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

Muir, W.M. 1996. Poultry Science 75:447-458



Mortality in the final generation



The resulting birds

Individually selected



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

 \rightarrow competition

Corn

Rice

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
 - ETBV = EDBV + (n-1)ESBV
- Selected for 25 Hatches





Results: 6 Week Weight



Genetic Trend: Social breeding value



Genetic Trend: Direct breeding value



Mortality at Termination of Experiment (Hatch 25)



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 ΔG (additive model)

 $\Delta G = i r_{IH} \sigma_{TRV}$

- -i = selection intensity
- r_{IH} = accuracy = correlation between selection criterion and TBV
- σ_{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) - $\Delta x_{avg} = Cov(w,x)/w_{avg}$

You can also regress the TBV on the selection criterion



Application 1

Selection on individual phenotype (mass selection)

Example1: accuracy of mass selection with **unrelated** group members

• Selection criterion = $P_i \rightarrow Accuracy: Corr(P_i, TBV_i)$

$$\begin{aligned} r_{IH} &= \frac{Cov(P_i, TBV_i)}{\sigma_P \sigma_{TBV}} = \frac{Cov[A_{D,i} + \sum_{n=1}^{i} A_{S,j}, A_{D,i} + (n-1)A_{S,i}]}{\sigma_P \sigma_{TBV}} \\ &= \frac{Cov[A_{D,i}, A_{D,i} + (n-1)A_{S,i}]}{\sigma_P \sigma_{TBV}} + \frac{Cov[\sum_{n=1}^{i} A_{S,j}, A_{D,i} + (n-1)A_{S,i}]}{\sigma_P \sigma_{TBV}} \\ r_{ij} &= 0 \rightarrow Cov[\sum_{n=1}^{i} A_{S,j}, A_{D,i} + (n-1)A_{S,i}] = 0 \rightarrow \\ r_{IH} &= \frac{Cov[A_{D,i}, A_{D,i} + (n-1)A_{S,i}]}{\sigma_P \sigma_{TBV}} \rightarrow \end{aligned}$$
The accuracy is negative when
$$r_{ADS} < -\frac{\sigma_{AD}}{(n-1)\sigma_{AS}}$$

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

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

$$\begin{split} r_{IH} &= \frac{Cov(P_{i}, TBV_{i})}{\sigma_{P}\sigma_{TBV}} = \frac{Cov\left[A_{D,i} + \sum_{n=1}^{i} A_{S,j}, A_{D,i} + (n-1)A_{S,i}\right]}{\sigma_{P}\sigma_{TBV}} \\ &= \frac{Cov[A_{D,i}, A_{D,i} + (n-1)A_{S,i}]}{\sigma_{P}\sigma_{TBV}} + \frac{Cov\left[\sum_{n=1}^{i} A_{S,j}, A_{D,i} + (n-1)A_{S,i}\right]}{\sigma_{P}\sigma_{TBV}} \\ Cov[A_{D,i}, A_{D,i} + (n-1)A_{S,i}] = \sigma_{A_{D}}^{2} + (n-1)\sigma_{A_{DS}} \\ Cov\left[\sum_{n=1}^{i} A_{S,j}, A_{D,i} + (n-1)A_{S,i}\right] = Cov\left(\sum_{n=1}^{i} A_{S,j}, A_{D,i}\right) + Cov\left[\sum_{n=1}^{i} A_{S,j}, (n-1)A_{S,i}\right] \\ &= (n-1)r\sigma_{A_{DS}} + (n-1)^{2}r\sigma_{A_{S}}^{2} \\ r_{IH} &= \frac{\sigma_{A_{D}}^{2} + (n-1)\sigma_{A_{DS}} + (n-1)r[\sigma_{A_{DS}} + (n-1)^{2}r\sigma_{A_{S}}^{2}}{\sigma_{P}\sigma_{TBV}} \\ r_{IH} &= \frac{\sigma_{A_{D}}^{2} + (n-1)\sigma_{A_{DS}} + (n-1)r[\sigma_{A_{DS}} + (n-1)\sigma_{A_{S}}^{2}]}{\sigma_{P}\sigma_{TBV}} \\ \end{split}$$

Example 2: accuracy of mass selection with **related** group members



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:

$$Cov(P, TBV)_{g,r=0}$$

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

$$r = 1 \rightarrow r_{IH} = \frac{\sigma_{TBV}^2}{\sigma_P \sigma_{TBV}} = \frac{\sigma_{TBV}}{\sigma_P}$$

$$f$$
This is like $\sqrt{h^2}$

-Relatedness equals the proportion of selection pressure that acts directly on the TBV

 With full relatedness among group members accuracy is always positive
 → Relatedness prevents increased competition Example 2: phenotypic variance with **related** group members

- Phenotypic variance
 - □ Phenotypic variance also depends on relatedness
 - $\Box Var(P) = Var(P)_{within} + Var(P)_{between}$
 - Var(P)_{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 Var(P) usually increases with r
 - □ This is like wright's F-statistics

$$Var(P) = \sigma_{A_D}^2 + \sigma_{E_D}^2 + (n-1)(\sigma_{A_S}^2 + \sigma_{E_S}^2) + (n-1)r \left[2\sigma_{A_{DS}} + (n-2)\sigma_{A_S}^2 \right]$$

Example 2: phenotypic variance with **related** group members



Relatedness among group members increases phenotypic variance

Example 2: phenotypic variance with **related** group members

$$r = 0 \rightarrow Var(P) = \left[\sigma_{A_D} + (n-1)\sigma_{A_S}^2\right] + \left[\sigma_{E_D} + (n-1)\sigma_{E_S}^2\right]$$
$$r = 1 \rightarrow Var(P) = \left[\sigma_{TBV}^2\right] + \left[\sigma_{E_D} + (n-1)\sigma_{E_S}^2\right]$$

- With full relatedness, there is no hidden genetic variance
- Var(P) = Var(TBV) + non-genetic variance
- This is because, with r = 1, an individuals TBV is an element of its phenotype

-
$$P_i = A_{D,i} + Sum(A_{S,i}) + non-genetic terms$$

- r = 1 \rightarrow A_{S,j} = A_{S,i} \rightarrow A_{D,i} + Sum(A_{S,j}) = A_{D,i} + (n-1) A_{S,i}
- $P_i = TBV_i + non-genetic terms$, just like P = A + E

If $P_i = TBV_i + non-genetic terms$, then mass selection directly targets an individual's TBV \rightarrow that's why relatedness prevents negative accuracy



Application 2

Selection of individuals based on group performance (Group Selection)



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)

Example3: accuracy of group selection with **unrelated** group members

• Selection criterion = I_i , Accuracy: Corr(I_i , TBV_i)

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

$$Cov(P, TBV)_{g,r=0}$$

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

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: Corr(I_i , TBV_i)

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

$$r_{IH} = \frac{[g + r + (n - 2)gr]\sigma_{TBV}^{2} + (1 - g)(1 - r)[\sigma_{A_{D}}^{2} + (n - 1)\sigma_{A_{DS}}]}{\sigma_{I}\sigma_{TBV}}$$

The numerator of this expression is symmetric in g and r \rightarrow relatedness and group selection have the same impact on the sign of r_{IH}

Accuracy as a function of both g and r



Conclusions

- Accuracy increases almost linearly with r
- For g > ~0.4 accuracy increases only little

Check for your own genetic parameters!

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

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
 - $\hfill\square$ How to weigh all the info in an index?
- Step 1: Define the breeding goal (H)
 - $\Box H = v_1 A_1 + v_2 A_2 + ... + v_k A_k = v'a$
 - □ k is the number of traits to be improved
 - □ A_i is the true breeding values for trait i
 - \Box v_i is the (economic) value of trait I
- Step 2: define the index (I)
 - \Box I = b₁x₁ + b₂x₂ + + b_mx_m = **b**'**x**
 - m is the number of observations for each individual
 - \Box x_i is the ith information source
 - \Box 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: $\mathbf{b} = \text{Cov}(\mathbf{x}, H)/\text{Var}(\mathbf{x})$
 - \square **b** is the vector of regression coefficients of H on **x**
 - □ Substitute $H = \mathbf{v}'\mathbf{a} \rightarrow \mathbf{b} = [Var(\mathbf{x})]^{-1} Cov(\mathbf{x},\mathbf{a}) \mathbf{v}$
 - □ Usual notation: $\mathbf{b} = \mathbf{P}^{-1}\mathbf{G}\mathbf{v}$
 - \square P = Var(**x**)
 - Matix with (co)variances between all info sources
 - $\Box \quad G = Cov(\mathbf{x}, \mathbf{a})$
 - Matrix with covariances between info and breeding values in a
 - \Box **v** = vector of economic values
- Response to selection
 - □ In underlying trait values: $\Delta \mathbf{a} = \mathbf{b'G} i / \sigma_1$
 - □ In breeding goal: $\Delta H = \mathbf{b}' \mathbf{G} \mathbf{v} i / \sigma$
- Accuracy
 - $\Box \ \mathbf{r}_{\mathsf{IH}} = \mathbf{b}'\mathbf{G}\mathbf{v} / (\sigma_{\mathsf{I}}\sigma_{\mathsf{H}})$

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 ΔG
- □ 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
 - $\Box \quad H = v_1 A_D + v_2 A_S = A_D + (n-1)A_S$
 - \square H = v'a

$$\Box \quad \mathbf{a}' = [\mathsf{A}_\mathsf{D} \; \mathsf{A}_\mathsf{s}]$$

Index

- Direct effect is expressed in P_i
- \Box Social effect is expressed in sum(P_i)

$$\Box I_i = b_1 P_i + b_2 sum(P_j)$$

- \Box I = b'x
- \Box **b**' = [b₁ b₂]
- $\square \mathbf{x}' = [P_i \text{ sum}(P_j)]$

Application of selection index theory to socially affected traits

- The relationship between the index and group selection
 - $\Box I_i = b_1 P_i + b_2 sum(P_j)$
 - □ This is proportional to $I = P_i + (b_2/b_1) \text{ sum}(P_i)$
 - □ 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: **b** = **P**⁻¹**Gv**

$$\mathbf{x}_{i} = \begin{bmatrix} P_{i} \\ \sum P_{j} \end{bmatrix} \implies \mathbf{P} = Var(\mathbf{x}) = \begin{bmatrix} Var(P_{i}) & Cov\left(P_{i}, \sum P_{j}\right) \\ Cov\left(P_{i}, \sum P_{j}\right) & Var\left(\sum P_{i}, \sum P_{j}\right) \end{bmatrix}$$

$$P_{11} = Var(P_i) = \sigma_{P_D}^2 + (n-1)\sigma_{P_S}^2 + (n-1)r \left[2\sigma_{A_{DS}} + (n-2)\sigma_{A_S}^2 \right]$$

$$P_{12} = P_{21} = Cov(P_i, \sum P_j) = (n-1)Cov(P_i, P_j)$$
$$Cov(P_i, P_j) = 2\sigma_{P_{DS}} + (n-2)\sigma_{P_S}^2 + r\left[\sigma_{A_D}^2 + 2(n-2)\sigma_{A_{DS}} + (n^2 - 3n + 3)\sigma_{A_S}^2\right]$$

 $P_{22} = Var(\sum P_j) = (n-1)Var(P_i) + (n-1)(n-2)Cov(P_i, P_j)$

Application of selection index theory to socially affected traits

Solving the index weights: b = P⁻¹Gv

$$\mathbf{x}_{i} = \begin{bmatrix} P_{i} \\ \sum_{n-1} P_{j} \end{bmatrix}, \ \mathbf{a} = \begin{bmatrix} A_{D,i} \\ A_{S,i} \end{bmatrix} \Rightarrow \ \mathbf{G} = Cov(\mathbf{x}, \mathbf{a}) = \begin{bmatrix} Cov(P_{i}, A_{D,i}) & Cov(P_{i}, A_{S,i}) \\ Cov\left(\sum_{n-1} P_{j}, A_{D,i}\right) & Cov\left(\sum_{n-1} P_{j}, A_{S,i}\right) \end{bmatrix}$$

$$\begin{aligned} G_{11} &= Cov(P_i, A_{D,i}) = \sigma_{A_D}^2 + (n-1)r\sigma_{A_{DS}} \\ G_{12} &= Cov(P_i, A_{S,i}) = \sigma_{A_{DS}} + (n-1)r\sigma_{A_S}^2 \\ G_{21} &= Cov(\sum P_j, A_{D,i}) = (n-1) \left[r\sigma_{A_D}^2 + \sigma_{A_{DS}} + (n-2)r\sigma_{A_{DS}} \right] \\ G_{22} &= Cov(\sum P_j, A_{S,i}) = (n-1) \left[r\sigma_{A_{DS}}^2 + \sigma_{A_S}^2 + (n-2)r\sigma_{A_S}^2 \right] \end{aligned}$$

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, b₁ 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</p>

Response to selection

Sib and progeny testing schemes

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



Groups with unrelated individuals

What is in the full sib info? $P_{sib} = A_{D,sib}$ + unrelated components $\rightarrow P_{sibs} = \frac{1}{2}A_{D,sire} + \frac{1}{2}A_{D,dam}$

> The sibs provide no info on the social breeding value of the candidate!

Classical sib and progeny testing dont work for socially affected traits
 You may get negative response

Sib and progeny testing using family groups



Groups with full sibs

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

Sib selection with family groups is effective and robust

Accuracy of sib selection schemes

- Classical situation: $r_{IH} = \frac{rh}{\sqrt{t + (1 t)/N}}$
 - r = relatedness between candidate and relatives
 - \square N = number of relatives
 - \Box 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 $(N \rightarrow \infty)$:
 - □ FS: √0.5 = ~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

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

$$\square \eta^2 \text{ is an analogy of } h^2: \quad \eta^2 = \frac{\sigma_{TBV}^2}{\sigma_{TPV}^2} \quad , \quad \sigma_{TPV}^2 = \sigma_{P_S}^2 + 2(n-1)\sigma_{P_{DS}} + (n-1)^2\sigma_{P_S}^2$$

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

This accuracy is always positive

- □ N is the number of relatives
 - N = number of groups times group size

Sib schemes vs group or individual selection



FIGURE 1.—Accuracy of selection methods as a function of the associative phenotypic variance $(\sigma_{P_s}^2)$ $(n = 4; m = 1; \sigma_{P_p}^2 = 1; h_D^2 = 0.10; h_S^2 = 0.10; r_A = r_E = 0)$. The accuracy is shown for individual selection when the animals in a group are full sibs (\blacklozenge) or unrelated (\diamondsuit); for group selection with groups of full sibs (\bigstar); and for selection based on relatives where relatives can be half sibs (\blacksquare), full sibs (\divideontimes), or half-sib offspring (\bigcirc).

Sib schemes are robust against social effects

Results will depend on the genetic parameters \rightarrow check for your own situation !

Sib schemes vs group or individual selection



FIGURE 2.—Accuracy of selection methods as a function of the genetic correlation (r_A) when $r_A = r_E$ $(n = 4; m = 1; \sigma_{P_D}^2 = 1; \sigma_{P_S}^2 = 0.33; h_D^2 = 0.10; h_S^2 = 0.10)$. The accuracy is shown for individual selection when the animals in a group are full sibs (\blacklozenge) or unrelated (\diamondsuit); for group selection with groups of full sibs (\blacktriangle); and for selection based on relatives where relatives can be half sibs (\blacksquare), full sibs (\ast), or half-sib offspring (\bigcirc). Sib and group selection schemes are robust against competition ($r_A < 0$)

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)

FIGURE 3.—Accuracy of selection methods as a function of the number of groups per selection candidate (m) $(n = 4; \sigma_{P_D}^2 = 1; \sigma_{P_S}^2 = 0.33; h_D^2 = 0.10; h_S^2 = 0.10; r_A = r_E = 0)$. The accuracy is shown for individual selection when the animals in a group are full sibs (\blacklozenge) or unrelated (\diamondsuit); for group selection with groups of full sibs (\blacktriangle); and for selection based on relatives, where relatives can be half sibs (\blacksquare), full sibs (\ast), or half-sib offspring (\bigcirc). When m = 1, selection based on full sibs and selection based on half-sib offspring received the same symbol, because the accuracy is, respectively, 0.29 and 0.31.

Accuracy of sib selection schemes with social effects (Ellen et al., 2008)

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 ΔG
 - □ Selection index theory (pseudo-BLUP)
 - Wray and Hill, 1989; Villanueva et al., 1993
 - This is really tedious, **P** = 24x24
 - 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
 - □ But I have not tried it

Design problem

- $Max(\Delta G) \rightarrow full sib groups$
 - $\hfill\square$ Random groups give poor ΔG , even with BLUP
- Estimate VC → avoid full sib groups
 □ Random groups are fine
- Problem: how to combine VCE and ΔG ?
- 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

 $\Box \rightarrow$ genotype x group-size interaction

$$r_{G}(n_{1},n_{2}) = \frac{Cov(TBV_{n_{1}},TBV_{n_{2}})}{\sigma_{TBV_{n_{1}}}\sigma_{TBV_{n_{2}}}}$$

$$TBV_{n_{1}} = \begin{bmatrix} 1 & n_{1}-1 \end{bmatrix} \begin{bmatrix} A_{D,i} \\ A_{S,i} \end{bmatrix} \rightarrow \sigma_{TBV_{n_{1}}}^{2} = \begin{bmatrix} 1 & n_{1}-1 \end{bmatrix} \begin{bmatrix} \sigma_{A_{D}}^{2} & \sigma_{A_{DS}} \\ \sigma_{A_{DS}} & \sigma_{A_{S}}^{2} \end{bmatrix} \begin{bmatrix} 1 \\ n_{1}-1 \end{bmatrix} = \mathbf{n}_{1}^{'} \mathbf{Cn}_{1}$$

$$Cov(TBV_{n_{1}},TBV_{n_{2}}) = \begin{bmatrix} 1 & n_{1}-1 \end{bmatrix} \begin{bmatrix} \sigma_{A_{D}}^{2} & \sigma_{A_{DS}} \\ \sigma_{A_{DS}} & \sigma_{A_{S}}^{2} \end{bmatrix} \begin{bmatrix} 1 \\ n_{2}-1 \end{bmatrix} = \mathbf{n}_{1}^{'} \mathbf{Cn}_{2}$$

 $r_G(n_1, n_2) = \frac{\mathbf{n}_1 \mathbf{C} \mathbf{n}_2}{\sqrt{\mathbf{n}_1 \mathbf{C} \mathbf{n}_1 \mathbf{n}_2 \mathbf{C} \mathbf{n}_2}}$ This expresses the degree of GxE interaction



Inputs Var(A_D) = 1 Var(A_S) = 0.2 $r_{A,DS}$ = 0

Impact is largest when either n_1 or n_2 is small







Inputs Var(A_D) = 1 Var(A_S) = 0.2

The impact is bigger when direct and social effects are negatively correlated

 $Var(A_S) = 0.2$

 $Var(A_{s}) = 0.05$



Inputs Var(A_D) = 1 r_{A,DS} = -0.6

The GxE also depends on the size of social effects

- 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 \rightarrow

$$\begin{split} A_{S,i,n} &= \frac{A_{S,i,n=2}}{n-1} & \text{This will differ between e.g.} \\ A_{S,i,n=3} &= \frac{1}{2} A_{S,i,n=2} \text{ , etc} \\ TBV_{i,n} &= \sigma_{A_D}^2 + 2\sigma_{A_{DS},n=2} + \sigma_{A_S,n=2}^2 = TBV_{i,n=2} \end{split}$$

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

Conclusions GxE

Because the TBV depends on n

- □ Variation in n may cause GxE interaction
- \Box This depends critically on the relationship of 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