} u_1 \\ u_2 \\ u_3 \\ u_4 \\ u_5 \\ u_6 \\ u_7 \end{bmatrix} = \left[\begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix} + \begin{bmatrix} 13/6 & 1/2 & -2/3 & -2/3 & -1 & 0 & 0 \\ 1/2 & 11/6 & 0 & 0 & -1 & -2/3 & 0 \\ -2/3 & 0 & 4/3 & 0 & 0 & 0 & 0 \\ -2/3 & 0 & 0 & 4/3 & 0 & 0 & 0 \\ -1 & -1 & 0 & 0 & 2 & 0 & 0 \\ 0 & -2/3 & 0 & 0 & 0 & 4/3 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix} \right]^{-1} \begin{bmatrix} 45.3 \\ -57.7 \\ 18.3 \\ 19.3 \\ -7.7 \\ -38.7 \\ 21.3 \end{bmatrix}$$

$$\begin{pmatrix} \hat{u}_1 \\ \hat{u}_2 \\ \hat{u}_3 \\ \hat{u}_4 \\ \hat{u}_5 \\ \hat{u}_6 \\ \hat{u}_7 \end{pmatrix} = \begin{pmatrix} .410 & -.030 & .117 & .117 & .127 & -.008 & 0 \\ -.030 & .435 & -.008 & -.008 & .135 & .124 & 0 \\ .117 & -.008 & .462 & .033 & .036 & -.002 & 0 \\ .117 & -.008 & .033 & .462 & .036 & -.002 & 0 \\ .127 & .135 & .036 & .036 & .421 & .039 & 0 \\ -.008 & .124 & -.002 & -.002 & .039 & .464 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & .5 \end{pmatrix} \begin{pmatrix} 45.3 \\ -57.7 \\ 18.3 \\ 19.3 \\ -7.7 \\ -38.7 \\ 21.3 \end{pmatrix}$$

BLP is the same as the classical selection index, except that there is a custom set of index weights for each candidate animal whose breeding value is to be estimated.

BLP results

The result is: $\begin{pmatrix} \hat{u}_1 \\ \hat{u}_2 \\ \hat{u}_3 \\ \hat{u}_4 \\ \hat{u}_5 \\ \hat{u}_6 \\ \hat{u}_7 \end{pmatrix} = \begin{pmatrix} 24.01 \\ -32.63 \\ 14.70 \\ 15.13 \\ -5.44 \\ -25.91 \\ 10.64 \end{pmatrix}$

Does this make sense?

$$\hat{u}_7 = (1 + \lambda)^{-1}(330 - 308.72) = h^2 \times 21.28 = 10.64$$

Animal 1 leans on its three offspring.

For animal 1, there is a negative weight on animal 2's phenotype.

MIXED MODELS: Best Linear Unbiased Prediction

breeding values → random effects
herds, years etc → fixed effects

We want

- **to estimate breeding values**
- **estimate/correct for fixed effects**

Jointly in a MIXED MODEL

Y = Xb + Zu + e

Mixed Model equations

$$\begin{pmatrix} X'X & X'Z \\ Z'X & Z'Z + \lambda A^{-1} \end{pmatrix} \begin{pmatrix} \hat{b} \\ \hat{u} \end{pmatrix} = \begin{pmatrix} X'y \\ Z'y \end{pmatrix}$$

Example Mixed Model for BLUP analysis

Y = X b + Z u + e

$$\begin{bmatrix} 354 \\ 251 \\ 327 \\ 328 \\ 301 \\ 270 \\ 330 \end{bmatrix} = \begin{bmatrix} 1 & 1 & 0 \\ 1 & 1 & 0 \\ 1 & 0 & 1 \\ 1 & 0 & 1 \\ 1 & 0 & 1 \\ 1 & 0 & 1 \\ 1 & -1 & -1 \end{bmatrix} \begin{bmatrix} b_{mean} \\ b_{1990} \\ b_{1991} \end{bmatrix} + \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} u1 \\ u2 \\ u3 \\ u4 \\ u5 \\ u6 \\ u7 \end{bmatrix} + \begin{bmatrix} e1 \\ e2 \\ e3 \\ e4 \\ e5 \\ e6 \\ e7 \end{bmatrix}$$

Mixed Model Equations

Fixed bit

$$\begin{pmatrix} \mathbf{X'X} & \mathbf{X'Z} \\ \mathbf{Z'X} & \mathbf{Z'Z} + \lambda \mathbf{A}^{-1} \end{pmatrix} \begin{pmatrix} \hat{\mathbf{b}} \\ \hat{\mathbf{u}} \end{pmatrix} = \begin{pmatrix} \mathbf{X'y} \\ \mathbf{Z'y} \end{pmatrix}$$

Random bit

Fixed by
Random bit

Coefficient matrix

Solution

Right Hand Side

Mixed Model Equations

$$\begin{pmatrix} \mathbf{X'X} & \mathbf{X'Z} \\ \mathbf{Z'X} & \mathbf{Z'Z} + \lambda\mathbf{A}^{-1} \end{pmatrix} \begin{pmatrix} \hat{\mathbf{b}} \\ \hat{\mathbf{u}} \end{pmatrix} = \begin{pmatrix} \mathbf{X'y} \\ \mathbf{Z'y} \end{pmatrix}$$

$$\begin{pmatrix} \hat{b} \\ \hat{u} \end{pmatrix} = \begin{pmatrix} X'X & X'Z \\ Z'X & Z'Z + \lambda A^{-1} \end{pmatrix}^{-1} \begin{pmatrix} X'y \\ Z'y \end{pmatrix}$$

Solution = Inverse of Coefficient matrix . Right Hand Side

Example of BLUP solutions

Solution to MME

$$\begin{pmatrix} \hat{b} \\ \hat{u} \end{pmatrix} = \begin{pmatrix} X'X & X'Z \\ Z'X & Z'Z + \lambda A^{-1} \end{pmatrix}^{-1} \begin{pmatrix} X'y \\ Z'y \end{pmatrix}$$

Coefficient matrix

RHS

Solution to MME

$$\begin{bmatrix} \mu \\ \mathbf{b}_1 \\ \mathbf{b}_2 \\ \hat{\mathbf{u}}_1 \\ \hat{\mathbf{u}}_2 \\ \hat{\mathbf{u}}_3 \\ \hat{\mathbf{u}}_4 \\ \hat{\mathbf{u}}_5 \\ \hat{\mathbf{u}}_6 \\ \hat{\mathbf{u}}_7 \end{bmatrix} = \begin{bmatrix} 7 & 1 & 3 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\ 1 & 3 & 1 & 1 & 1 & 0 & 0 & 0 & 0 & -1 \\ 3 & 1 & 5 & 0 & 0 & 1 & 1 & 1 & 1 & -1 \\ 1 & 1 & 0 & 19/6 & 1/2 & -2/3 & -2/3 & -1 & 0 & 0 \\ 1 & 1 & 0 & 1/2 & 17/6 & 0 & 0 & -1 & -2/3 & 0 \\ 1 & 0 & 1 & -2/3 & 0 & 7/3 & 0 & 0 & 0 & 0 \\ 1 & 0 & 1 & -2/3 & 0 & 0 & 7/3 & 0 & 0 & 0 \\ 1 & 0 & 1 & -1 & -1 & 0 & 0 & 3 & 0 & 0 \\ 1 & 0 & 1 & 0 & -2/3 & 0 & 0 & 7/3 & 7/3 & 0 \\ 1 & -1 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 2 \end{bmatrix}^{-1} \begin{bmatrix} 2161 \\ 275 \\ 896 \\ 354 \\ 251 \\ 327 \\ 328 \\ 301 \\ 270 \\ 330 \end{bmatrix} = \begin{bmatrix} 311.9 \\ -9.15 \\ -8.9 \\ 28.26 \\ -28.85 \\ 18.34 \\ 18.77 \\ -0.87 \\ -22.4 \\ 0 \end{bmatrix}$$

Example of BLUP solutions

$$\begin{pmatrix} \hat{b} \\ \hat{u} \end{pmatrix} = \begin{pmatrix} X'X & X'Z \\ Z'X & Z'Z + \lambda A^{-1} \end{pmatrix}^{-1} \begin{pmatrix} X'y \\ Z'y \end{pmatrix}$$

Counting records in different herds

$$\begin{bmatrix} \mu \\ b_1 \\ b_2 \\ \hat{u}_1 \\ \hat{u}_2 \\ \hat{u}_3 \\ \hat{u}_4 \\ \hat{u}_5 \\ \hat{u}_6 \\ \hat{u}_7 \end{bmatrix} = \begin{bmatrix} 7 & 1 & 3 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\ 1 & 3 & 1 & 1 & 1 & 0 & 0 & 0 & 0 & -1 \\ 3 & 1 & 5 & 0 & 0 & 1 & 1 & 1 & 1 & -1 \\ 1 & 1 & 0 & 19/6 & 1/2 & -2/3 & -2/3 & -1 & 0 & 0 \\ 1 & 1 & 0 & 1/2 & 17/6 & 0 & 0 & -1 & -2/3 & 0 \\ 1 & 0 & 1 & -2/3 & 0 & 7/3 & 0 & 0 & 0 & 0 \\ 1 & 0 & 1 & -2/3 & 0 & 0 & 7/3 & 0 & 0 & 0 \\ 1 & 0 & 1 & -1 & -1 & 0 & 0 & 3 & 0 & 0 \\ 1 & 0 & 1 & 0 & -2/3 & 0 & 0 & 7/3 & 7/3 & 0 \\ 1 & -1 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 2 \end{bmatrix}^{-1} \begin{bmatrix} 2161 \\ 275 \\ 896 \\ 354 \\ 251 \\ 327 \\ 328 \\ 301 \\ 270 \\ 330 \end{bmatrix} = \begin{bmatrix} 311.9 \\ -9.15 \\ -8.9 \\ 28.26 \\ -28.85 \\ 18.34 \\ 18.77 \\ -0.87 \\ -22.4 \\ 0 \end{bmatrix}$$

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Counting animals in diff. herds

$$\begin{bmatrix} \mu \\ b_1 \\ b_2 \\ \hat{u}_1 \\ \hat{u}_2 \\ \hat{u}_3 \\ \hat{u}_4 \\ \hat{u}_5 \\ \hat{u}_6 \\ \hat{u}_7 \end{bmatrix} = \begin{bmatrix} 7 & 1 & 3 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\ 1 & 3 & 1 & 1 & 1 & 0 & 0 & 0 & 0 & -1 \\ 3 & 1 & 5 & 0 & 0 & 1 & 1 & 1 & 1 & -1 \\ 1 & 1 & 0 & 19/6 & 1/2 & -2/3 & -2/3 & -1 & 0 & 0 \\ 1 & 1 & 0 & 1/2 & 17/6 & 0 & 0 & -1 & -2/3 & 0 \\ 1 & 0 & 1 & -2/3 & 0 & 7/3 & 0 & 0 & 0 & 0 \\ 1 & 0 & 1 & -2/3 & 0 & 0 & 7/3 & 0 & 0 & 0 \\ 1 & 0 & 1 & -1 & -1 & 0 & 0 & 3 & 0 & 0 \\ 1 & 0 & 1 & 0 & -2/3 & 0 & 0 & 7/3 & 7/3 & 0 \\ 1 & -1 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 2 \end{bmatrix}^{-1} \begin{bmatrix} 2161 \\ 275 \\ 896 \\ 354 \\ 251 \\ 327 \\ 328 \\ 301 \\ 270 \\ 330 \end{bmatrix} = \begin{bmatrix} 311.9 \\ -9.15 \\ -8.9 \\ 28.26 \\ -28.85 \\ 18.34 \\ 18.77 \\ -0.87 \\ -22.4 \\ 0 \end{bmatrix}$$

Example of BLUP solutions

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Counting animals' records and their relationships and heritability

$$\begin{bmatrix} \mu \\ b_1 \\ b_2 \\ \hat{u}_1 \\ \hat{u}_2 \\ \hat{u}_3 \\ \hat{u}_4 \\ \hat{u}_5 \\ \hat{u}_6 \\ \hat{u}_7 \end{bmatrix} = \begin{bmatrix} 7 & 1 & 3 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\ 1 & 3 & 1 & 1 & 1 & 0 & 0 & 0 & 0 & -1 \\ 3 & 1 & 5 & 0 & 0 & 1 & 1 & 1 & 1 & -1 \\ 1 & 1 & 0 & 19/6 & 1/2 & -2/3 & -2/3 & -1 & 0 & 0 \\ 1 & 1 & 0 & 1/2 & 17/6 & 0 & 0 & -1 & -2/3 & 0 \\ 1 & 0 & 1 & -2/3 & 0 & 7/3 & 0 & 0 & 0 & 0 \\ 1 & 0 & 1 & -2/3 & 0 & 0 & 7/3 & 0 & 0 & 0 \\ 1 & 0 & 1 & -1 & -1 & 0 & 0 & 3 & 0 & 0 \\ 1 & 0 & 1 & 0 & -2/3 & 0 & 0 & 7/3 & 7/3 & 0 \\ 1 & -1 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 2 \end{bmatrix}^{-1} \begin{bmatrix} 2161 \\ 275 \\ 896 \\ 354 \\ 251 \\ 327 \\ 328 \\ 301 \\ 270 \\ 330 \end{bmatrix} = \begin{bmatrix} 311.9 \\ -9.15 \\ -8.9 \\ 28.26 \\ -28.85 \\ 18.34 \\ 18.77 \\ -0.87 \\ -22.4 \\ 0 \end{bmatrix}$$

Notice that:

1. The X'X and X'Y are as fixed effects analysis.

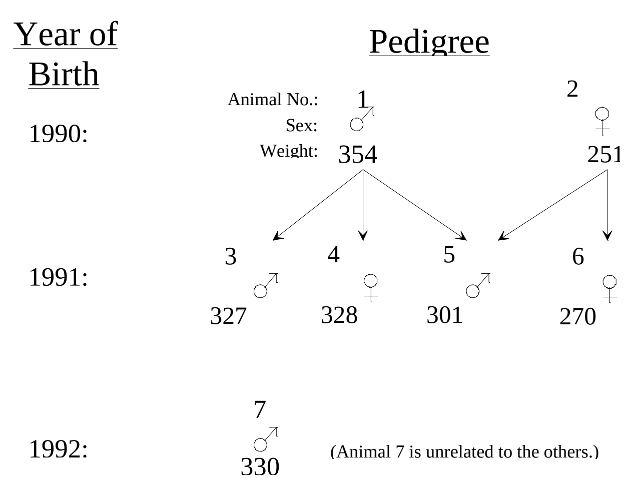
2. $Z'Z + A^{-1}\lambda$ is as in random model

4. Because the mean is fitted, raw data can be used (in Z'Y = Y) rather that deviations from the overall mean, as used for the random model in the last lecture.

   Note that there is a " Z'X block " which is used to account for fixed effects when calculating EBV's.

BLUP solutions

$$
\begin{bmatrix} \mu \\ \mathbf{b}_1 \\ \mathbf{b}_2 \\ \hat{\mathbf{u}}_1 \\ \hat{\mathbf{u}}_2 \\ \hat{\mathbf{u}}_3 \\ \hat{\mathbf{u}}_4 \\ \hat{\mathbf{u}}_5 \\ \hat{\mathbf{u}}_6 \\ \hat{\mathbf{u}}_7 \end{bmatrix}
=
\begin{bmatrix}
7 & 1 & 3 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\
1 & 3 & 1 & 1 & 1 & 0 & 0 & 0 & 0 & -1 \\
3 & 1 & 5 & 0 & 0 & 1 & 1 & 1 & 1 & -1 \\
1 & 1 & 0 & 19/6 & 1/2 & -2/3 & -2/3 & -1 & 0 & 0 \\
1 & 1 & 0 & 1/2 & 17/6 & 0 & 0 & -1 & -2/3 & 0 \\
1 & 0 & 1 & -2/3 & 0 & 7/3 & 0 & 0 & 0 & 0 \\
1 & 0 & 1 & -2/3 & 0 & 0 & 7/3 & 0 & 0 & 0 \\
1 & 0 & 1 & -1 & -1 & 0 & 0 & 3 & 0 & 0 \\
1 & 0 & 1 & 0 & -2/3 & 0 & 0 & 7/3 & 7/3 & 0 \\
1 & -1 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 2
\end{bmatrix}^{-1}
\begin{bmatrix} 2161 \\ 275 \\ 896 \\ 354 \\ 251 \\ 327 \\ 328 \\ 301 \\ 270 \\ 330 \end{bmatrix}
=
\begin{bmatrix} 311.9 \\ -9.15 \\ -8.9 \\ 28.26 \\ -28.85 \\ 18.34 \\ 18.77 \\ -0.87 \\ -22.4 \\ 0 \end{bmatrix}
\begin{matrix} \text{Mean} \\ \text{Yr1} \\ \text{yr2} \\ \\ \\ \\ \text{EBVs} \\ \\ \\ \\ \end{matrix}
$$



BLUP solutions

$$
\begin{bmatrix} \mu \\ b_1 \\ b_2 \\ \hat{u}_1 \\ \hat{u}_2 \\ \hat{u}_3 \\ \hat{u}_4 \\ \hat{u}_5 \\ \hat{u}_6 \\ \hat{u}_7 \end{bmatrix}
=
\begin{bmatrix}
7 & 1 & 3 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\
1 & 3 & 1 & 1 & 1 & 0 & 0 & 0 & 0 & -1 \\
3 & 1 & 5 & 0 & 0 & 1 & 1 & 1 & 1 & -1 \\
1 & 1 & 0 & 19/6 & 1/2 & -2/3 & -2/3 & -1 & 0 & 0 \\
1 & 1 & 0 & 1/2 & 17/6 & 0 & 0 & -1 & -2/3 & 0 \\
1 & 0 & 1 & -2/3 & 0 & 7/3 & 0 & 0 & 0 & 0 \\
1 & 0 & 1 & -2/3 & 0 & 0 & 7/3 & 0 & 0 & 0 \\
1 & 0 & 1 & -1 & -1 & 0 & 0 & 3 & 0 & 0 \\
1 & 0 & 1 & 0 & -2/3 & 0 & 0 & 7/3 & 7/3 & 0 \\
1 & -1 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 2
\end{bmatrix}^{-1}
\begin{bmatrix} 2161 \\ 275 \\ 896 \\ 354 \\ 251 \\ 327 \\ 328 \\ 301 \\ 270 \\ 330 \end{bmatrix}
=
\begin{bmatrix} 311.9 \\ -9.15 \\ -8.9 \\ 28.26 \\ -28.85 \\ 18.34 \\ 18.77 \\ -0.87 \\ -22.4 \\ 0 \end{bmatrix}
$$

Mean
Yr1
yr2

Av ~0

Ave >0

Year difference was 4 in fixed model (‘raw means’)

Now corrected for animal effects = ‘trend’

Further: Looking at the results

- **Year effect is different from fixed model**. Why?
- **Animal 7 has a zero EBV**. Why?

BLUP accounts for selection, genetic trend……

EBV of animals 1 and 2 are zero – on average

EBV of animals 3-6 are above zero – on average Why?

BLUP

How it works ☺

- A joint evaluation of all animals,
  - uses all additive genetic relationships
  - uses all data on all animal jointly
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  - jointly estimates animal effects and fixed effects (herds)
- ……..but has Selection Index properties

  (Regression with "heritability")