

OHP Picture 1

Recap  
Predictions of breeding values using  
Linear Mixed Effect Models (LME).

□ Model:  $y = X\beta + Z\underline{u} + \underline{e}$

$y$ : observations  
 $\beta$ : fixed effects  
 $\underline{u}$ : random effects  $\rightarrow$  breeding values  
 $\underline{e}$ : random residuals

□ Example: Sire Model  $\rightarrow$  Dairy Cattle  
- Replaced  $\underline{u}$  by  $\underline{s}$  ( $y = X\beta + Z\underline{s} + \underline{e}$ )

$y = X\beta + Z\underline{u}_s + \underline{e}$   
vector of breeding values for sires

⊕ Estimate fixed effects and predict breeding values for sires, simultaneously  
⊖ Dams do not get breeding values.

## □ Animal Model

- The problem with the sire model that only sires get predicted breeding values is solved with the animal model

- LME:

$$y = X\beta + Z\underline{u} + \underline{e}$$

breeding values for all animals

- Expectations and Variance-Covariances

$$E(\underline{y}) = \underline{0} ; E(\underline{e}) = \underline{0} ; E(\underline{y}) = X\beta$$

$$\text{var}(\underline{e}) = R = I \cdot \sigma_e^2$$

$$\text{var}(\underline{u}) = G = A \cdot \sigma_u^2$$

$$\text{var}(\underline{y}) = ZGZ^T + R$$

↳ numerator relationship matrix

OHP Picture 3

| Animal | Herd                  | Sire |
|--------|-----------------------|------|
| 3      | 1 → herd <sub>1</sub> | 1    |
| 4      | 2 → herd <sub>2</sub> | NA   |
| 5      | 2                     | 4    |
| 6      | 1                     | 5    |

} 2 herds

$$\begin{matrix} y \\ \rightarrow \begin{bmatrix} 4.5 \\ 2.9 \\ 3.9 \\ 3.5 \end{bmatrix} \end{matrix}$$

$$=$$

$$\begin{matrix} \text{herd}_1 & \text{herd}_2 \\ \begin{bmatrix} 1 & 0 \\ 0 & 1 \\ 0 & 1 \\ 1 & 0 \end{bmatrix} \end{matrix}$$

$$\beta \begin{bmatrix} \text{herd}_1 \\ \text{herd}_2 \end{bmatrix}$$

$$+$$

$$\begin{matrix} \mathcal{U} \\ \begin{bmatrix} 1 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix} \end{matrix}$$

$$\begin{matrix} U_s \\ \begin{bmatrix} U_1 \\ U_4 \\ U_5 \end{bmatrix} \end{matrix}$$

Solutions for estimate  $\hat{\beta}$  of fixed herd effect  $\beta$  and predictions  $\hat{U}_s$  for sire breeding values by Mixed Model Equations.

Mixed Model Equations (MME) :

$$\begin{bmatrix} X^T X & X^T Z \\ Z^T X & Z^T Z + I \end{bmatrix} \begin{bmatrix} \hat{\beta} \\ \hat{u}_s \end{bmatrix} = \begin{bmatrix} X^T y \\ Z^T y \end{bmatrix}$$

Annotations:
 

- mat\_x1x:  $X^T X$
- mat\_x1z:  $X^T Z$
- mat\_z1x:  $Z^T X$
- mat\_z1z:  $Z^T Z + I$
- right-hand side:  $\begin{bmatrix} X^T y \\ Z^T y \end{bmatrix}$
- var(e) =  $R = I \cdot \sigma_e^2$
- var(u<sub>s</sub>) =  $G = I \cdot \sigma_{u_s}^2$
- σ<sub>e</sub><sup>2</sup> / σ<sub>u<sub>s</sub></sub><sup>2</sup>
- λ = 1
- C:  $\begin{bmatrix} X^T X & X^T Z \\ Z^T X & Z^T Z + I \end{bmatrix}$
- â = r

Goal:  $\hat{a}$  as a solution to  $C \cdot \hat{a} = r$

- Multiply by  $C^{-1}$ :  $C^{-1} C \cdot \hat{a} = C^{-1} r$
- $\hat{a} = C^{-1} r$
- solve(mat\_C, mat\_R)

$$(X^T Z)^T = Z^T (X^T)^T = Z^T X$$

$$C^{-1} = \text{solve}(\text{mat}_C)$$

$$\text{mat}_a\_hat \leftarrow \text{solve}(\text{mat}_C) \%*\% \text{mat}_R$$


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Example II:  $y = X\beta + Zu_s + e$

$E(e) = \underline{0}$ ,  $E(u_s) = \underline{0}$ ,  $E(y) = X\beta$

Example II:

$$y = X\beta + Zu_3 + e$$

$E(e) = \underline{0}$ ,  $E(u_3) = \underline{0}$ ,  $E(y) = X\beta$

$\text{Var}(e) = R = I \cdot \sigma_e^2$

$\text{Var}(u_3) = \begin{bmatrix} \text{var}(u_1) & \text{cov}(u_1, u_4) & \text{cov}(u_1, u_5) \\ \text{cov}(u_1, u_4) & \text{var}(u_4) & \text{cov}(u_4, u_5) \\ \text{cov}(u_5, u_1) & \text{cov}(u_5, u_4) & \text{var}(u_5) \end{bmatrix} = G$

$u_3 = \begin{bmatrix} u_1 \\ u_4 \\ u_5 \end{bmatrix}$

$\rightarrow \neq 0$  because set is the father of 4

$$= \begin{bmatrix} \sigma_u^2 & \frac{1}{2} \sigma_u^2 & \frac{1}{4} \sigma_u^2 \\ \frac{1}{2} \sigma_u^2 & \sigma_u^2 & \frac{1}{2} \sigma_u^2 \\ \frac{1}{4} \sigma_u^2 & \frac{1}{2} \sigma_u^2 & \sigma_{u_5}^2 \end{bmatrix}$$

$u_i = \frac{1}{2} u_3 + \frac{1}{2} u_4 + w_i$

For sire model:  $u_4 = \frac{1}{2} u_1 + w_4$

$\text{cov}(u_1, u_4) = \text{cov}(u_1, \frac{1}{2} u_1 + w_4^*) = 0$

$= \text{cov}(u_1, \frac{1}{2} u_1) + \text{cov}(u_1, w_4^*)$

$= \frac{1}{2} \text{cov}(u_1, u_1) = \frac{1}{2} \sigma_u^2$

Animal Model:

- LME
- random vector  $\underline{u}$  contains breeding values for all animals in the pedigree
- fixed effects, the same as for sire model

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|        |                                     |     |  |  |     |   |     |  |
|--------|-------------------------------------|-----|--|--|-----|---|-----|--|
| Animal | $\underline{y}$                     | $=$ | $X$  | $\beta$  | $+$ | $\underline{u}$   | $+$ | $\underline{e}$  |
| 3      | $\begin{bmatrix} 4.5 \end{bmatrix}$ |     | $\begin{bmatrix} 1 & 0 \\ 0 & 1 \\ 0 & 1 \\ 1 & 0 \end{bmatrix}$ | $\begin{bmatrix} \text{head} \\ \text{nose} \\ \vdots \end{bmatrix}$ |     | $\begin{bmatrix} u_1 & u_2 & u_3 & u_4 & u_5 & u_6 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$ |     | $\begin{bmatrix} u \\ u_1 \\ u_2 \\ u_3 \\ u_4 \\ u_5 \\ u_6 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ e_3 \\ e_4 \end{bmatrix}$ |

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Solutions from Mixed Model Equations

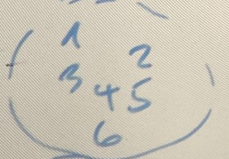
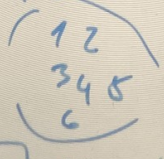
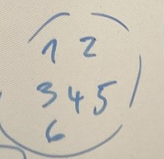
Solutions from Mixed Model Equations

$$R = I \cdot \sigma_e^2 ; G$$

$$\begin{bmatrix} X^T X & X^T Z \\ Z^T X & Z^T Z + G^{-1} \end{bmatrix} \begin{bmatrix} \hat{\beta} \\ \hat{u} \end{bmatrix} = \begin{bmatrix} X^T y \\ Z^T y \end{bmatrix}$$

$$G_{6 \times 6} = \text{var}(\underline{u}) = \begin{bmatrix} \text{var}(u_1) & \text{cov}(u_1, u_2) & \dots & \text{cov}(u_1, u_6) \\ \text{cov}(u_2, u_1) & \text{var}(u_2) & \dots & \text{cov}(u_2, u_6) \\ \vdots & \vdots & \ddots & \vdots \\ \vdots & \vdots & \vdots & \text{var}(u_6) \end{bmatrix}$$

\* Source of  $\text{var}(u_i)$  and  $\text{cov}(u_i, u_j)$  is based on the so-called "large-sampling" concept

| Universe 1  | Universe 2  | Universe 3   |
|---|---|--|
| Population  | Population  |  |
|  |  |  |
| $u_1, u_2, u_3, u_4, \dots$   | $u_1, u_2, \dots, u_6$  | $u_1, u_2, \dots, u_6$   |
|   |   | $E(u_2) = 0; \text{var}(u_2)$  |

$\rightarrow u_i$  are random variable with given expectation and variance

For animal  $i$ :  $E(u_i) = 0$

$\text{var}(u_i) = (1 + F_i) \sigma_u^2$

• Inbreeding coefficient of animal  $i$

•  $F_i = \frac{1}{2} A_{sd}$   
 where  $A_{sd}$  is the relationship between parent's and  $d$

$G = \text{var}(u)$

$$= \begin{bmatrix} \text{var}(u_1) & \text{cov}(u_1, u_2) & \text{cov}(u_1, u_3) & \text{cov}(u_1, u_6) \\ \text{cov}(u_2, u_1) & \text{var}(u_2) & & \\ & & & \\ & & & \end{bmatrix}$$

$$= \begin{bmatrix} (1+F_1) \sigma_u^2 & 0 & \frac{1}{2} \sigma_u^2 & \frac{1}{2} \sigma_u^2 \\ & (1+F_2) \sigma_u^2 & & \\ & & & \\ & & & \end{bmatrix}$$

$\text{cov}(u_1, u_2) = 0$ , because animals 1 and 2 do not share common ancestors

$$\begin{aligned} \text{cov}(u_1, u_3) &= \text{cov}(u_1, \frac{1}{2} u_1 + \frac{1}{2} u_2 + m_3) \\ &= \text{cov}(u_1, \frac{1}{2} u_1) + \text{cov}(u_1, \frac{1}{2} u_2) + \text{cov}(u_1, m_3) \\ &= \frac{1}{2} \text{cov}(u_1, u_1) + \frac{1}{2} \text{cov}(u_1, u_2) \\ &= \frac{1}{2} \text{var}(u_1) = \frac{1}{2} \sigma_u^2 \end{aligned}$$



OHP Picture 9

$$G = \begin{bmatrix} 1+F_1 & 0 & 1/2 & 1/2 & \dots \\ \vdots & \vdots & \vdots & \vdots & \vdots \end{bmatrix} \cdot \sigma_u^2$$

$G = A \cdot \sigma_u^2$  used in animal model

$A \rightarrow$  numerator relationship matrix

For Mixed Model Equations, we need  $G^{-1}$

$$G^{-1} = (A \cdot \sigma_u^2)^{-1} = A^{-1} \cdot \sigma_u^{-2}$$

$$\begin{bmatrix} X^T X & X^T Z \\ Z^T X & Z^T Z + A^{-1} \lambda \end{bmatrix} \begin{bmatrix} \hat{\beta} \\ \hat{u} \end{bmatrix} = \begin{bmatrix} X^T y \\ Z^T y \end{bmatrix}$$

$$\lambda = \sigma_e^2 / \sigma_u^2$$

Compute Numerator Relationship Matrix A

Background:  $\text{var}(y) = G = A \cdot \sigma_u^2$

## Compute Numerator Relationship Matrix A

Background:  $\text{var}(\underline{y}) = G = A \cdot \sigma_u^2$

- Diagonal elements of A:

$$(A)_{ii} = (1 + F_i) \text{ with } F_i = \frac{1}{2}(A)_{sd}$$

- Off diagonal:  $(A)_{ij} = \frac{\text{cov}(u_i, u_j)}{\sigma_u^2}$

### Receipts to compute A based on given pedigree:

- Step 1: Complete all animals in pedigree  
Result: Pedigree must be sorted such that parents are before offspring (topological sort)

|   |    |    |
|---|----|----|
| 3 | 1  | 2  |
| 4 | 1  | NA |
| 5 | 4  | 3  |
| 6 | 5  | 2  |
| 1 | NA | NA |
| 2 | NA | NA |

} in valid order

• Step 2: Empty Matrix A: square  
 Dimension is the number of animals  
 in pedigree  
 $A_{6 \times 6}$

|   |   |   |               |               |   |   |
|---|---|---|---------------|---------------|---|---|
|   | 1 | 2 | 3             | 4             | 5 | 6 |
| 1 | 1 | 0 | $\frac{1}{2}$ | $\frac{1}{2}$ |   |   |
| 2 |   |   |               |               |   |   |
| 3 |   |   |               |               |   |   |
| 4 |   |   |               |               |   |   |
| 5 |   |   |               |               |   |   |
| 6 |   |   |               |               |   |   |

Arrows point from the 1 in row 1, column 2 to the 0 in row 2, column 1, labeled  $(A)_{12}$ .  
 An arrow points from the 0 in row 2, column 1 to the 1 in row 1, column 1, labeled  $(A)_{11}$ .

• Step 3: Diagonal element  $(A)_{11} = 1 + F_1 = 1$   
 Because animal 1 has unknown parents  
 $F_1 = 0$

• Step 4: Off-diagonal:  
 $(A)_{12} = \frac{1}{2} [(A)_{1,1NA} + (A)_{1,2NA}] = 0$   
 $(A)_{13} = \frac{1}{2} [(A)_{1,1} + (A)_{1,2}]$   
 $= \frac{1}{2} [1 + 0] = \frac{1}{2}$   
 $(A)_{14} = \frac{1}{2} [(A)_{1,1} + (A)_{1,2NA}] = \frac{1}{2}$

• Step 5: Copy first row into first column

OHP Picture 12

Step 5: Copy first row into first column

$$A = \begin{bmatrix} 1 & 0 & \frac{1}{2} & \frac{1}{2} & \frac{1}{2} & \frac{1}{4} \\ 0 & \square & \square & \square & \square & \square \\ \frac{1}{2} & & & & & \\ \frac{1}{2} & & & & & \\ \frac{1}{2} & & & & & \\ \frac{1}{4} & & & & & \end{bmatrix}$$