

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)

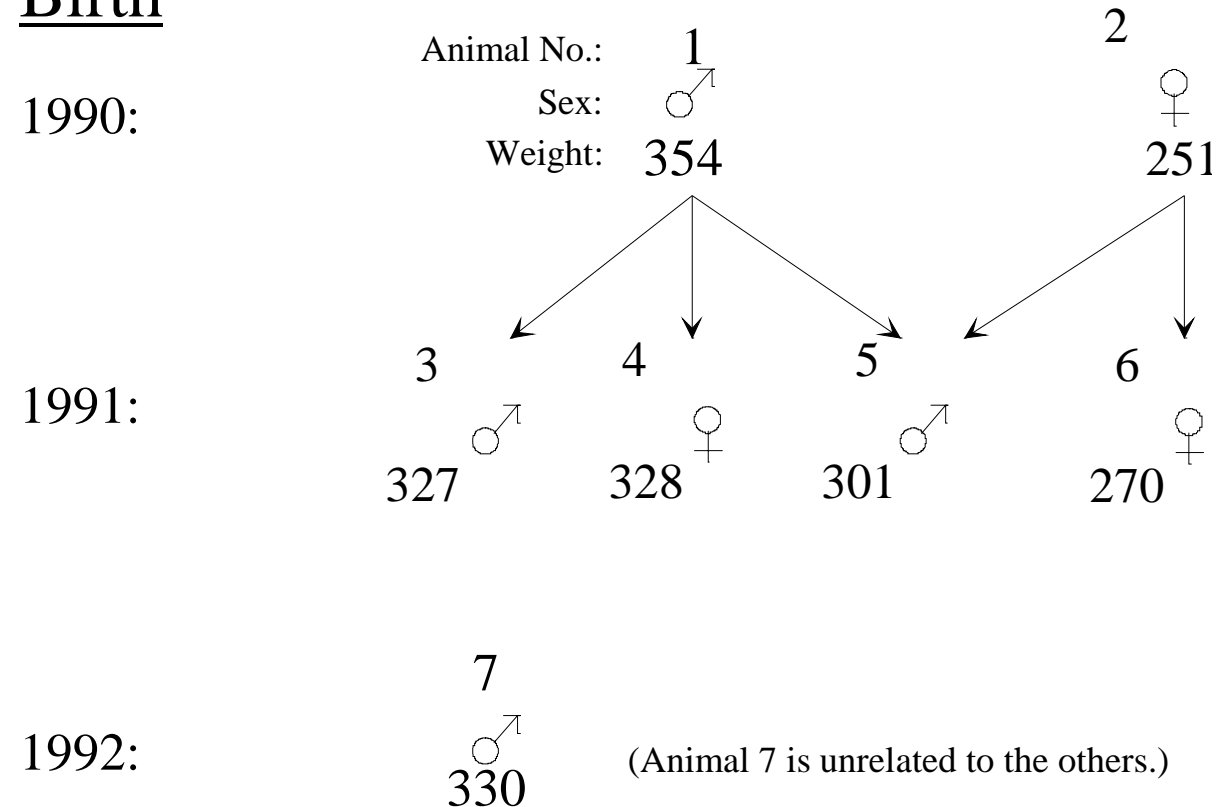
but has Selection Index properties (Regression with “heritability”)

Estimating EBV's with linear models

example:

Year of Birth

Pedigree



Example BLUP model

$$Y = X \quad b \quad + \quad Z \quad u \quad + \quad e$$

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

Example of BLUP solutions

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

$$\begin{pmatrix} \hat{b}_{\text{mean}} \\ \hat{b}_{1990} \\ \hat{b}_{1991} \\ \hat{u}_1 \\ \hat{u}_2 \\ \hat{u}_3 \\ \hat{u}_4 \\ \hat{u}_5 \\ \hat{u}_6 \\ \hat{u}_7 \end{pmatrix} = \begin{bmatrix} 7 & 1 & 3 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\ 1 & 3 & 1 & 1 & 1 & 0 & 0 & 0 & 0 & -1 \\ 3 & 1 & 5 & 0 & 0 & 1 & 1 & 1 & 1 & -1 \\ 1 & 1 & 0 & 19/6 & 1/2 & -2/3 & -2/3 & -1 & 0 & 0 \\ 1 & 1 & 0 & 1/2 & 17/6 & 0 & 0 & -1 & -2/3 & 0 \\ 1 & 0 & 1 & -2/3 & 0 & 7/3 & 0 & 0 & 0 & 0 \\ 1 & 0 & 1 & -2/3 & 0 & 0 & 7/3 & 0 & 0 & 0 \\ 1 & 0 & 1 & -1 & -1 & 0 & 0 & 3 & 0 & 0 \\ 1 & 0 & 1 & 0 & -2/3 & 0 & 0 & 0 & 7/3 & 0 \\ 1 & -1 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 2 \end{bmatrix}^{-1} \begin{pmatrix} 2161 \\ 275 \\ 896 \\ 354 \\ 251 \\ 327 \\ 328 \\ 301 \\ 270 \\ 330 \end{pmatrix} = \begin{pmatrix} 311.94 \\ -9.15 \\ -8.90 \\ 28.26 \\ -28.85 \\ 18.34 \\ 18.77 \\ -0.87 \\ -22.40 \\ 0 \end{pmatrix}$$

Example of BLUP solutions

Counting records in different herds

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

$$\begin{pmatrix} \hat{b}_{\text{mean}} \\ \hat{b}_{1990} \\ \hat{b}_{1991} \\ \hat{u}_1 \\ \hat{u}_2 \\ \hat{u}_3 \\ \hat{u}_4 \\ \hat{u}_5 \\ \hat{u}_6 \\ \hat{u}_7 \end{pmatrix} = \begin{pmatrix} 7 & 1 & 3 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\ 1 & 3 & 1 & 1 & 1 & 0 & 0 & 0 & 0 & -1 & \\ 3 & 1 & 5 & 0 & 0 & 1 & 1 & 1 & 1 & -1 & \\ 1 & 1 & 0 & 19/6 & 1/2 & -2/3 & -2/3 & -1 & 0 & 0 & \\ 1 & 1 & 0 & 1/2 & 17/6 & 0 & 0 & -1 & -2/3 & 0 & \\ 1 & 0 & 1 & -2/3 & 0 & 7/3 & 0 & 0 & 0 & 0 & \\ 1 & 0 & 1 & -2/3 & 0 & 0 & 7/3 & 0 & 0 & 0 & \\ 1 & 0 & 1 & -1 & -1 & 0 & 0 & 3 & 0 & 0 & \\ 1 & 0 & 1 & 0 & -2/3 & 0 & 0 & 0 & 7/3 & 0 & \\ 1 & -1 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 2 & \end{pmatrix}^{-1} \begin{pmatrix} 2161 \\ 275 \\ 896 \\ 354 \\ 251 \\ 327 \\ 328 \\ 301 \\ 270 \\ 330 \end{pmatrix} = \begin{pmatrix} 311.94 \\ -9.15 \\ -8.90 \\ 28.26 \\ -28.85 \\ 18.34 \\ 18.77 \\ -0.87 \\ -22.40 \\ 0 \end{pmatrix}$$

Example of BLUP solutions

Counting
animals in
diff. herds

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

$$\begin{pmatrix} \hat{b}_{\text{mean}} \\ \hat{b}_{1990} \\ \hat{b}_{1991} \\ \hat{u}_1 \\ \hat{u}_2 \\ \hat{u}_3 \\ \hat{u}_4 \\ \hat{u}_5 \\ \hat{u}_6 \\ \hat{u}_7 \end{pmatrix} = \begin{bmatrix} 7 & 1 & 3 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\ 1 & 3 & 1 & 1 & 1 & 0 & 0 & 0 & 0 & -1 \\ 3 & 1 & 5 & 0 & 0 & 1 & 1 & 1 & 1 & -1 \\ 1 & 1 & 0 & 19/6 & 1/2 & -2/3 & -2/3 & -1 & 0 & 0 \\ 1 & 1 & 0 & 1/2 & 17/6 & 0 & 0 & -1 & -2/3 & 0 \\ 1 & 0 & 1 & -2/3 & 0 & 7/3 & 0 & 0 & 0 & 0 \\ 1 & 0 & 1 & -2/3 & 0 & 0 & 7/3 & 0 & 0 & 0 \\ 1 & 0 & 1 & -1 & -1 & 0 & 0 & 3 & 0 & 0 \\ 1 & 0 & 1 & 0 & -2/3 & 0 & 0 & 0 & 7/3 & 0 \\ 1 & -1 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 2 \end{bmatrix}^{-1} \begin{pmatrix} 2161 \\ 275 \\ 896 \\ 354 \\ 251 \\ 327 \\ 328 \\ 301 \\ 270 \\ 330 \end{pmatrix} = \begin{pmatrix} 311.94 \\ -9.15 \\ -8.90 \\ 28.26 \\ -28.85 \\ 18.34 \\ 18.77 \\ -0.87 \\ -22.40 \\ 0 \end{pmatrix}$$

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 animals' records and their relationships and heritability

$$\begin{pmatrix} \hat{b}_{\text{mean}} \\ \hat{b}_{1990} \\ \hat{b}_{1991} \\ \hat{u}_1 \\ \hat{u}_2 \\ \hat{u}_3 \\ \hat{u}_4 \\ \hat{u}_5 \\ \hat{u}_6 \\ \hat{u}_7 \end{pmatrix} = \begin{bmatrix} 7 & 1 & 3 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\ 1 & 3 & 1 & 1 & 1 & 0 & 0 & 0 & 0 & 0 & -1 \\ 3 & 1 & 5 & 0 & 0 & 1 & 1 & 1 & 1 & 1 & -1 \\ 1 & 1 & 0 & 19/6 & 1/2 & -2/3 & -2/3 & -1 & 0 & 0 \\ 1 & 1 & 0 & 1/2 & 17/6 & 0 & 0 & -1 & -2/3 & 0 \\ 1 & 0 & 1 & -2/3 & 0 & 7/3 & 0 & 0 & 0 & 0 \\ 1 & 0 & 1 & -2/3 & 0 & 0 & 7/3 & 0 & 0 & 0 \\ 1 & 0 & 1 & -1 & -1 & 0 & 0 & 3 & 0 & 0 \\ 1 & 0 & 1 & 0 & -2/3 & 0 & 0 & 0 & 7/3 & 0 \\ 1 & -1 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 2 \end{bmatrix}^{-1} \begin{pmatrix} 2161 \\ 275 \\ 896 \\ 354 \\ 251 \\ 327 \\ 328 \\ 301 \\ 270 \\ 330 \end{pmatrix} = \begin{pmatrix} 311.94 \\ -9.15 \\ -8.90 \\ 28.26 \\ -28.85 \\ 18.34 \\ 18.77 \\ -0.87 \\ -22.40 \\ 0 \end{pmatrix}$$

The relationships matrix

What is $Z'Z + A^{-1} \frac{\sigma^2_e}{\sigma^2_g}$??

**All elements are straightforward, except the inverse of A,
i.e. the inverse of the Numerator Relationship Matrix**

$$A = \begin{pmatrix} 1 & 0 & 1/2 & 1/2 & 1/2 & 0 & 0 \\ 0 & 1 & 0 & 0 & 1/2 & 1/2 & 0 \\ 1/2 & 0 & 1 & 1/4 & 1/4 & 0 & 0 \\ 1/2 & 0 & 1/4 & 1 & 1/4 & 0 & 0 \\ 1/2 & 1/2 & 1/4 & 1/4 & 1 & 1/4 & 0 \\ 0 & 1/2 & 0 & 0 & 1/4 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix}$$

$$\lambda = 1 \text{ if } h^2 = 0.5$$

$$\lambda = 3 \text{ if } h^2 = 0.25$$

$$\mathbf{Z}'\mathbf{Z} + \mathbf{A}^{-1} \frac{\sigma_e^2}{\sigma_a^2}$$

$$\mathbf{I} + \mathbf{A}^{-1}\lambda$$

$$\left[\begin{pmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix} + \begin{pmatrix} 13/6 & 1/2 & -2/3 & -2/3 & -1 & 0 & 0 \\ 1/2 & 11/6 & 0 & 0 & -1 & -2/3 & 0 \\ -2/3 & 0 & 4/3 & 0 & 0 & 0 & 0 \\ -2/3 & 0 & 0 & 4/3 & 0 & 0 & 0 \\ -1 & -1 & 0 & 0 & 2 & 0 & 0 \\ 0 & -2/3 & 0 & 0 & 0 & 4/3 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix} \right]^{-1}$$

The need to shrink!

'wrong' single-animal version : $\hat{u} = y - Xb$

Correct is to regress properly: $\hat{u} = V_a / (V_a + V_e)(y - Xb)$

Divide top and bottom by V_a : $\hat{u} = 1 / (1 + (V_e / V_a))(y - Xb)$

Back to multi-animal: $\hat{u} = (Z'Z + A^{-1} \frac{\sigma^2_e}{\sigma^2_g})^{-1} Z'(y - Xb)$

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

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.

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

$$\begin{pmatrix} \hat{b}_{\text{mean}} \\ \hat{b}_{1990} \\ \hat{b}_{1991} \\ \hat{u}_1 \\ \hat{u}_2 \\ \hat{u}_3 \\ \hat{u}_4 \\ \hat{u}_5 \\ \hat{u}_6 \\ \hat{u}_7 \end{pmatrix} = \begin{bmatrix} 7 & 1 & 3 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\ 1 & 3 & 1 & 1 & 1 & 0 & 0 & 0 & 0 & -1 \\ 3 & 1 & 5 & 0 & 0 & 1 & 1 & 1 & 1 & -1 \\ 1 & 1 & 0 & 19/6 & 1/2 & -2/3 & -2/3 & -1 & 0 & 0 \\ 1 & 1 & 0 & 1/2 & 17/6 & 0 & 0 & -1 & -2/3 & 0 \\ 1 & 0 & 1 & -2/3 & 0 & 7/3 & 0 & 0 & 0 & 0 \\ 1 & 0 & 1 & -2/3 & 0 & 0 & 7/3 & 0 & 0 & 0 \\ 1 & 0 & 1 & -1 & -1 & 0 & 0 & 3 & 0 & 0 \\ 1 & 0 & 1 & 0 & -2/3 & 0 & 0 & 0 & 7/3 & 0 \\ 1 & -1 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 2 \end{bmatrix}^{-1} \begin{pmatrix} 2161 \\ 275 \\ 896 \\ 354 \\ 251 \\ 327 \\ 328 \\ 301 \\ 270 \\ 330 \end{pmatrix} = \begin{pmatrix} 311.94 \\ -9.15 \\ -8.90 \\ 28.26 \\ -28.85 \\ 18.34 \\ 18.77 \\ -0.87 \\ -22.40 \\ 0 \end{pmatrix}$$

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 EQUATIONS

$$\begin{pmatrix} \hat{b}_{\text{mean}_1} \\ \hat{b}_{1990} \\ \hat{b}_{1991} \\ \hat{u}_1 \\ \hat{u}_2 \\ \hat{u}_3 \\ \hat{u}_4 \\ \hat{u}_5 \\ \hat{u}_6 \\ \hat{u}_7 \end{pmatrix} = \begin{bmatrix} 7 & 1 & 3 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\ 1 & 3 & 1 & 1 & 1 & 0 & 0 & 0 & 0 & -1 & -1 \\ 3 & 1 & 5 & 0 & 0 & 1 & 1 & 1 & 1 & -1 & -1 \\ 1 & 1 & 0 & 19/6 & 1/2 & -2/3 & -2/3 & -1 & 0 & 0 & 0 \\ 1 & 1 & 0 & 1/2 & 17/6 & 0 & 0 & -1 & -2/3 & 0 & 0 \\ 1 & 0 & 1 & -2/3 & 0 & 7/3 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 1 & -2/3 & 0 & 0 & 7/3 & 0 & 0 & 0 & 0 \\ 1 & 0 & 1 & -1 & -1 & 0 & 0 & 3 & 0 & 0 & 0 \\ 1 & 0 & 1 & 0 & -2/3 & 0 & 0 & 0 & 7/3 & 0 & 0 \\ 1 & -1 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 2 \end{bmatrix}^{-1} \begin{pmatrix} 2161 \\ 275 \\ 896 \\ 354 \\ 251 \\ 327 \\ 328 \\ 301 \\ 270 \\ 330 \end{pmatrix} = \begin{pmatrix} 311.94 \\ -9.15 \\ -8.90 \\ 28.26 \\ -28.85 \\ 18.34 \\ 18.77 \\ -0.87 \\ -22.40 \\ 0 \end{pmatrix}$$

- Write out equations:

For **animal 6**:

$$\underline{\mu + b_{1991} - \frac{2}{3}\hat{u}_2 + \frac{7}{3}\hat{u}_6 = 270} \quad \rightarrow \quad \underline{\hat{u}_6 = \frac{3}{7}(270 - \mu - b_{1991}) + \frac{2}{7}\hat{u}_2}$$

$$\rightarrow \underline{\hat{u}_6 = \frac{3}{7}(270 - \mu - b_{1991} - \frac{1}{2}\hat{u}_2) + \frac{1}{2}\hat{u}_2}$$

Similarly for **animal 5**:

$$\underline{\mu + b_{1991} - \hat{u}_1 - \hat{u}_2 + 3\hat{u}_5 = 301}$$

→

$$\underline{\hat{u}_5 = \frac{1}{3}(301 - \mu - b_{1991} - \frac{1}{2}(\hat{u}_1 + \hat{u}_2)) + \frac{1}{2}(\hat{u}_1 + \hat{u}_2)}$$

EBV is estimated as a deviation of an expected mean

(FE + family mean)

animal 2:

$$\mu + b_{1990} + \frac{1}{2}\hat{u}_1 + \frac{17}{6}\hat{u}_2 - \hat{u}_5 - \frac{2}{3}\hat{u}_6 = 251$$

$$\rightarrow \hat{u}_2 = \frac{6}{17}(251 - \mu - b_{1990}) - \frac{6}{17}(\hat{u}_5 - \frac{1}{2}\hat{u}_1) + \frac{4}{17}\hat{u}_6$$

parents:

- own record
- progeny records
- correction for mates

Weights are same as in selection index

BLUP accounts for selection!!

Animals are from selected parents

year	sire 1	sire 2	sire 3
1	350	300	250
	↙	↓	↘
	offspr. 1	offspr. 2	offspr. 3
2	365	325	310

as years/generations go by, the genetic mean changes

- need to account for selection (evaluate jointly)
- calculate genetic trend from increase in EBV over years

EBV's without BLUP (within year)

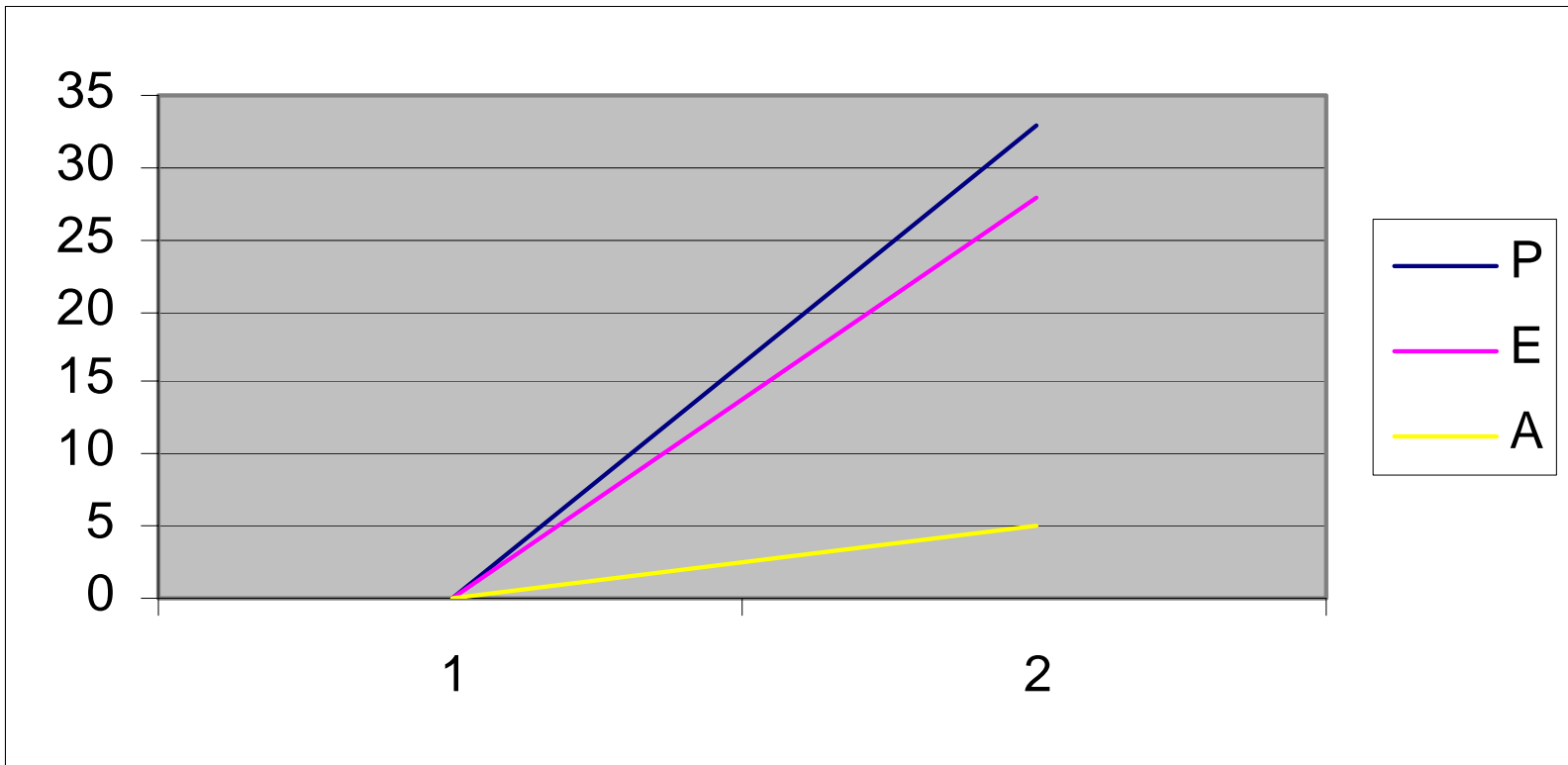
year		sire 1	sire 2	sire 3
1	300	350	300	250
		13	0	-13
		offspr. 1	offspr. 2	offspr. 3
2	333	365	325	310
		8	-2	-6

EBV's with BLUP (across year)

year		sire 1	sire 2	sire 3
1	300	350	300	250
		14	-2	-13
		↙	↓	↘
		offspr. 1	offspr. 2	offspr. 3
2	329	365	325	310
		13	5	-4

as years/generations go by, the genetic mean changes

- need to account for selection (evaluate jointly)
- calculate genetic trend from increase in EBV over years



BLUP allows to separate between environmental and

Genetic Trend

Simply as mean EBV's per year of birth

Genetic Properties of the animal model

- Numerator Relationships Matrix

NRM is constructed using recurrent rules

$$a_{ii} = (1 + F_i)$$

$$F_i = 0.5a_{sd}$$

$$a_{ij} = 0.5 a_{i,js} + 0.5 a_{i,jd} \quad \text{for } i \neq j$$

Consider a vector \mathbf{u} with additive genetic values

(breeding values)

$$\text{var}(\mathbf{u}) = \mathbf{A}\sigma_a^2$$

$$\mathbf{u}_p = .5\mathbf{u}_s + .5\mathbf{u}_d + \mathbf{m}_s$$

write \mathbf{u} as

$$\mathbf{u} = \mathbf{P} \mathbf{u} + \boldsymbol{\phi}$$

$$(\mathbf{I}-\mathbf{P}) \mathbf{u} = \boldsymbol{\phi}$$

$$\mathbf{u} = (\mathbf{I}-\mathbf{P})^{-1} \boldsymbol{\phi}$$

$$\begin{pmatrix} u_b \\ u_p \end{pmatrix} = \begin{pmatrix} 0 & 0 \\ P_{21} & P_{22} \end{pmatrix} \begin{pmatrix} u_b \\ u_p \end{pmatrix} + \begin{pmatrix} u_b \\ \phi \end{pmatrix}$$

BV's are linear function of independent genetic values!

See example!

$$\mathbf{u} = (\mathbf{I}-\mathbf{P})^{-1} \phi$$

$$\mathbf{u} = \mathbf{T} \phi$$

T describes the flow of genes

,

$$T = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0.5 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0.5 & 0.5 & 0 & 1 & 0 & 0 & 0 \\ 0.25 & 0.5 & 0.5 & 0 & 1 & 0 & 0 \\ .375 & .25 & .75 & 0 & .5 & 1 & 0 \\ .4375 & 0.125 & 0.875 & 0 & 0.25 & 0.5 & 1 \end{pmatrix}$$

$$\begin{aligned}
\mathbf{var}(\mathbf{u}) &= \mathbf{A} \\
&= (\mathbf{I}-\mathbf{P})^{-1} \mathbf{var}(\phi) (\mathbf{I}-\mathbf{P}')^{-1} \\
&= (\mathbf{I}-\mathbf{P})^{-1} \mathbf{D} (\mathbf{I}-\mathbf{P}')^{-1} \\
&= \mathbf{TDT}'
\end{aligned}$$

The matrix \mathbf{D} is a diagonal

$d_i=1$ if no parents are known,

$d_i= .75$ if one of the parents is known

$d_i= .5$ if both parents are known.

\mathbf{P} is a matrix with at most two elements of 0.5 in each row, one in the column for each parent

derive rules for A^{-1}

$$A^{-1} = [TDT']^{-1} = (I-P')D^{-1}(I-P)$$

Multiplication of $(I-P')$ and $(I-P)$ gives symmetric matrix

$$(I-P')(I-P) = I - (P + P') + P'P$$

1 on diagonal

-0.5 for a parent-progeny

0.25 between mates (and on parents diagonal)

Multiply with $d_i^{-1} = 1, 4/3$ or 2 [see example!](#)

Rules for A-inverse

pedigree knowledge:	element added to		value
<hr/>			
<i>no parents known</i>			
(i,0,0)	animals' diagonal	i,i	1.0
<i>one parent known</i>			
(i,j,0) or (i,0,k)	animals' diagonal	i,i	1.0 * 4/3
	parent-offspring off-diagonal	i,j and j,i or I,k and k,i	-0.5* 4/3
	parents' diagonal	j,j or k,k	0.25* 4/3
<i>two parents known</i>			
(i,j,k)	animals' diagonal	i,i	1.0 * 2
	parent-offspring off-diagonal	i,j; j,i; i,k and k,i	-0.5* 2
	parents' diagonal	j,j and k,k	0.25* 2
	mates' off-diagonal	j,k and k,j	0.25 * 2

Deriving rules for A-inverse in case of inbreeding

$$\begin{aligned}\text{var}(u) &= (1+F) && \text{is the diagonal for inbred animal} \\ &= \frac{1}{4} \text{var}(u_s) + \frac{1}{4} \text{var}(u_d) + \frac{1}{2} \text{cov}(u_s, u_d) + \text{var}(\phi)\end{aligned}$$

so that the within family variance is equal to

$$\begin{aligned}\text{var}(\phi) &= (1+F_i) - \frac{1}{4}(1+F_s) - \frac{1}{4}(1+F_d) - F_i \\ &= \frac{1}{2}(1 - \frac{1}{2}(F_s + F_d))\end{aligned}$$

MS term variance reduced if parents are inbred

Deriving rules for A-inverse in case of inbreeding

MS term variance reduced if parents are inbred

The diagonal for D becomes

$$d_i = 1 - 0.25a_{ss} - 0.25a_{dd} = \frac{1}{2}(1 - \frac{1}{2}(F_s + F_d))$$

And if only one parent known:

$$d_{ii} = 1 - 0.25a_{jj} = \frac{3}{4} - 0.25F_j$$

note that we need diagonal of A!

Further, rules are same as with no inbreeding

- 1** * d_{ii} on diagonal
- 0.5** * d_{ii} for a parent-progeny
- 0.25** * d_{ii} between mates (and on parents diagonal)

algorithms: Quaas, Tier et al., Meuwissen and Luo

Bulmer effect: Variance reduces after selection

(P-males=10%, P-females = 50%)

Gen	VA	V(sire)	V(dam)	Herit	Mean	R
1	1.000	0.584	0.682	0.500	0	0.902
2	0.817	0.511	0.583	0.450	0.902	0.773
3	0.774	0.493	0.559	0.436	1.676	0.741
4	0.763	0.488	0.553	0.433	2.417	0.733
5	0.760	0.487	0.552	0.432	3.151	0.731
6	0.759	0.487	0.551	0.432	3.882	0.731
7	0.759	0.487	0.551	0.432	4.613	0.730
8	0.759	0.487	0.551	0.432	5.344	0.730
9	0.759	0.486	0.551	0.432	6.075	0.730
10	0.759	0.486	0.551	0.432	6.806	0.730

Mixed models account for changes of variance due to gametic disequilibrium

Pearson's result gives the variance of a variable x after selection on a correlated variable y as

$$\begin{aligned}\sigma_{sx}^2 &= \sigma_x^2 - \text{cov}(x, y)^2 \sigma_y^{-2} (1 - (\sigma_{ys}^2 / \sigma_y^2)) \\ &= \sigma_x^2 - \text{cov}(x, y)^2 \sigma_y^{-2} \sigma_x^{-2} (1 - (1 - k)) \sigma_x^2 = \\ &= (1 - r^2 k) \sigma_x^2\end{aligned}$$

Using Pearson's result, we can write the genetic variance in a selected group (after mass selection) as $(1-h^2k)$

result also found by Bulmer (1971)

Henderson 1975 Kennedy & Sorenson 1988

if the base population is unselected, and the next generation descends from the best parents of the previous generation, than both generations can be evaluated in an unbiased fashion.

Although the 2nd generation animals are not random animals (but from selected parents), they are unselected within their families.

In statistical terms, the distribution (i.e. mean as well as variance) of the second generation conditional on the first generation is not affected by selection.

In quantitative genetic terminology, this conditional variance is equal to the within family variance, or the Mendelian sampling variance. The parental contributions are evaluated unbiasedly if their contemporaries that they were selected from are in the model

**Recall $A = TDT'$ where T describes
the flow of genes**

breeding values can be written as $a = T\phi$,

$$T = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0.5 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0.5 & 0.5 & 0 & 1 & 0 & 0 & 0 \\ 0.25 & 0.5 & 0.5 & 0 & 1 & 0 & 0 \\ .375 & .25 & .75 & 0 & .5 & 1 & 0 \\ .4375 & 0.125 & 0.875 & 0 & 0.25 & 0.5 & 1 \end{pmatrix}$$

**base population must be unselected
Mendelian sampling terms not affected by selection
then effects of linkage disequilibrium and
inbreeding are accommodated**

Which variance is to be used?

'base population' variance

variance in later generation t

**but we are mainly interested in the variation in
each generation generated by Mendelian
Sampling**

both variances are valid!

Is base really unselected?

Genetic groups

- Consider them as fixed effect in the model
- But add those to breeding values.....
- **$EBV_{\text{across}} = EBV_{\text{within}} + \text{group_solution}$**
- Grouping needed whenever there is a **genetic** difference in base animals
 - (to account for selection: breeds, origin,....)
- Only need to group the unknown parents
 - Remember that relationships matrix accounts for other selection

Example of genetic groups

Michael Angus	315	Mean Angus	300
Whiskey Hereford	315	Mean Hereford	320

	<u>EBV_{within}</u>	<u>EBV_{across}</u>
Michael Angus	+ 6	+ 6
Whiskey Hereford	- 2	+ 18

The mixed model including grouping would now be

$$\mathbf{y} = \mathbf{Xb} + \mathbf{ZQg} + \mathbf{Za}^* + \mathbf{e}$$

$$\mathbf{a} = \mathbf{Qg} + \mathbf{a}^*$$

$$\begin{bmatrix} \mathbf{X}'\mathbf{X} & \mathbf{X}'\mathbf{ZQ} & \mathbf{X}'\mathbf{Z} \\ \mathbf{Q}'\mathbf{Z}'\mathbf{X} & \mathbf{Q}'\mathbf{Z}'\mathbf{ZQ} & \mathbf{Q}'\mathbf{Z}'\mathbf{Z} \\ \mathbf{Z}'\mathbf{X} & \mathbf{Z}'\mathbf{ZQ} & \mathbf{Z}'\mathbf{Z} + \alpha \mathbf{A}^{-1} \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{g} \\ \mathbf{a}^* \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{y} \\ \mathbf{Q}'\mathbf{Z}'\mathbf{y} \\ \mathbf{Z}'\mathbf{y} \end{bmatrix}$$

Modified Equations

$$\begin{bmatrix} X'X & 0 & X'Z \\ 0 & \alpha Q'A^{-1}Q & -\alpha Q'A^{-1} \\ Z'X & -\alpha A^{-1}Q & Z'Z + \alpha A^{-1} \end{bmatrix} \begin{bmatrix} b \\ g \\ a \end{bmatrix} = \begin{bmatrix} X'y \\ 0 \\ Z'y \end{bmatrix}$$

Can use rules for A-inverse to form the grouping equations

Groups are 'phantom parents'

Rules for pedigree with groups

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

Then add:

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

Calf	Sire	Dam
1	unknown	unknown
2	unknown	unknown
3	unknown	unknown
4	1	unknown
5	3	2
6	1	2
7	4	5
8	3	6

Calf	Sire	Dam
1	G1	G2
2	G1	G2
3	G1	G2
4	1	G2
5	3	2
6	1	2
7	4	5
8	3	6

The flow of genes is described

	G1	G2	A1	A2			
$T =$	1	0	0	0	0	0	0
	0	1	0	0	0	0	0
	0.5	0	1	0	0	0	0
	0.5	0.5	0	1	0	0	0
	0.25	0.5	0.5	0	1	0	0
	.375	.25	.75	0	.5	1	0
	.4375	0.125	0.875	0	0.25	0.5	1

Conclusion on across breed evaluations

- First have first moments correct
 - grouping/fixed effects/heterosis etc
- Then worry about second moments
 - Variance if pure- and crossbreds