BLUP

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Recap: Linear Mixed Effects Model

$$y = X \cdot b + Z \cdot u + e$$

where

y	vector of phenotypic observations of all animals
b	vector of unknown fixed effects and unknown regression coefficients
u	vector of random breeding values of all animals
e	vector of random environmental effects
X	design matrix with regression covariates or indicator values for fixed effects
Z	design matrix relating breeding values to observations

Solution - BLUP

- Solution to correction problem in selection index: BLUP
- Estimates environmental effects at the same time as breeding values are predicted
- Linear mixed effects model
- Meaning of BLUP
  - **B** stands for **best** $\rightarrow$ correlation between true (u) and its prediction ($\hat{u}$) is maximal or the prediction error variance ($var(u - \hat{u})$) is minimal.
  - **L** stands for **linear** $\rightarrow$ predicted breeding values are linear functions of the observations (y)
  - **U** stands for **unbiased** $\rightarrow$ expected values of the predicted breeding values are equal to the true breeding values
  - **P** stands for **prediction**

Example Dataset I

Animal	Sire	Dam	Herd	Weaning Weight	Breast Circumference
14	1	5	1	2.44	1.48
15	1	5	1	2.41	1.47
16	1	6	2	2.51	1.50
17	1	6	2	2.55	1.47
20	2	8	1	2.34	1.46
21	2	8	1	1.99	1.38

Example Dataset II

Animal	Sire	Dam	Herd	Weaning Weight
12	1	4	1	2.61
13	1	4	1	2.31
14	1	5	1	2.44
15	1	5	1	2.41
16	1	6	2	2.51
17	1	6	2	2.55
18	1	7	2	2.14
19	1	7	2	2.61
20	2	8	1	2.34
21	2	8	1	1.99
22	2	9	1	3.10
23	2	9	1	2.81
24	2	10	2	2.14
25	2	10	2	2.41
26	3	11	2	2.54
27	3	11	2	3.16

Linear Models

- Simple linear model

$$y_{ij} = \mu + herd_j + e_{ij}$$

- Result: Estimate of effect of herd j
- Try with given dataset

Linear Mixed Effects Model

- What about breeding value u_i for animal i?
  - Problem: breeding values have a variance σ_u^2 and co-variances
  - Cannot be specified in simple linear model

$\rightarrow$ **Linear Mixed Effects Model** (LME)

$$y_{ijk} = \mu + \beta_j + u_i + e_{ijk}$$

Matrix-Vector Notation

- LME for all animals of a population

$\rightarrow$ use matrix-vector notation

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

where

y	vector of length n of all observations
β	vector of length p of all fixed effects
X	$n \times p$ design matrix linking the fixed effects to the observations
u	vector of length n_u of random effects
Z	$n \times n_u$ design matrix linking random effect to the observations
e	vector of length n of random residual effects.

Expected Values and Variances

- Expected values

$$E(u) = 0 \text{ and } E(e) = 0 \rightarrow E(y) = X\beta$$

- Variances

$$var(u) = U \text{ and } var(e) = R$$

with $cov(u, e^T) = 0$,

$$var(y) = Z * var(u) * Z^T + var(e) = ZUZ^T + R = V$$

Estimates of unknown Parameters

Use properties of BLUP to design predictor $\widehat{u}$

- Linear: predictor $\widehat{u}$ is a linear function of data

$$\widehat{u} = M \cdot (y - k)$$

- Unbiased: $E(\widehat{u}) = E(u)$. Above we have specified $E(u) = 0$

$$k = E(y)$$

- Best: Prediction error variance $var(u - \widehat{u})$ is minimal

$$M = UZ^T V^{-1}$$

Result

- Summary of above results, using $E(y) = X\beta$

$$\hat{u} = UZ^T V^{-1}(y - X\beta)$$

- For u and y following a Gaussian normal distribution

$$\hat{u} = E(u|y)$$

- β unknown, replace it by general least squares estimate

$$\hat{\beta} = (X^T V^{-1} X)^{-} X^T V^{-1} y$$

Mixed Model Equations

- Problem: V^{-1}
- Same solutions obtained with following set of equations

$$\left[\begin{array}{lr} X^T R^{-1} X & X^T R^{-1} Z \\ Z^T R^{-1} X & Z^T R^{-1} Z + U^{-1} \end{array}\right] \left[\begin{array}{c} \hat{\beta} \\ \hat{u} \end{array}\right] = \left[\begin{array}{c} X^T R^{-1} y \\ Z^T R^{-1} y \end{array}\right]$$

Sire Model

- Breeding value of sire as random effect:

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

* Expected values

$$E(s) = 0 \text{ and } E(e) = 0 \to E(y) = X\beta$$

- Variances

$$var(s) = U_s \text{ and } var(e) = R$$

- Unrelated sires: $var(s) = U_s = I\sigma_s^2$

Example

$$\begin{bmatrix} 2.61 \\ 2.31 \\ 2.44 \\ 2.41 \\ 2.51 \\ 2.55 \\ 2.14 \\ 2.61 \\ 2.34 \\ 1.99 \\ 3.1 \\ 2.81 \\ 2.14 \\ 2.41 \\ 2.54 \\ 3.16 \end{bmatrix} = \begin{bmatrix} 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 0 & 1 \\ 0 & 1 \\ 0 & 1 \\ 0 & 1 \\ 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 0 & 1 \\ 0 & 1 \\ 0 & 1 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} \beta_1 \\ \beta_2 \end{bmatrix} + \begin{bmatrix} 1 & 0 & 0 \\ 1 & 0 & 0 \\ 1 & 0 & 0 \\ 1 & 0 & 0 \\ 1 & 0 & 0 \\ 1 & 0 & 0 \\ 1 & 0 & 0 \\ 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 1 & 0 \\ 0 & 1 & 0 \\ 0 & 1 & 0 \\ 0 & 1 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \\ 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} s_1 \\ s_2 \\ s_3 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ e_3 \\ e_4 \\ e_5 \\ e_6 \\ e_7 \\ e_8 \\ e_9 \\ e_{10} \\ e_{11} \\ e_{12} \\ e_{13} \\ e_{14} \\ e_{15} \\ e_{16} \end{bmatrix}$$

Animal Model

- Breeding value for all animals as random effects

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

- Expected values

$$E(u) = 0 \text{ and } E(e) = 0 \rightarrow E(y) = X\beta$$

- Variances

$$var(u) = U = A * \sigma_u^2 \text{ and } var(e) = R$$

- Matrix A: numerator relationship matrix and σ_u^2 the genetic additive variance