BLUP properties

• Correction for mates and selection over generations.
• Allows estimation of genetic trend
• Selection across age classes
• Accuracy and linkage between herds/CGs
• BLUP and inbreeding
## Properties of BLUP solutions

<table>
<thead>
<tr>
<th>Solutions</th>
<th>Accuracy</th>
</tr>
</thead>
<tbody>
<tr>
<td>311.94</td>
<td></td>
</tr>
<tr>
<td>-9.15</td>
<td>0.54</td>
</tr>
<tr>
<td>-8.90</td>
<td></td>
</tr>
<tr>
<td>28.26</td>
<td>0.54</td>
</tr>
<tr>
<td>-28.85</td>
<td>0.56</td>
</tr>
<tr>
<td>18.34</td>
<td>0.56</td>
</tr>
<tr>
<td>18.77</td>
<td>0.56</td>
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<tr>
<td>-0.87</td>
<td>0.50</td>
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<tr>
<td>-22.40</td>
<td>0.58</td>
</tr>
<tr>
<td>0.00</td>
<td>0.00</td>
</tr>
</tbody>
</table>

EBV of animals 1 and 2 are zero – on average

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

BLUP provides genetic trend
Possible bias in genetic evaluation:
Some sires have better mates

<table>
<thead>
<tr>
<th>Sire 1</th>
<th>Dam 1</th>
<th>Sire 2</th>
<th>Dam2</th>
</tr>
</thead>
<tbody>
<tr>
<td>300</td>
<td>200</td>
<td>300</td>
<td>300</td>
</tr>
<tr>
<td>250</td>
<td></td>
<td>275</td>
<td></td>
</tr>
</tbody>
</table>

Blup accounts for this (see next)

Need to evaluate all animals jointly
Possible bias in genetic evaluation: Animals are from selected parents

<table>
<thead>
<tr>
<th>year</th>
<th>sire 1</th>
<th>sire 2</th>
<th>sire 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>350</td>
<td>300</td>
<td>250</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>offspr. 1</td>
<td>offspr. 2</td>
<td>offspr. 3</td>
</tr>
<tr>
<td>2</td>
<td>365</td>
<td>325</td>
<td>310</td>
</tr>
</tbody>
</table>

As years/generations go by, the genetic mean changes. Blup accounts for this (see next)

• Need to account for selection (evaluate jointly)
• Calculate genetic trend from increase in EBV over years
Properties of BLUP
how are individual EBV’s estimated?

• Look at equations for individual animals
\[
\begin{pmatrix}
7 & 1 & 3 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\
1 & 3 & 1 & 1 & 1 & 0 & 0 & 0 & 0 & -1 \\
3 & 1 & 5 & 0 & 0 & 1 & 1 & 1 & 1 & -1 \\
1 & 1 & 5 & \frac{19}{6} & \frac{1}{2} & -\frac{2}{3} & -\frac{2}{3} & -1 & 0 & 0 \\
1 & 1 & 0 & \frac{1}{2} & \frac{17}{6} & 0 & 0 & 0 & -\frac{2}{3} & 0 \\
1 & 0 & 0 & -\frac{2}{3} & 0 & \frac{7}{3} & 0 & 0 & 0 & 0 \\
1 & 0 & 1 & -\frac{2}{3} & 0 & 0 & \frac{7}{3} & 0 & 0 & 0 \\
1 & 0 & 1 & -1 & 1 & 0 & 0 & 3 & 0 & 0 \\
1 & 0 & 1 & 0 & -\frac{2}{3} & 0 & 0 & 0 & \frac{7}{3} & 0 \\
1 & -1 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 2 \\
\end{pmatrix}
\begin{pmatrix}
\mu \\
b_{1990} \\
b_{1991} \\
\hat{u}_1 \\
\hat{u}_2 \\
\hat{u}_3 \\
\hat{u}_4 \\
\hat{u}_5 \\
\hat{u}_6 \\
\hat{u}_7 \\
\end{pmatrix} =
\begin{pmatrix}
2161 \\
275 \\
896 \\
354 \\
251 \\
327 \\
328 \\
301 \\
270 \\
330 \\
\end{pmatrix}
\]

Look at animal 6

\[
\mu + b_{1991} - \frac{2}{3} \hat{u}_2 + \frac{7}{3} \hat{u}_6 = 270
\]
Look at animal 6

\[
\mu + b_{1991} - \frac{2}{3} \hat{u}_2 + \frac{7}{3} \hat{u}_6 = 270
\]

\[
\hat{u}_6 = \frac{3}{7} (270 - \mu - b_{1991}) + \frac{2}{7} \hat{u}_2
\]

Selection index weight:
\[
\frac{3}{4} VA / (\frac{3}{4} VA + VE)
\]

This is own performance as deviation from expected, given its sire

This comes from sire
\[
\begin{pmatrix}
7 & 1 & 3 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\
1 & 3 & 1 & 1 & 1 & 0 & 0 & 0 & 0 & -1 \\
3 & 1 & 5 & 0 & 0 & 1 & 1 & 1 & 1 & -1 \\
1 & 1 & 5 & \frac{19}{6} & \frac{1}{2} & -\frac{2}{3} & -\frac{2}{3} & -1 & 0 & 0 \\
1 & 1 & 0 & \frac{1}{2} & \frac{17}{6} & 0 & 0 & 0 & -\frac{2}{3} & 0 \\
1 & 0 & 0 & -\frac{2}{3} & 0 & \frac{7}{3} & 0 & 0 & 0 & 0 \\
1 & 0 & 1 & -\frac{2}{3} & 0 & 0 & \frac{7}{3} & 0 & 0 & 0 \\
1 & 0 & 1 & -1 & 1 & 0 & 0 & 3 & 0 & 0 \\
1 & 0 & 1 & 0 & -\frac{2}{3} & 0 & 0 & 0 & \frac{7}{3} & 0 \\
1 & -1 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 2
\end{pmatrix}
\begin{pmatrix}
\mu \\
{b_{1990}} \\
{b_{1991}} \\
\hat{u}_1 \\
\hat{u}_2 \\
\hat{u}_3 \\
\hat{u}_4 \\
\hat{u}_5 \\
\hat{u}_6 \\
\hat{u}_7
\end{pmatrix}
= \begin{pmatrix}
2161 \\
275 \\
896 \\
354 \\
251 \\
327 \\
328 \\
301 \\
270 \\
330
\end{pmatrix}
\]

Look at animal 5

\[\mu + b_{1991} - \hat{u}_1 - \hat{u}_2 + 3\hat{u}_5 = 301\]
For animal 5

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

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

This is own performance as deviation from expected, given its sire and dam

Mean of parents

Selection index weight:

\[ \frac{1}{2} VA / (\frac{1}{2} VA + VE) \]
\[
\begin{pmatrix}
7 & 1 & 3 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\
1 & 3 & 1 & 1 & 1 & 0 & 0 & 0 & 0 & -1 \\
3 & 1 & 5 & 0 & 0 & 1 & 1 & 1 & 1 & -1 \\
1 & 1 & 5 & \frac{19}{6} & \frac{1}{2} & -\frac{2}{3} & -\frac{2}{3} & -1 & 0 & 0 \\
1 & 1 & 0 & \frac{1}{2} & \frac{17}{6} & 0 & 0 & 0 & -\frac{2}{3} & 0 \\
1 & 0 & 0 & -\frac{2}{3} & 0 & \frac{7}{3} & 0 & 0 & 0 & 0 \\
1 & 0 & 1 & -\frac{2}{3} & 0 & 0 & \frac{7}{3} & 0 & 0 & 0 \\
1 & 0 & 1 & -1 & 1 & 0 & 0 & 3 & 0 & 0 \\
1 & 0 & 1 & 0 & -\frac{2}{3} & 0 & 0 & 0 & \frac{7}{3} & 0 \\
1 & -1 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 2
\end{pmatrix}
\begin{pmatrix}
\mu \\
b_{1990} \\
b_{1991} \\
\hat{u}_1 \\
\hat{u}_2 \\
\hat{u}_3 \\
\hat{u}_4 \\
\hat{u}_5 \\
\hat{u}_6 \\
\hat{u}_7
\end{pmatrix}
= \begin{pmatrix}
2161 \\
275 \\
896 \\
354 \\
251 \\
327 \\
328 \\
301 \\
270 \\
330
\end{pmatrix}
\]

Look at animal 2

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

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

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

This is own performance as deviation from expected,

Prog 1, corrected for dam

Prog 2, no dam

Parents themselves estimated based on:

- own record
- progeny records
- correction for mates

Weights are same as in selection index. BLUP accounts for selection!!
### Possible bias in genetic evaluation:

Animals are from selected parents

<table>
<thead>
<tr>
<th>Year</th>
<th>Sire 1</th>
<th>Sire 2</th>
<th>Sire 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>350</td>
<td>300</td>
<td>250</td>
</tr>
<tr>
<td>2</td>
<td>365</td>
<td>325</td>
<td>310</td>
</tr>
</tbody>
</table>

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
<table>
<thead>
<tr>
<th>year</th>
<th>sire 1</th>
<th>sire 2</th>
<th>sire 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>300</td>
<td>350</td>
<td>300</td>
</tr>
<tr>
<td></td>
<td>13</td>
<td>0</td>
<td>-13</td>
</tr>
<tr>
<td>2</td>
<td>333</td>
<td>365</td>
<td>325</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>-2</td>
<td>-6</td>
</tr>
</tbody>
</table>

EBV’s without BLUP (within year)
EBV’s with BLUP (across year)

<table>
<thead>
<tr>
<th>year</th>
<th>sire 1</th>
<th>sire 2</th>
<th>sire 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>300</td>
<td>350</td>
<td>300</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>250</td>
</tr>
<tr>
<td></td>
<td></td>
<td>14</td>
<td>-2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>-13</td>
</tr>
<tr>
<td></td>
<td>offspr. 1 offspr. 2 offspr. 3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>329</td>
<td>365</td>
<td>325</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>310</td>
</tr>
<tr>
<td></td>
<td></td>
<td>13</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>-4</td>
</tr>
</tbody>
</table>

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
Optimizing Generation Interval

- Dilemma between young and old sires
Genetic Evaluation helps

BLUP EBV Optimizes generation interval

- Dilemma between young and old sires
BLUP and Inbreeding

BLUP uses family information
→ co-selection of relatives
→ more inbreeding
  loss of variance
  and inbreeding depression

• Does it balance out increased accuracy?
## Simulation:

### Selection on INDidual performance vs selection on BLUP

<table>
<thead>
<tr>
<th>Heritability</th>
<th>Year</th>
<th>Merit genetic merit</th>
<th></th>
<th></th>
<th></th>
<th>Inbreeding</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>IND</td>
<td>BLUP</td>
<td>BLUP/IND</td>
<td>IND</td>
<td>BLUP</td>
</tr>
<tr>
<td>0.1</td>
<td>5</td>
<td>0.38</td>
<td>0.63</td>
<td>1.66</td>
<td>0.067</td>
<td>0.167</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>0.78</td>
<td>1.41</td>
<td>1.81</td>
<td>0.174</td>
<td>0.383</td>
</tr>
<tr>
<td>0.3</td>
<td>5</td>
<td>1.1</td>
<td>1.41</td>
<td>1.28</td>
<td>0.078</td>
<td>0.141</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>2.4</td>
<td>3.14</td>
<td>1.31</td>
<td>0.193</td>
<td>0.332</td>
</tr>
<tr>
<td>0.6</td>
<td>5</td>
<td>2.25</td>
<td>2.29</td>
<td>1.02</td>
<td>0.087</td>
<td>0.13</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>5.16</td>
<td>5.31</td>
<td>1.03</td>
<td>0.205</td>
<td>0.293</td>
</tr>
</tbody>
</table>

1. BLUP more response than phenotypic selection (IND)
   
   *Difference is larger for smaller heritability.*

2. BLUP more inbreeding
   
   *Especially for low heritabilities*

3. BLUP still better after 10 years (???)
Advantages BLUP EBVs

- Optimal weights for all information sources

- **Flexible:** Lots of different sets exist of optimal weighting factors, BLUP does it automatically

- Allows comparisons of EBV’s of animals in different herd (possibly with different genetic means)
  - *But links need to exist in the data!*

- Accounts for culling and selection, non-random mating
  - *But non selected animals need to be included in analysis!*

- Allows selection across age classes

- Provides an estimate of genetic trend
Consequences of BLUP selection

- Maximize genetic response in next generation

- Can compare animals over age classes → BLUP optimises generation interval

- Tend to select more related animals the more so with lower heritability → BLUP leads to more inbreeding

- Optimal selection uses BLUP + restricted inbreeding (but by how much?)

- BLUP only optimises next generation merit!
Accuracy of BLUP EBV’s

The accuracy of an EBV depends on:

‘the amount of information used’

own info / relatives

The value of information (say a phenotype) depends on

1) the heritability,
2) the additive genetic relationship
3) the genetic correlation
4) the effective number of records.
How is **Accuracy** \((r)\) of BLUP-EBV's calculated?

- Use *inverse* of coefficient matrix of mixed model equations
  \[
  \begin{pmatrix}
  X'X & X'Z \\
  Z'X & Z'Z + \lambda A^{-1}
  \end{pmatrix}^{-1}
  \]

  *independent of data values !!!*

  Diagonal of Coeff. Matrix is basically the number of records per class/animal \((N)\)

  Inverse of Coeff. Matrix is basically \(1/n\)

- Use diagonal for animal \(i\): \(C_{ii}\)
- Prediction Error Variance: \(PEV = C_{ii}.\text{var}(e) \sim \sigma^2/N\)

Remember \(PEV = (1-r^2_{IA}).V_A\)

\[
\begin{align*}
  &\quad \Rightarrow \quad r^2_{IA} = (V_A - PEV)/V_A \\
  &\quad r^2_{IA} = 1 - \lambda C_{ii} \\
  &\quad \text{Accuracy} = r_{IA} = \sqrt{(1 - \lambda C_{ii})}
\end{align*}
\]

\(C_{ii}\) is diagonal of MME
Effective number of records
a record has less value when in a small contemporary group

• A single observation is effectively worth

\[ n_e = 1 - \left( \frac{1}{N} \right) \]

where \( N \) is the number of animals in the contemporary group

• Sire with \( n \) progeny in CG of \( N \):

\[ n_e = \frac{n^* (N-n)}{N} \]
**Examples effective number of records**

<table>
<thead>
<tr>
<th>Contemporary group size</th>
<th>1 record is effectively</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>0.5</td>
</tr>
<tr>
<td>4</td>
<td>0.75</td>
</tr>
<tr>
<td>20</td>
<td>0.95</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Contemporary group size</th>
<th># sire A</th>
<th>effective # sire A</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>10</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td>10</td>
<td>9</td>
<td>0.9</td>
</tr>
<tr>
<td>10</td>
<td>1</td>
<td>0.9</td>
</tr>
<tr>
<td>10</td>
<td>5</td>
<td>2.5</td>
</tr>
</tbody>
</table>
BLUP accuracy depends on the model used!

<table>
<thead>
<tr>
<th>animal</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.7683</td>
<td>0.6082</td>
<td>0.5404</td>
<td>0.3809</td>
</tr>
<tr>
<td>2</td>
<td>0.7516</td>
<td>0.6264</td>
<td>0.5561</td>
<td>0.5181</td>
</tr>
<tr>
<td>3</td>
<td>0.7335</td>
<td>0.609</td>
<td>0.5647</td>
<td>0.4164</td>
</tr>
<tr>
<td>4</td>
<td>0.7335</td>
<td>0.609</td>
<td>0.5647</td>
<td>0.5554</td>
</tr>
<tr>
<td>5</td>
<td>0.7612</td>
<td>0.5664</td>
<td>0.504</td>
<td>0.4243</td>
</tr>
<tr>
<td>6</td>
<td>0.7321</td>
<td>0.6175</td>
<td>0.5788</td>
<td>0.5124</td>
</tr>
<tr>
<td>7</td>
<td>0.7071</td>
<td>0.6304</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

model 1: \( y = \text{animal} \) (mean is known)

m2: \( y = \text{mean} + \text{animal} \)

m3: \( y = \text{mean} + \text{year} + \text{animal} \)

m4: \( y = \text{mean} + \text{year} + \text{sex} + \text{animal} \)

Need to find a balance.
Conclusion

Need to find a balance between

unbiasedness > many (i.e. small) fixed effect classes

and

accuracy > few large fixed effect classes

An observation is more worth when compared with many others

In progeny testing designs, we don’t need necessarily many progeny of the same sire tested in the same flock/herd, in fact better spread across as many flocks as possible