Genetic improvement of socially affected traits

Predicting response to selection
Impacts on breeding program design
Empirical results

1. Selecting on group performance rather than individual performance may be beneficial

2. Relatedness among group members plays a key role
Mortality due to cannibalism in laying hens (Bill Muir)

- Cannibalistic laying hens
- No beak-trimming
- 7 generations of selection:
  - FS-Group Selection for egg number
    - Select the FS-group with highest egg number
  - Control
  - Individual Selection for egg number
    - Select the individual with highest egg number

Mortality in the final generation

![Graph showing mortality over age in weeks for different groups.](image)
The resulting birds

Individually selected

6 out of 12 alive
The resulting birds

Group selected

12 out of 12 Alive
Group vs. individual selection in plants

- Goodnight, 1985
- Group vs. Individual Bi-directional Selection for Leaf Area in Cress (tobacco)
- Group Selection produced a Positive responses in both directions
- Individual selection Failed in both directions
  - Correlated response in competitiveness
Plant breeders use group selection

Natural selection for individual fitness

→ competition

Artificial selection for clone group yield

Group selection also increases uniformity
Can animal breeders achieve the same?

Can we breed for decreased competition, and does that improve uniformity?
Conclusion

Selection between groups can be very effective
6wk weight in quail, selection on EBV

- Experiment of Bill Muir
- Experimental Model
  - Quail
  - Trait: 6 Week Weight (wt)
- Selection Methods applied:
  - Animal Model BLUP (AM-BLUP)
    - Selection for classical EBV
  - Competitive Model BLUP: (CE-BLUP)
    - Selection for ETBV
    - \( \text{ETBV} = \text{EDBV} + (n-1)\text{ESBV} \)
- Selected for 25 Hatches
Results: 6 Week Weight

![Bar chart showing weight changes over 6 weeks for CE-BLUP and AM-BLUP methods. The chart indicates a significant increase in weight for CE-BLUP compared to AM-BLUP.](chart.png)
Genetic Trend: Social breeding value

- AM-BLUP
- CE-BLUP
Genetic Trend: Direct breeding value
Mortality at Termination of Experiment (Hatch 25)

<table>
<thead>
<tr>
<th>Line</th>
<th>CE-BLUP</th>
<th>AM-BLUP</th>
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<tr>
<td>Initial</td>
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Feed Conversion

Gain/Feed

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<tr>
<td>CE-BLUP</td>
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<tr>
<td>AM-BLUP</td>
<td>1.4</td>
</tr>
</tbody>
</table>

CE-BLUP vs AM-BLUP in Feed Conversion
Conclusion

Selection on EBV can also be effective
Theory of response to selection
Predicting response to selection

1. The general expression
   1. Applications to individual selection
   2. Application to group selection
2. A selection index approach
3. Sib and progeny testing schemes
General expression for $\Delta G$ (additive model)

$$\bar{\Delta G} = ir_{IH} \sigma_{TBV}$$

- $i =$ selection intensity
- $r_{IH} =$ accuracy = correlation between selection criterion and TBV
- $\sigma_{TBV} =$ (total) genetic standard deviation

This is simply the mean TBV of the selected parents, expressed as a deviation from the mean TBV of all individuals

This result can e.g. be derived from Price’s Theorem (Lynch and Walsh)

$$\Delta x_{avg} = \text{Cov}(w,x)/w_{avg}$$

You can also regress the TBV on the selection criterion
Accuracy

Application 1

Selection on individual phenotype
(mass selection)
Example 1: accuracy of mass selection with unrelated group members

- Selection criterion = $P_i$  →  Accuracy: $\text{Corr}(P_i, TBV_i)$

$$r_{IH} = \frac{\text{Cov}(P_i, TBV_i)}{\sigma_P \sigma_{TBV}} = \frac{\text{Cov}[A_{D,i} + \sum_{n-1} A_{S,j}, A_{D,i} + (n-1)A_{S,i}]}{\sigma_P \sigma_{TBV}}$$

$$r_{ij} = 0 \quad \rightarrow \quad \text{Cov}[\sum_{n-1} A_{S,j}, A_{D,i} + (n-1)A_{S,i}] = 0 \quad \rightarrow$$

$$r_{IH} = \frac{\text{Cov}[A_{D,i}, A_{D,i} + (n-1)A_{S,i}]}{\sigma_P \sigma_{TBV}}$$

The accuracy is negative when:

$$r_{ADS} < -\frac{\sigma_A}{(n-1)\sigma_A}$$

Negative response may occur when:
- Direct and social effects are negatively correlated
- Social effects are relatively large
Example 2: accuracy of mass selection with related group members

\[
\begin{align*}
\rho_{IH} &= \frac{\text{Cov}(P_i, TBV_i)}{\sigma_P \sigma_{TBV}} = \frac{\text{Cov}\left[A_{D,i} + \sum_{n-1} A_{S,j}, A_{D,i} + (n-1)A_{S,i}\right]}{\sigma_P \sigma_{TBV}} \\
&= \frac{\text{Cov}\left[A_{D,i}, A_{D,i} + (n-1)A_{S,i}\right]}{\sigma_P \sigma_{TBV}} + \frac{\text{Cov}\left[\sum_{n-1} A_{S,j}, A_{D,i} + (n-1)A_{S,i}\right]}{\sigma_P \sigma_{TBV}} \\
\text{Cov}\left[A_{D,i}, A_{D,i} + (n-1)A_{S,i}\right] &= \sigma^2_{AD} + (n-1)\sigma_{ADS} \\
\text{Cov}\left[\sum_{n-1} A_{S,j}, A_{D,i} + (n-1)A_{S,i}\right] &= \text{Cov}\left[\sum_{n-1} A_{S,j}, A_{D,i}\right] + \text{Cov}\left[\sum_{n-1} A_{S,j}, (n-1)A_{S,i}\right] \\
&= (n-1)r\sigma_{ADS} + (n-1)^2 r\sigma^2_{AS} \\
\rho_{IH} &= \frac{\sigma^2_{AD} + (n-1)\sigma_{ADS} + (n-1)r\sigma_{ADS} + (n-1)^2 r\sigma^2_{AS}}{\sigma_P \sigma_{TBV}} \\
\rho_{IH} &= \frac{\sigma^2_{AD} + (n-1)\sigma_{ADS} + (n-1)r(\sigma_{ADS} + (n-1)\sigma^2_{AS})}{\sigma_P \sigma_{TBV}}
\end{align*}
\]

Accuracy depends on relatedness (r) among group members.
Effect of relatedness on accuracy

Example 2: accuracy of mass selection with related group members

\[ n = 8 \]
\[ \text{Var}(P_D) = 1 \]
\[ \text{Var}(P_S) = 0.2 \]
\[ h_D^2 = h_S^2 = 0.3 \]
\[ r_{A,DS} = -0.6 \]

Relatedness among group members increases the accuracy of mass selection.
Example 2: accuracy of mass selection with related group members

Accuracy can also be expressed as:

\[ r_{IH} = \frac{r \sigma_{TBV}^2 + (1 - r)[\sigma_{AD}^2 + (n - 1)\sigma_{ADS}^2]}{\sigma_P \sigma_{TBV}} \]

\[ r = 1 \Rightarrow r_{IH} = \frac{\sigma_{TBV}^2}{\sigma_P \sigma_{TBV}} = \frac{\sigma_{TBV}}{\sigma_P} \]

- Relatedness equals the proportion of selection pressure that acts directly on the TBV
- With full relatedness among group members, accuracy is always positive
  \[ \rightarrow \text{Relatedness prevents increased competition} \]
Example 2: phenotypic variance with related group members

- Phenotypic variance
  - Phenotypic variance also depends on relatedness
  - \( \text{Var}(P) = \text{Var}(P)_{\text{within}} + \text{Var}(P)_{\text{between}} \)
    - \( \text{Var}(P)_{\text{between}} \) is the variance of the group means
  - Effects of relatedness
    - Relatedness increases the variance between groups
    - Relatedness decreases the variance within groups
    - The net effect is that \( \text{Var}(P) \) usually increases with \( r \)
      - This is like Wright’s F-statistics

\[
\text{Var}(P) = \sigma_{AD}^2 + \sigma_{ED}^2 + (n-1)(\sigma_{AS}^2 + \sigma_{ES}^2) + (n-1)r \left[ 2\sigma_{ADS}^2 + (n-2)\sigma_{AS}^2 \right]
\]
Example 2: phenotypic variance with related group members

Relatedness among group members increases phenotypic variance

Inputs
n = 8
Var(P_D) = 1
Var(P_S) = 0.2
h_D^2 = h_S^2 = 0.3
r_{A,DS} = -0.6
Example 2: phenotypic variance with related group members

\[ r = 0 \quad \rightarrow \quad \text{Var}(P) = \left[ \sigma_{AD} + (n-1)\sigma_{AS}^2 \right] + \left[ \sigma_{ED} + (n-1)\sigma_{ES}^2 \right] \]

\[ r = 1 \quad \rightarrow \quad \text{Var}(P) = \left[ \sigma_{TBV}^2 \right] + \left[ \sigma_{ED} + (n-1)\sigma_{ES}^2 \right] \]

- With full relatedness, there is no hidden genetic variance
- \text{Var}(P) = \text{Var}(TBV) + \text{non-genetic variance}
- This is because, with \( r = 1 \), an individual’s TBV is an element of its phenotype
- \( P_i = A_{D,i} + \text{Sum}(A_{S,j}) + \text{non-genetic terms} \)
- \( r = 1 \quad \rightarrow \quad A_{S,j} = A_{S,i} \rightarrow A_{D,i} + \text{Sum}(A_{S,j}) = A_{D,i} + (n-1)A_{S,i} \)
- \( P_i = TBV_i + \text{non-genetic terms}, \text{just like } P = A + E \)

If \( P_i = TBV_i + \text{non-genetic terms} \), then mass selection directly targets an individual’s TBV
\( \rightarrow \) that’s why relatedness prevents negative accuracy
Accuracy

Application 2

Selection of individuals based on group performance
(Group Selection)
Individual vs. Group Selection

<table>
<thead>
<tr>
<th>Eggs</th>
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<tr>
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</tr>
<tr>
<td>19</td>
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<td>15</td>
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<tr>
<td>23</td>
<td>5.7</td>
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Group Selected

Individual Selected
The degree of group selection (g)

Selection criterion: \( I_i = P_i + g \sum_{n-1} P_j \)

- \( g \) represents the degree of between-group selection

\[ g = 0 \rightarrow I_i = P_i \rightarrow \text{mass selection} \]

\[ g = 1 \rightarrow I_i = P_i + \sum_{n-1} P_j = \sum_{n} P \rightarrow \text{group selection} \]

\( g \) is on the same scale as relatedness (0,1)
Example 3: accuracy of group selection with **unrelated** group members

- **Selection criterion** = $I_i$,  **Accuracy:** $\text{Corr}(I_i, TBV_i)$

$$r_{IH} = \frac{\text{Cov}(I_i, TBV_i)}{\sigma_I \sigma_{TBV}} = \frac{\text{Cov}[P_i + g \sum_{j} P_j, A_{D,i} + (n-1)A_{S,i}]}{\sigma_I \sigma_{TBV}}$$

\[ = \frac{\text{Cov}(P, TBV)_{g,r=0}}{\sigma_I \sigma_{TBV}} \]

$$r_{IH} = \frac{g \sigma_{TBV}^2 + (1-g) [\sigma_{A_D}^2 + (n-1)\sigma_{A_{DS}}]}{\sigma_I \sigma_{TBV}}$$

$g$ is the proportion of selection pressure that acts directly on the TBV

**The effect of $g$ is very similar to that of relatedness**
Effect of either r or g on accuracy

- Accuracy increases more with r than with g
- Accuracy crosses 0 at same value of r = g

Relatedness has the biggest impact
Example 4: accuracy with both group selection and relatedness

- Selection criterion = $I_i$, Accuracy: $\text{Corr}(I_i, TBV_i)$

$$r_{IH} = \frac{\text{Cov}(I_i, TBV_i)}{\sigma_i \sigma_{TBV}} = \frac{\text{Cov}[P_i + g \sum_{j} P_{j}, A_{D,i} + (n-1)A_{S,i}]}{\sigma_i \sigma_{TBV}}$$

The numerator of this expression is symmetric in $g$ and $r$→ relatedness and group selection have the same impact on the sign of $r_{IH}$.
Conclusions
- Accuracy increases almost linearly with $r$
- For $g > \sim 0.4$ accuracy increases only little

Check for your own genetic parameters!

Inputs
$n = 8$
$\text{Var}(P_D) = 1$
$\text{Var}(P_S) = 0.2$
$h_D^2 = h_S^2 = 0.3$
$r_{A,DS} = -0.6$
Response to selection

A selection index approach
Basics of selection index theory

- Improvement of multiple traits, using multiple observations
- Problem: how to optimize selection?
  - E.g. The best animal for growth rate may be poor for feed intake
  - How to weigh all the info in an index?
- Step 1: Define the breeding goal (H)
  - \[ H = v_1 A_1 + v_2 A_2 + \ldots + v_k A_k = \mathbf{v}' \mathbf{a} \]
  - k is the number of traits to be improved
  - \( A_i \) is the true breeding values for trait i
  - \( v_i \) is the (economic) value of trait i
- Step 2: define the index (I)
  - \[ I = b_1 x_1 + b_2 x_2 + \ldots + b_m x_m = \mathbf{b}' \mathbf{x} \]
  - m is the number of observations for each individual
  - \( x_i \) is the ith information source
  - \( b_i \) is the index weight on the ith information source
- Step 3: find \( b \) so that accuracy is maximized
Basics of selection index theory

- Step 3: Find b so that accuracy is maximized
  - Optimum index weights: \( b = \text{Cov}(x, H)/\text{Var}(x) \)
  - \( b \) is the vector of regression coefficients of \( H \) on \( x \)
  - Substitute \( H = v'a \rightarrow b = [\text{Var}(x)]^{-1} \text{Cov}(x,a) v \)
  - Usual notation: \( b = P^{-1}Gv \)
  - \( P = \text{Var}(x) \)
    - Matrix with (co)variances between all info sources
  - \( G = \text{Cov}(x,a) \)
    - Matrix with covariances between info and breeding values in \( a \)
  - \( v = \text{vector of economic values} \)

- Response to selection
  - In underlying trait values: \( \Delta a = b'Gv/\sigma_i \)
  - In breeding goal: \( \Delta H = b'Gv/\sigma \)

- Accuracy
  - \( r_{IH} = b'Gv/(\sigma_i\sigma_H) \)
Application of selection index theory to socially affected traits

Aims

- Express response to selection within a framework common for animal breeders
- Structure the calculations of $\Delta G$
- Find optimum degree of group selection
Application of selection index theory to socially affected traits

- “Traits” of interest
  - Direct effect, $A_D$
  - Social effect, $A_S$

- Breeding goal
  - $H = v_1 A_D + v_2 A_S = A_D + (n-1)A_S$
  - $H = \mathbf{v}' \mathbf{a}$
  - $\mathbf{v}' = [1 \ (n-1)]$
  - $\mathbf{a}' = [A_D \ A_S]$

- Index
  - Direct effect is expressed in $P_i$
  - Social effect is expressed in $\text{sum}(P_j)$
  - $I_i = b_1 P_i + b_2 \text{sum}(P_j)$
  - $I = \mathbf{b}' \mathbf{x}$
  - $\mathbf{b}' = [b_1 \ b_2]$
  - $\mathbf{x}' = [P_i \ \text{sum}(P_j)]$
Application of selection index theory to socially affected traits

- The relationship between the index and group selection
  - $I_i = b_1 P_i + b_2 \text{sum}(P_j)$
  - This is proportional to $I = P_i + (b_2/b_1) \text{sum}(P_j)$
  - Hence, $b_2/b_1$ represents $g$, the degree of between group selection
  - Solving the index weights yields the optimum degree of between group selection, $g_{opt}$
  - Hence, we can use selection index theory to optimize group vs. individual selection
Application of selection index theory to socially affected traits

- Solving the index weights: \( \mathbf{b} = \mathbf{P}^{-1} \mathbf{Gv} \)

\[
x_i = \left[ \frac{p_i}{\sum_{n=1} P_j} \right] \quad \Rightarrow \quad \mathbf{P} = \text{Var}(\mathbf{x}) = \begin{bmatrix}
\text{Var}(P_i) & \text{Cov}\left(P_i, \sum_{n=1} P_j\right) \\
\text{Cov}\left(P_i, \sum_{n=1} P_j\right) & \text{Var}\left(\sum_{n=1} P_j\right)
\end{bmatrix}
\]

\[
P_{11} = \text{Var}(P_i) = \sigma_{PD}^2 + (n-1)\sigma_{PS}^2 + (n-1)r\left[2\sigma_{ADS} + (n-2)\sigma_{AS}^2\right]
\]

\[
P_{12} = P_{21} = \text{Cov}(P_i, \sum P_j) = (n-1)\text{Cov}(P_i, P_j)
\]

\[
\text{Cov}(P_i, P_j) = 2\sigma_{PDS}^2 + (n-2)\sigma_{PS}^2 + r\left[\sigma_{AD}^2 + 2(n-2)\sigma_{ADS} + (n^2 - 3n + 3)\sigma_{AS}^2\right]
\]

\[
P_{22} = \text{Var}(\sum P_j) = (n-1)\text{Var}(P_i) + (n-1)(n-2)\text{Cov}(P_i, P_j)
\]
Application of selection index theory to socially affected traits

- Solving the index weights: \( \mathbf{b} = \mathbf{P}^{-1} \mathbf{Gv} \)

\[
x_i = \left[ \begin{array}{c} P_i \\ \sum_{n=1}^{k} P_j \end{array} \right], \quad \mathbf{a} = \left[ \begin{array}{c} A_{D,i} \\ A_{S,i} \end{array} \right] \quad \Rightarrow \quad \mathbf{G} = \text{Cov}(\mathbf{x}, \mathbf{a}) = \left[ \begin{array}{cc} \text{Cov}(P_i, A_{D,i}) & \text{Cov}(P_i, A_{S,i}) \\ \text{Cov} \left( \sum_{n=1}^{k} P_j, A_{D,i} \right) & \text{Cov} \left( \sum_{n=1}^{k} P_j, A_{S,i} \right) \end{array} \right]
\]

\[
G_{11} = \text{Cov}(P_i, A_{D,i}) = \sigma_{AD}^2 + (n-1)r\sigma_{ADS}
\]

\[
G_{12} = \text{Cov}(P_i, A_{S,i}) = \sigma_{ADS} + (n-1)r\sigma_{AS}^2
\]

\[
G_{21} = \text{Cov} \left( \sum_{n=1}^{k} P_j, A_{D,i} \right) = (n-1) \left[ r\sigma_{AD}^2 + \sigma_{ADS} + (n-2)r\sigma_{ADS} \right]
\]

\[
G_{22} = \text{Cov} \left( \sum_{n=1}^{k} P_j, A_{S,i} \right) = (n-1) \left[ r\sigma_{ADS} + \sigma_{AS}^2 + (n-2)r\sigma_{AS}^2 \right]
\]
Application of selection index theory to socially affected traits

- When the genetic parameters are known, the index always outperforms individual and group selection.
- The optimum $b$ may correspond to a $g$ outside the range 0…1
  - E.g. when $r_A$ is strongly negative, $b_1$ tends to be negative.
- Hence, optimum selection is not an intermediate of individual and group selection.
- When $r_{A,DS} < 0$, group selection ($g=1$) is rather robust
  - Group selection acts directly on the TBV.
  - Useful when genetic parameters are unsure.
- Individual selection is not at all robust against $r_{A,DS} < 0$. 

Response to selection

Sib and progeny testing schemes
Does classical sib or progeny testing work for socially affected traits?

- Classical sib and progeny testing don't work for socially affected traits
  - You may get a negative response

What is in the full sib info?

\[ P_{\text{sib}} = A_{D,\text{sib}} + \text{unrelated components} \]
\[ \Rightarrow P_{\text{sibs}} = \frac{1}{2}A_{D,\text{sire}} + \frac{1}{2}A_{D,\text{dam}} \]

The sibs provide no info on the social breeding value of the candidate!
Sib and progeny testing using **family** groups

- Sib selection with family groups is effective and robust

What is in the full sib info?

\[ P_{sib} = A_{D,sib} + (n-1)A_{S,sib} \]

\[ \rightarrow P_{sibs} = \frac{1}{2}TBV_{sire} + \frac{1}{2}TBV_{dam} \]

Using sibs in family groups provides info on the TBV of the selection candidate
Accuracy of sib selection schemes

- Classical situation:
  \[ r_{IH} = \frac{rh}{\sqrt{t + (1 - t) / N}} \]
  - \( r \) = relatedness between candidate and relatives
  - \( N \) = number of relatives
  - \( t \) = intraclass correlation among the relatives
    - Correlation between the phenotypes of the relatives
    - \( t = r_w h^2 \), \( r_w \) is relatedness among the relatives

- Full sib info: \( r = \frac{1}{2} \), \( t_{FS} = \frac{1}{2} h^2 \)

- Half sib info: \( r = \frac{1}{4} \), \( t_{HS} = \frac{1}{4} h^2 \)

- Progeny info: \( r = \frac{1}{2} \), \( t_{HS} = \frac{1}{4} h^2 \)
Accuracy of sib selection schemes

Classical sib selection schemes, no social effects

- Assymptotic values for \((N \to \infty)\):
  - FS: \(\sqrt{0.5} \approx 0.71\)
  - HS: 0.5
  - Progeny: 1

Assymptotic accuracies do not depend on heritability
Accuracy of sib selection schemes with social effects (Ellen et al., 2008)

- When using groups composed of relatives, accuracy is an analogy of the classical situation

$$r_{IH} = \frac{r \eta}{\sqrt{\tau + (1 - \tau) / N}}$$

- $\eta^2$ is an analogy of $h^2$: $\eta^2 = \frac{\sigma^2_{TBV}}{\sigma^2_{TPV}}$, $\sigma^2_{TPV} = \sigma^2_{PS} + 2(n - 1)\sigma_{PDS} + (n - 1)^2 \sigma^2_{PS}$

- $\tau$ is an analogy of $t$: $\tau = r_W \eta^2$

- $N$ is the number of relatives
  - $N = \text{number of groups times group size}$

This accuracy is always positive
Sib schemes vs group or individual selection

Sib schemes are robust against social effects

Results will depend on the genetic parameters → check for your own situation!
Sib schemes vs group or individual selection

- Individual selection (r = 0.5)
- Group selection (r = 0.5)
- Progeny and Full sibs
- Individual selection (r = 0)
- Half sibs

Figure 2.—Accuracy of selection methods as a function of the genetic correlation ($r_A$) when $r_A = r_E$ ($n = 4$; $m = 1$; $\sigma_P^2 = 1$; $\sigma_R^2 = 0.33$; $k_D = 0.10$; $k_S = 0.10$). The accuracy is shown for individual selection when the animals in a group are full sibs (●) or unrelated (◇); for group selection with groups of full sibs (▲); and for selection based on relatives where relatives can be half sibs (■), full sibs (★), or half-sib offspring (●).
Impact of number of groups on $r_{IH}$

This is very similar to the effect of the number of sibs with classical sib selection.

High accuracies are feasible which may not be feasible with group selection ($m = 1$).
Conclusions

- Sib selection works with groups composed of relatives
  - Negative response “cannot” occur

- Useful when
  - The candidate must be kept individually
  - Group size differs between nucleus and commercial environment
  - The candidate does not express the trait (e.g. sex-limited traits)
  - The breeding goal refers to a crossbred
  - “heritability” is low
  - Strong competition ($r_A << 0$)
  - Genetic parameters are unknown
  - ……

- Limiting accuracies are the same as for classical sib selection
  - FS: 0.71, HS: 0.5, Progeny: 1
  - This ignores Bulmer effects
Application of sibs selection against mortality due to cannibalism

Results of one generation of divergent sib selection against mortality due to cannibalism in laying hens
BLUP selection

- BLUP $\rightarrow$ EBV$_D$, EBV$_S$
- Optimum index: ETBV = EBV$_D$ + (n–1) EBV$_S$
- You don’t have to worry about optimum weights
- Which breeding designs yield most accurate EBTV?
  - Little research has been done
  - Relatedness within groups increases accuracy of the ETBV substantially
  - Benefits of BLUP
    - Estimation of fixed effects
    - Low heritabilities
    - Accounting for genetic trend and selection
  - Disadvantage: you need to know the genetic parameters
    - Which cannot be estimated from sib group data
- “Nothing can beat BLUP” when the design is the same
- Group selection with FS beats “BLUP with unrelated group members”
Optimum breeding schemes for BLUP

- Optimization requires prediction of $\Delta G$
  - Selection index theory (pseudo-BLUP)
    - Wray and Hill, 1989; Villanueva et al., 1993
    - This is really tedious, $P = 24 \times 24$
  - Stochastic simulation
  - Use a sib-index as approximation

- The main result will be that higher relatedness within groups yields higher accuracy
  - But I have not tried it
Design problem

- Max($\Delta G$) $\rightarrow$ full sib groups
  - Random groups give poor $\Delta G$, even with BLUP

- Estimate VC $\rightarrow$ avoid full sib groups
  - Random groups are fine

- Problem: how to combine VCE and $\Delta G$?

- Are there intermediate solutions?
  - Maybe: always combine only two families in a group
  - With multiple combinations between families
  - More research is needed
Variation in group size (n)

Genotype by environment (n) interaction
Variation in group size

- The TBV depends on n: \[ TBV_i = A_{D,i} + (n - 1)A_{S,i} \]
  - → the value of an animal depends on n
  - → genotype x group-size interaction

\[
 r_G(n_1, n_2) = \frac{Cov(TBV_{n_1}, TBV_{n_2})}{\sigma_{TBV_{n_1}} \sigma_{TBV_{n_2}}}
\]

\[
 TBV_{n_1} = [1 \quad n_1 - 1] \begin{bmatrix} A_{D,i} \\ A_{S,i} \end{bmatrix} \rightarrow \sigma^2_{TBV_{n_1}} = [1 \quad n_1 - 1] \begin{bmatrix} \sigma^2_{A_D} & \sigma_{A_D S} \\ \sigma_{A_D S} & \sigma^2_{A_S} \end{bmatrix} \begin{bmatrix} 1 \\ n_1 - 1 \end{bmatrix} = n_1' Cn_1
\]

\[
 Cov(TBV_{n_1}, TBV_{n_2}) = [1 \quad n_1 - 1] \begin{bmatrix} \sigma^2_{A_D} & \sigma_{A_D S} \\ \sigma_{A_D S} & \sigma^2_{A_S} \end{bmatrix} \begin{bmatrix} 1 \\ n_2 - 1 \end{bmatrix} = n_1' Cn_2
\]

\[
 r_G(n_1, n_2) = \frac{n_1' Cn_2}{\sqrt{n_1' Cn_1 n_2' Cn_2}} \quad \text{This expresses the degree of GxE interaction}
\]
Genotype by group size interaction

Impact is largest when either $n_1$ or $n_2$ is small

Inputs
$\text{Var}(A_D) = 1$
$\text{Var}(A_S) = 0.2$
$r_{A,DS} = 0$
Genotype by group size interaction

$r_{A,DS} = 0$

$r_{A,DS} = -0.6$

The impact is bigger when direct and social effects are negatively correlated.
The GxE also depends on the size of social effects.
Genotype by group size interaction

- The above assumes that Var(A_S) is constant
  - In larger groups, social effects per individual *may* be smaller
  - “Dilution” of the effect over n−1 group members

- Full dilution →

  \[ A_{S,i,n} = \frac{A_{S,i,n=2}}{n-1} \]

  \[ A_{S,i,n=3} = \frac{1}{2} A_{S,i,n=2} \text{ , etc} \]

  \[ TBV_{i,n} = \sigma_{A_D}^2 + 2\sigma_{A_{DS},n=2} + \sigma_{A_S,n=2}^2 = TBV_{i,n=2} \]

With full dilution, the TBV is the same for any n, → there is no GxE-interaction

This will differ between e.g. Food Sharing vs Infectious Disease
Conclusions GxE

- Because the TBV depends on $n$
  - Variation in $n$ may cause GxE interaction
  - This depends critically on the relationship of $\text{Var}(A_S)$ with $n$
  - Problem: Prediction requires VCE in data with varying $n$
    - Large data sets required
    - You may not have data for certain $n$ values
  - Once you have the genetic parameters use can use selection index theory or BLUP