Social Interactions in Livestock

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Social Interactions:

Trait values of individuals are affected by other individuals

Examples

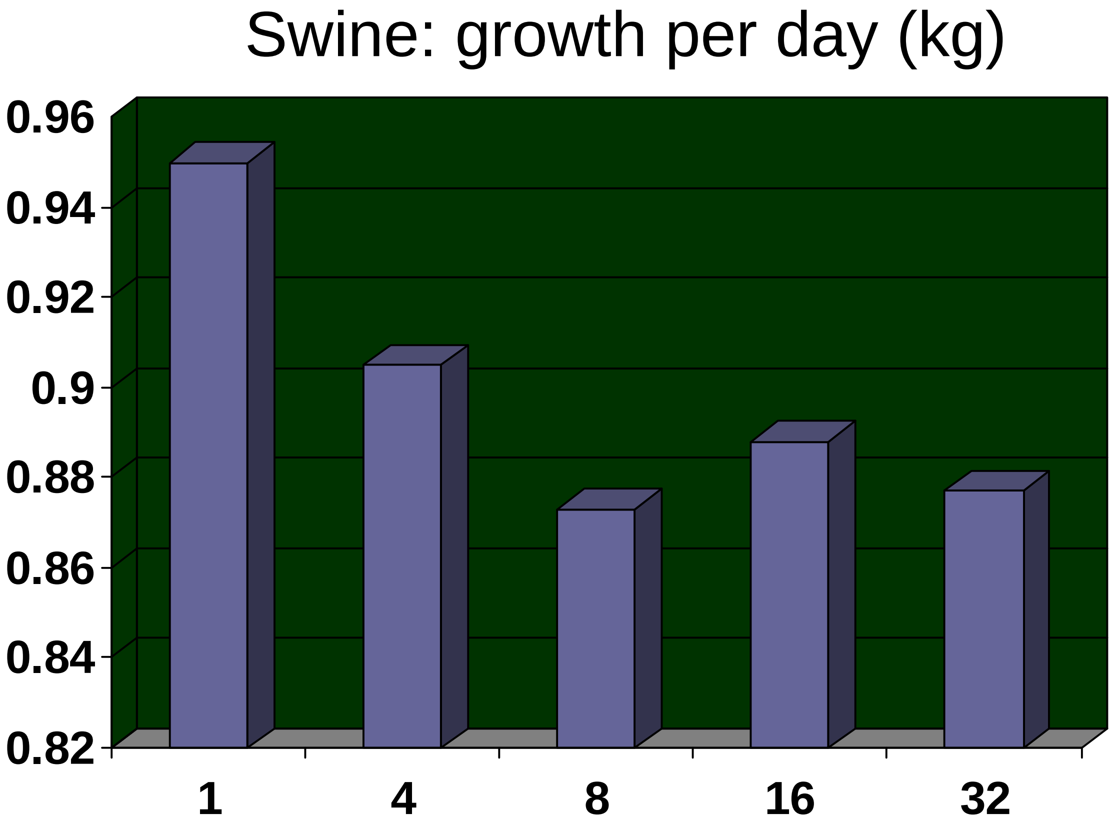
Examples

Mortality due to cannibalism in domestic chicken (Bill Muir)

Examples

Tail biting in swine affects welfare and probably also yield

Examples



Frank et al 1997a. J. Anim. Sci. Vol. 75(Suppl. 1):37

Frank et al 1997b. J. Anim. Sci.(Suppl. 1):38

Social interactions may suppress performance

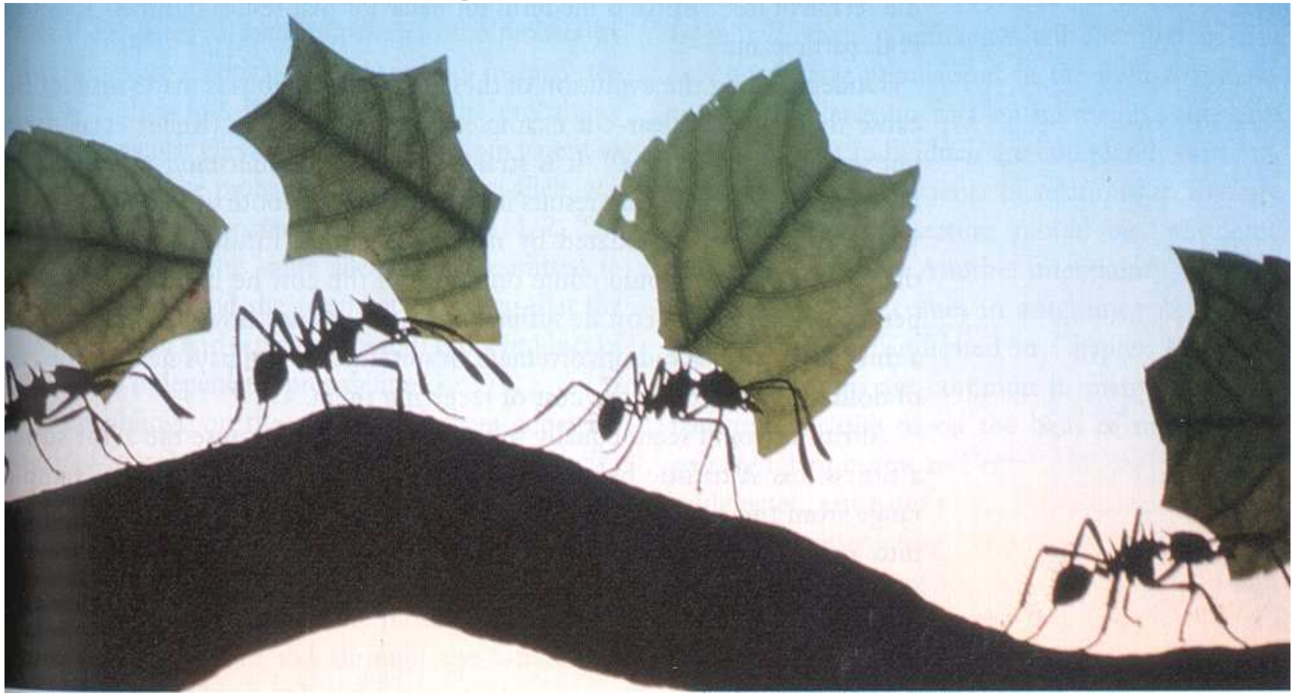
Examples

Competition inflates size variation in aquaculture

Relationship with uniformity

Examples in natural populations

Sterile helpers in social insects



Leaf cutter ants

Examples in plant breeding

Wild variety

Domestic variety

Competition for light and soil nutrients in plants

Example in plant breeding

Corn

Rice

Wild variety

Link with uniformity

Domestic variety

Classical example in livestock

Maternal effects

Examples

Beef cattle in feedlot?

Examples

Competition for light and soil nutrients in trees

Relevance for breeding?

Do social effects merit special attention?

- Why not simply:
  - Treat it as environmental noise
  - Correct for it in breeding value estimation
    - e.g. include fixed effect for group size
    - e.g. fit a random group effect (pigs, beef cattle)
    - e.g. fit distance to a neighbor (trees)

- This is not sufficient

Selection for size in aquaculture

- Simply selecting the largest fish may increase competition
  - → reduced benefits and increased inefficiency
  - Trade-off between individual benefit and group benefit

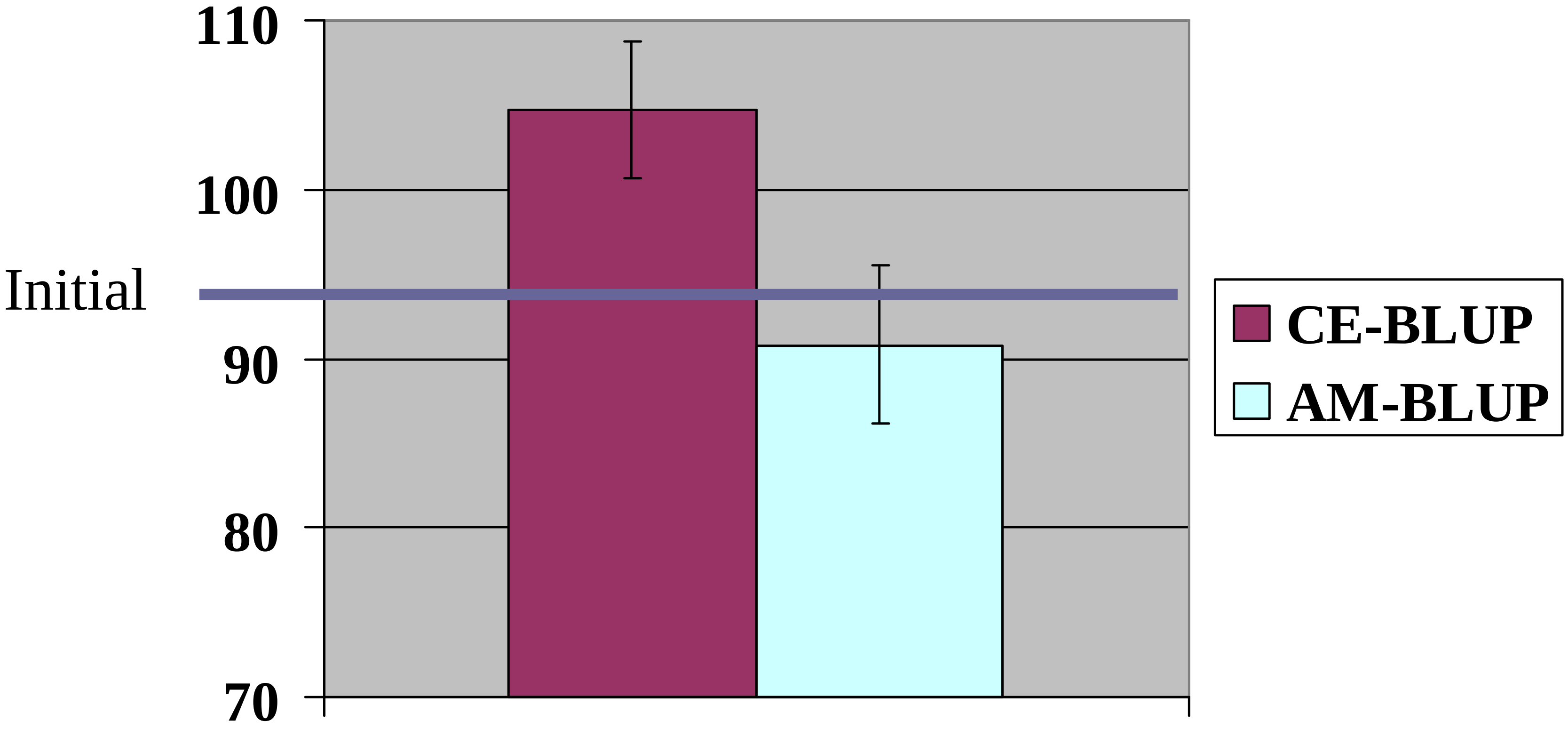
Selection for 6wk weight in quail

Experiment by Bill Muir (Purdue University)

25 generations of selection on either:

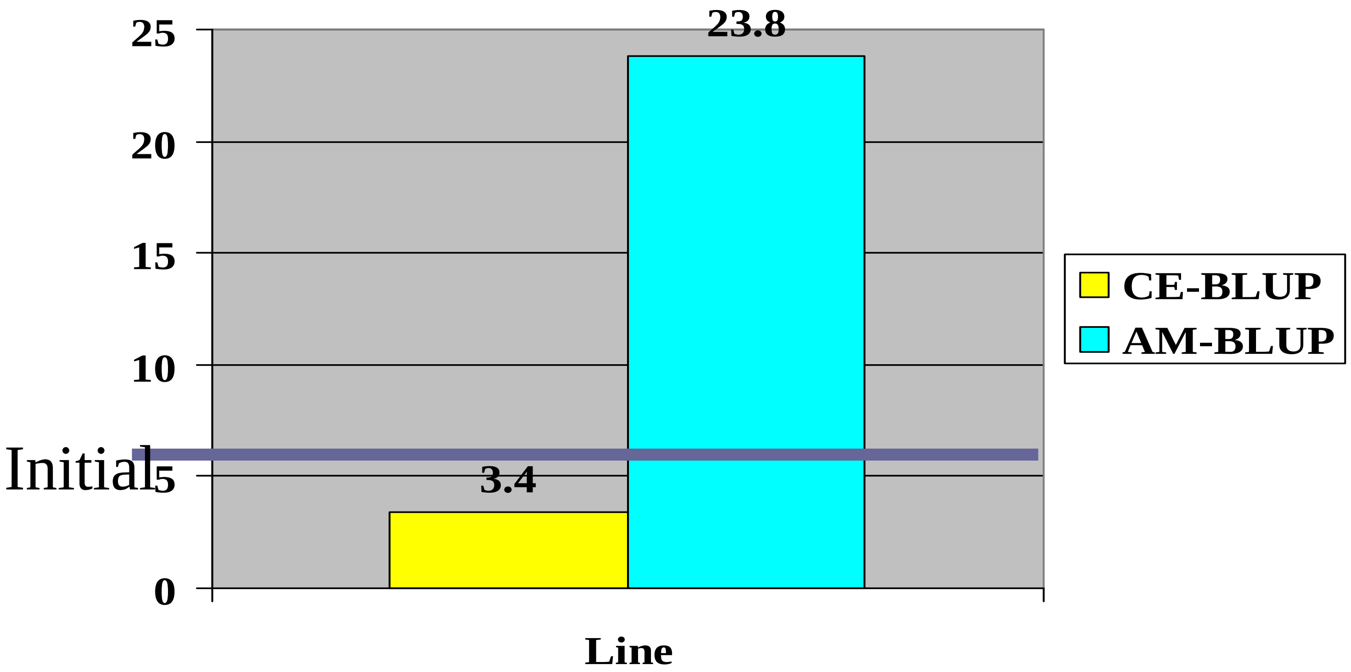
- Classical animal model BLUP-EBV
- EBV taking into account social effects (CE-BLUP)

Results: 6 Week Weight



Selection on classical BLUP-EBV yielded response in the wrong direction

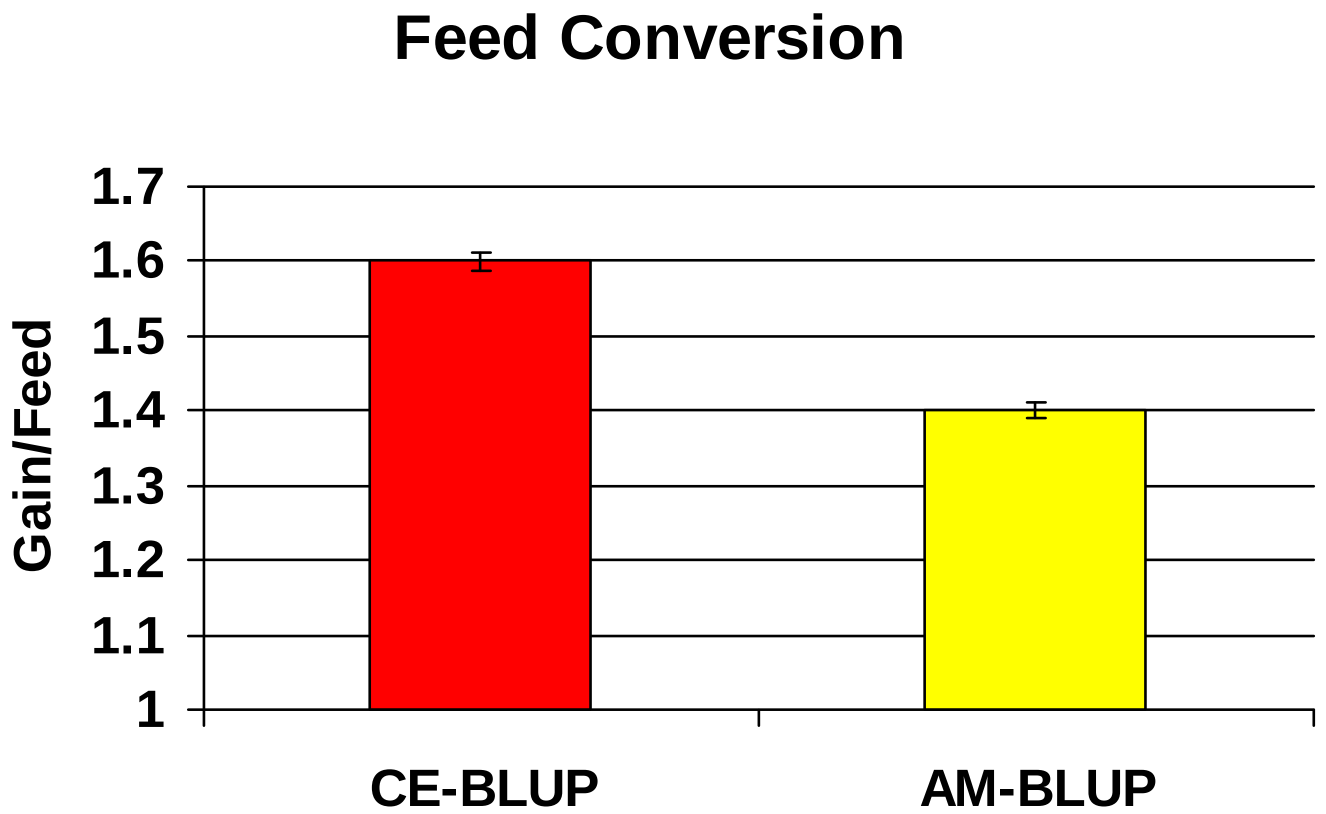
Results: Mortality at Termination of Experiment



Selection on classical EBV has dramatically increased mortality

Apparantly: the fastest growing individuals are most competitive

Results: feed conversion



Increased competition may lead to a loss in efficiency

Selection on individual performance in a group setting may select for the most competitive animals

Conclusion

When traits are affected by social interactions,

then breeders should take this into account.

Otherwise they risk suboptimal or even negative response.

However

- Classical breeding theory does not explain negative response to selection

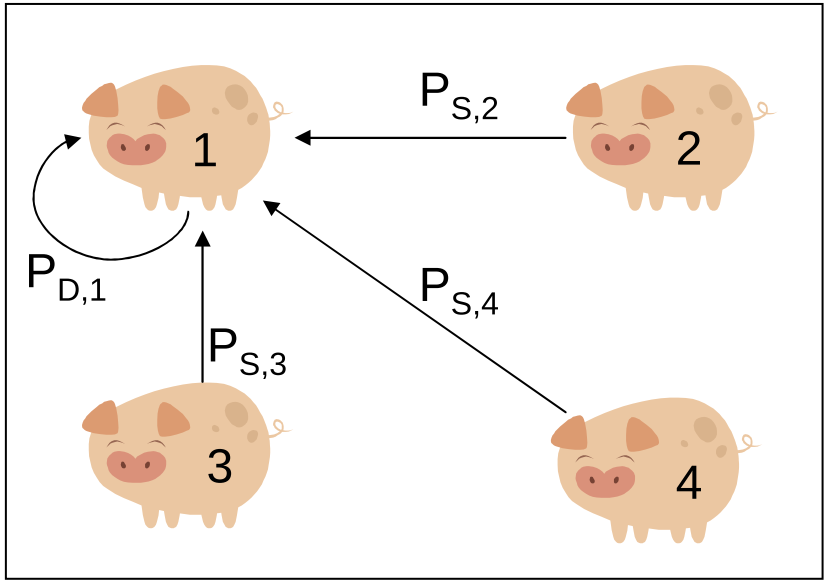
- Breeder's Equation: $\Delta G = h^2 S$
- or, $\Delta G = i \, r_{IH} \, \sigma_G$
- In theory, response is always greater than zero

We need to extend our models

Improvement of socially affected traits

- What is needed?
  - A quantitative genetic model to understand inheritance of socially affected traits
  - Methods to estimate variance components
  - Breeding designs to efficiently improve socially affected traits

The Basic Model



Individual $i: P_i = P_{D,i} + \sum_{j \neq i}^{n} P_{S,j}$

Each individual has:
- Direct effect on self (P_D)
- Social effect on others (P_S)

$P_1 = P_{D,1} + P_{S,2} + P_{S,3} + P_{S,4}$

$P_2 = P_{D,2} + P_{S,1} + P_{S,3} + P_{S,4}$

$P_3 = P_{D,3} + P_{S,1} + P_{S,2} + P_{S,4}$

$P_4 = P_{D,4} + P_{S,1} + P_{S,2} + P_{S,3}$

- The social effect is “phenotypic”
  - It may contain both genetic and non-genetic components
  - $P_S \neq A_S$, but $P_S = A_S + E_S$

The Basic Model

$$\text{Individual } i: P_i = P_{D,i} + \sum_{j \neq i}^{n} P_{S,j}$$

- Split phenotypic effects in heritable and environmental component
  - $P_{D,i} = A_{D,i} + E_{D,i}$
  - $P_{S,i} = A_{S,i} + E_{S,i}$

- Genetic model: $$P_i = \underbrace{A_{D,i}}_{\text{Direct Breeding Value}} + E_{D,i} + \sum_{i \neq j} \underbrace{A_{S,j}}_{\text{Social Breeding Value}} + \sum_{i \neq j} E_{S,j}$$

e.g. with *n* = 4: each phenotype is the sum of:
-The direct breeding value of the individual itself
-The social breeding values of its three group members
-And the corresponding non-heritable terms

The Basic Model: response

Response = genetic change in mean trait value

$$P_i = A_{D,i} + \sum_{n-1} A_{S,j} + \text{terms in } E$$

$$\overline{P} = \overline{A_D} + (n-1)\overline{A_S} + \text{terms in } E$$

$$\Delta\overline{G} = \Delta\overline{A_D} + (n-1)\Delta\overline{A_S}$$

Response equals
- Response in direct effect
- plus (group size minus one) times response in social effect

-e.g. with groups of 4 individuals: $\Delta G = \Delta A_D + 3\Delta A_S$

Basic model: variance components

- Two traits
  - Direct effects
  - Social effects

- Three genetic variance components:
  - Direct genetic variance: $Var(A_D)$
  - Social genetic variance: $Var(A_S)$
  - Direct-social genetic covariance: $Cov(A_D,A_S)$

- Direct-social genetic correlation: $r_{A_{DS}} = \dfrac{Cov(A_D, A_S)}{\sigma_{A_D}\sigma_{A_S}}$

$r_A > 0 \rightarrow$ "cooperation"
- positive effects on self go together with positive effects on others

$r_A < 0 \rightarrow$ "competition"
- positive effects on self go together with negative effects on others

Can this model explain the observed negative responses to selection?

e.g. Mass selection with unrelated group members (Griffing, 1967)

Response to mass selection with unrelated group members

$$\Delta\overline{G} = \Delta\overline{A_D} + (n-1)\Delta\overline{A_S}$$

Method: regress $A_D + (n-1)A_S$ on the selection criterion (phenotype)

$$\Delta\overline{G} = b_{A_D+(n-1)A_S,P} \times S$$

Selection differential : $S = i\sigma_P$

Regression coefficient :

$$b = Cov[A_{D,i} + (n-1)A_{S,i}, P_i]/\sigma_P^2$$

Note: i versus j

Unrelated group members

$$Cov[A_{D,i} + (n-1)A_{S,i}, P_i] = Cov[A_{D,i} + (n-1)A_{S,i} ; A_{D,i} + \sum_{n-1} A_{S,j}] = \sigma_{A_D}^2 + (n-1)\sigma_{A_{DS}}$$

$$\Delta\overline{G} = \left[\sigma_{A_D}^2 + (n-1)\sigma_{A_{DS}}\right]\frac{i}{\sigma_P}$$

Response to mass selection with unrelated group members

$$\Delta\overline{G} = \left[\sigma^2_{A_D} + (n-1)\sigma_{A_{DS}}\right]\frac{i}{\sigma_P}$$

$$\sigma^2_{A_D}\frac{i}{\sigma_P} = \overline{\Delta A_D}$$ is response in direct effects (= i h σ_A , the usual breeder's eqn)

$$(n-1)\sigma_{A_{DS}}\frac{i}{\sigma_P} = (n-1)\overline{\Delta A_S}$$ is correlated response in social effects

Response in negative when: $$r_{A_{DS}} < \frac{-\sigma_{A_D}}{(n-1)\sigma_{A_S}}$$

In that case: $(n-1)\Delta\overline{A_S} < 0$ and $\left|(n-1)\Delta\overline{A_S}\right| > \left|\Delta\overline{A_D}\right|$

Conclusion response to selection

If group members are unrelated

and selection is on individual phenotype, then

correlated response in social effects can be negative and greater than response in direct effects,

causing negative net response.

Breeding value and heritable variance

- Classical model: $P = A + E$
  - A = breeding value, heritable variance = Var(A)
  - Var(A) $\leq$ Var(P); h^2 is proportion of Var(P) that is heritable
  - Response to selection equals ΔA

- Breeding value in social effects models
  - Each individual expresses its direct effect once and its social effect (n-1) times
  - Total breeding value: $TBV_i = A_{D,i} + (n-1)A_{S,i}$
  - TBV = heritable impact of an individual on the mean trait value of the population
  - $\Delta G = \Delta A_D + (n-1)\Delta A_S = \Delta TBV$
  - The TBV is a generalization of breeding value to account for social effects

Breeding value and heritable variance

- Heritable variance with social effects
  - Classical: Var(A)
  - Social effects: Var(TBV)

$$TBV_i = A_{D,i} + (n-1)A_{S,i}$$

$$\boxed{\sigma^2_{TBV} = \sigma^2_{A_D} + 2(n-1)\sigma_{A_{DS}} + (n-1)^2\sigma^2_{A_S}}$$

- Hence:
  - Heritable variance depends on group size (n)
  - Competition [Cov(A_D,A_S) < 0] reduces the heritable variance that can be used to generate response to selection

A measure of heritability

- Phenotypic variance with unrelated group members

$$P_i = P_{D,i} + \sum_{j=1,n-1} P_{S,j}$$

Cov($P_{D,i,}$$P_{S,j}$) = Cov($P_{S,j}$,$P_{S,j'}$) = 0
when group members are unrelated $\rightarrow$

$$\boxed{Var(P) = \sigma^2_{P_D} + (n-1)\sigma^2_{P_S}}$$

- A measure of "heritability"
  - T^2 = Var(TBV)/Var(P)
  - T^2 expresses heritable variance relative to phenotypic variance

Heritable variance in traits: example

- Groups of 8 individuals

$$n = 8,\ h_D^2 = h_S^2 = 0.3, \sigma_{P_D}^2 = 1.0, \sigma_{P_S}^2 = 0.15, r_A = r_E = 0$$

$$Var(P) = 1 + (8-1) \times 0.15 = 2.05$$

$$\sigma_{A_D}^2 = 0.3 \times 1 = 0.3$$

$$\sigma_{A_S}^2 = 0.3 \times 0.15 = 0.045$$

In this example,
50% of Var(P) is due to social effects,
but 88% of Var(TBV) is due to social effects !

$$Var(TBV) = 0.3 + 2 \times (8-1) \times 0 + (8-1)^2 \times 0.045 = 2.505$$

$$\text{"heritability": } T^2 = 2.505 / 2.05 = 1.22$$

Apparently, heritable variance can be greater than phenotypic variance!

Can heritable variance truly exceed phenotypic variance?

- Does Var(TBV) really reflect the heritable variance <u>that we can use for genetic improvement</u>?

- Classical: $\Delta\overline{G} = i\, r_{IH}\, \sigma_G$
  - Intensity and accuracy are scale free parameters
  - σ_G represents the genetic "variability" that can be used for genetic improvement

- Does this result also apply to the TBV?
  - Can we write: $\Delta\overline{G} = i\, r_{IH}\, \sigma_{TBV}$
  - If yes, then Var(TBV) really reflects the heritable variance that we can use for response to selection.

$$\overline{P} = \overline{A_D} + (n-1)\overline{A_S} + \text{terms in E} \quad \Rightarrow$$

Selection response indeed equals the change in mean TBV

$$\Delta\overline{G} = \Delta\overline{A_D} + (n-1)\Delta\overline{A_S} = \Delta\overline{TBV}$$

$$\Delta\overline{TBV} = b_{TBV,C}\,(C - \overline{C}) \;\Rightarrow$$

C is the selection criterion

$$= \frac{Cov(TBV,C)}{\sigma_C^2} i\sigma_C = Cov(TBV,C)\frac{i}{\sigma_C}$$

$$= Cov(TBV,C)\frac{i}{\sigma_C} \times \frac{\sigma_{TBV}}{\sigma_{TBV}} = i\,\frac{Cov(TBV,C)}{\sigma_C\sigma_{TBV}}\sigma_{TBV} \;\Rightarrow$$

$$\Delta\overline{G} = i r_{IH}\sigma_{TBV}$$

Accuracy is the correlation between the selection criterion and the TBV of individuals

Var(TBV) truly reflects the heritable variance that can be used for improvement

Why can heritable variance exceed phenotypic variance?

- Classical model
  - Breeding value is an element of the phenotype
    - P = A + E
  - Consequently, Var(P) = Var(A) + Var(E)
  - $\rightarrow$ Var(A) < Var(P)

- Socially affected traits
  - An individual's total breeding value is not an element of its phenotype
    - P $\neq$ TBV + E
  - Hence, Var(P) $\neq$ Var(TBV) + Var(E)
  - There is no need for Var(TBV) < Var(P)

- Heritable variance is "hidden" because an individual's TBV is distributed over multiple (*n*) individuals

Heritable variance with social effects

- Conclusions
  - In theory, social effects may contribute substantially to heritable variance in traits
  - Heritable variance can exceed phenotypic variance
  - Part of the heritable variance is hidden because social effects are distributed over multiple individuals
  - We have to investigate how important this is in real populations

Evidence for social genetic effects from the literature

1. Results from data analysis

2. Results from selection experiments

Evidence for social genetic effects from the literature

1. Results from data analysis

2. Results from selection experiments

Survival in cannibalistic laying hens

- Laying hens of Hendrix-ISA
- **Survival time** in non-beak trimmed laying hens, 4 individuals per cage
- Three genetic lines with ~6,000, 7,000 and 4,000 individuals per line
- Survival at and of lay 55% (W1,WB) and 75% (WF)

Table 2. Breeding scheme of the 3 layer lines per laying house

	Laying house 1		Laying house 2	
Line	Sires	Dams	Sires	Dams
W1	36	287	32	250
WB	35	276	33	261
WF	20	159	18	135

Ellen et al., Poultry Science, 2008

Table 4. Estimates of genetic parameters[1] with SE for direct effect on survival days in 3 layer lines using a traditional linear animal model

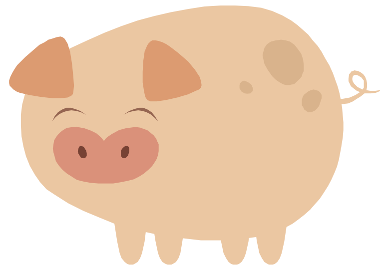
Parameter	Unit	W1	WB	WF
σ_A	d	30 ± 4	44 ± 5	16 ± 5
σ_P^2	d^2	12,814 ± 239	20,066 ± 367	13,936 ± 333
h^2		0.07 ± 0.02	0.10 ± 0.02	0.02 ± 0.01

Table 5. Estimates of genetic parameters[1] with SE for direct and associative effect on survival days in 3 layer lines using the linear animal model of Bijma et al. (2007a)

Parameter	Unit	W1	WB	WF
$\sigma_{A_D}^2$	d^2	915 ± 218	1,917 ± 394	246 ± 159
$\sigma_{A_S}^2$	d^2	134 ± 51	273 ± 85	60 ± 61
$\sigma_{A_{DS}}$	d^2	62 ± 76	−228 ± 132	13 ± 69
σ_{TBV}	d	50 ± 8	55 ± 9	30 ± 21
σ_P^2	d^2	12,847 ± 245	20,111 ± 374	13,999 ± 343
T^2		0.19 ± 0.06	0.15 ± 0.05	0.06 ± 0.06
r_A		0.18 ± 0.21	−0.31 ± 0.18	0.11 ± 0.55
ρ		0.08 ± 0.02	0.08 ± 0.02	0.10 ± 0.02

Clear evidence for heritable social effects on survival time

Yield traits in fattening pigs



Number of observations and means of traits per feeding strategy

	Feeding strategy		
	Restricted[a]	*Ad libitum*	All
No. of animals penned	11,469	4,965	16,434
Penning weight (kg)	27.7	27.2	27.6
No. of animals with slaughter records	9,541	4,491	14,032
Hot carcass weight (kg)	86.3	88.9	87.1
Growth rate (g/day)	823	881	841
Back fat thickness (mm)	16.6	17.6	16.9
Muscle depth (mm)	57.2	58.6	57.6
No. of animals with individual feed intake	0[b]	4,342	4,342
Feed intake (g/day)	—[b]	2,141	2,141

[a] The amount of feed was restricted per pen.
[b] Individual feed intake of restricted fed animals was unknown.

Bergsma et al., 2008 Genetics

Yield traits in fattening pigs

Estimates from the classical approach

Trait	$\hat{\sigma}^2_A$	$\hat{\sigma}^2_c$	$\hat{\sigma}^2_e$	$\hat{\sigma}^2_P$	$\hat{h}^2$
Growth rate (g/day)	2,583 ± 249	868 ± 70	3,820 ± 141	7,272 ± 133	0.36 ± 0.03
Back fat thickness (mm)	2.83 ± 0.23	0.28 ± 0.05	4.67 ± 0.14	7.78 ± 0.13	0.36 ± 0.03
Muscle depth (mm)	7.94 ± 0.76	1.09 ± 0.21	23.07 ± 0.52	32.10 ± 0.48	0.25 ± 0.02
Feed intake (g/day)	41,275 ± 3,384	15,201 ± 2,019	39,749 ± 6,050	96,226 ± 2,982	0.41 ± 0.04

Estimates were obtained using model 1 (Equation 6); ± indicates standard errors of estimates.

Inclusion of a random **pen effect** to account for non-heritable social effects

TABLE 4

Estimates from the classical approach including random pen effects

Trait	$\hat{\sigma}^2_A$	$\hat{\sigma}^2_c$	$\hat{\sigma}^2_g$	$\hat{\sigma}^2_e$	$\hat{\sigma}^2_P$	$\hat{h}^2$
Growth rate (g/day)	1,780 ± 172	259 ± 43	1,929 ± 90	3,057 ± 101	7,023 ± 122	0.25 ± 0.02
Back fat thickness (mm)	2.79 ± 0.23	0.18 ± 0.05	0.44 ± 0.05	4.37 ± 0.14	7.78 ± 0.13	0.36 ± 0.02
Muscle depth (mm)	7.69 ± 0.74	0.86 ± 0.21	1.03 ± 0.18	22.44 ± 0.51	32.02 ± 0.47	0.24 ± 0.02
Feed intake (g/day)	17,678 ± 3,244	2,689 ± 1,092	41,018 ± 3,346	35,780 ± 1,986	97,165 ± 3,573	0.18 ± 0.03

Estimates were obtained using model 2 (Equation 7); ± indicates standard errors of estimates.

A substantial drop in h^2 when including pen effects → when not accounted for, non-heritable social effects may bias estimates of heritability

Yield traits in fattening pigs

Table 5. Variance components when including social interactions

Trait	σ^2_{direct}	σ^2_{social}	σ^2_{TBV} 1)	T^2	$r_{A_{DS}}$
daily gain	1523 ± 157	46 ± 7	4602 ± 518	0.71 ±0.07	0.21 ± 0.10
Backfat	2.74 ± 0.23	0.006 ± 0.003	3.04 ± 0.34	0.40 ± 0.04	0.32 ± 0.18
Muscle depth	6.68± 0.51	0.015 ± 0.012	9.59 ± 1.13	0.31± 0.04	0.49± 0.30
Feed intake	14150 ± 3426	843 ± 239	70491±16460	1.02 ± 0.25	0.31 ± 0.19

Large contribution of social effects to heritable variance in growth rate and feed intake

Zero or positive genetic correlation between direct and social effects → “cooperation”

No evidence of social effects for back fat and muscle depth

Yield traits in fattening pigs

Comparison between restricted and *ad libitum* feeding

Table 6. Variance components and percentage of heritable variation (T^2) for net daily gain.

	σ^2_{direct}	σ^2_{social}	σ^2_{TBV} [1)]	T^2	$r_{A_{DS}}$
restricted fed	1619 ± 199	54 ± 9	4982 ± 642	0.79 ± 0.11	0.18 ± 0.11
ad libitum fed	1747 ± 272	92 ± 18	6745 ± 1141	1.19 ± 0.22	0.08 ± 0.14
Total	1484 ± 160	45 ± 7	4423 ± 514	R[3)] 0.66 ± 0.08	0.20 ± 0.10
				A[3)] 0.74 ± 0.09	

Surprise:
- Social effects seem largest with *ad libitum* feeding
- Restricted feeding yielded highest r_A

Other results

- Beef cattle
  - Gain of Hereford bulls in feed lot
  - Van Vleck et al., 2007, JAS (~1,800 obs)
  - Social effects in gain only during first 28 days in feedlot, $T^2 \approx 1$ to 2.
  - Small size of data set limiting factor.

- Growth of pigs
  - Arango et al., 2005, JAS (~5,000 obs.)
  - Large effects, $T^2 \approx 4.8$
    - Convergence problems
  - Chen et al., 2008, JAS (~11,000 obs)
    - $h_D^2 = 0.2$ and $T^2 = 0.60 \rightarrow$ 3-fold increase
    - $r_A = 0.25 \rightarrow$ "cooperation"

- Many authors did not realize that their estimates are extremely large
  - Judging $h_S^2 = Var(A_S)/Var(P)$, rather than $T^2 = Var(TBV)/Var(P)$

Evidence for social genetic effects from the literature

1. Results from data analysis

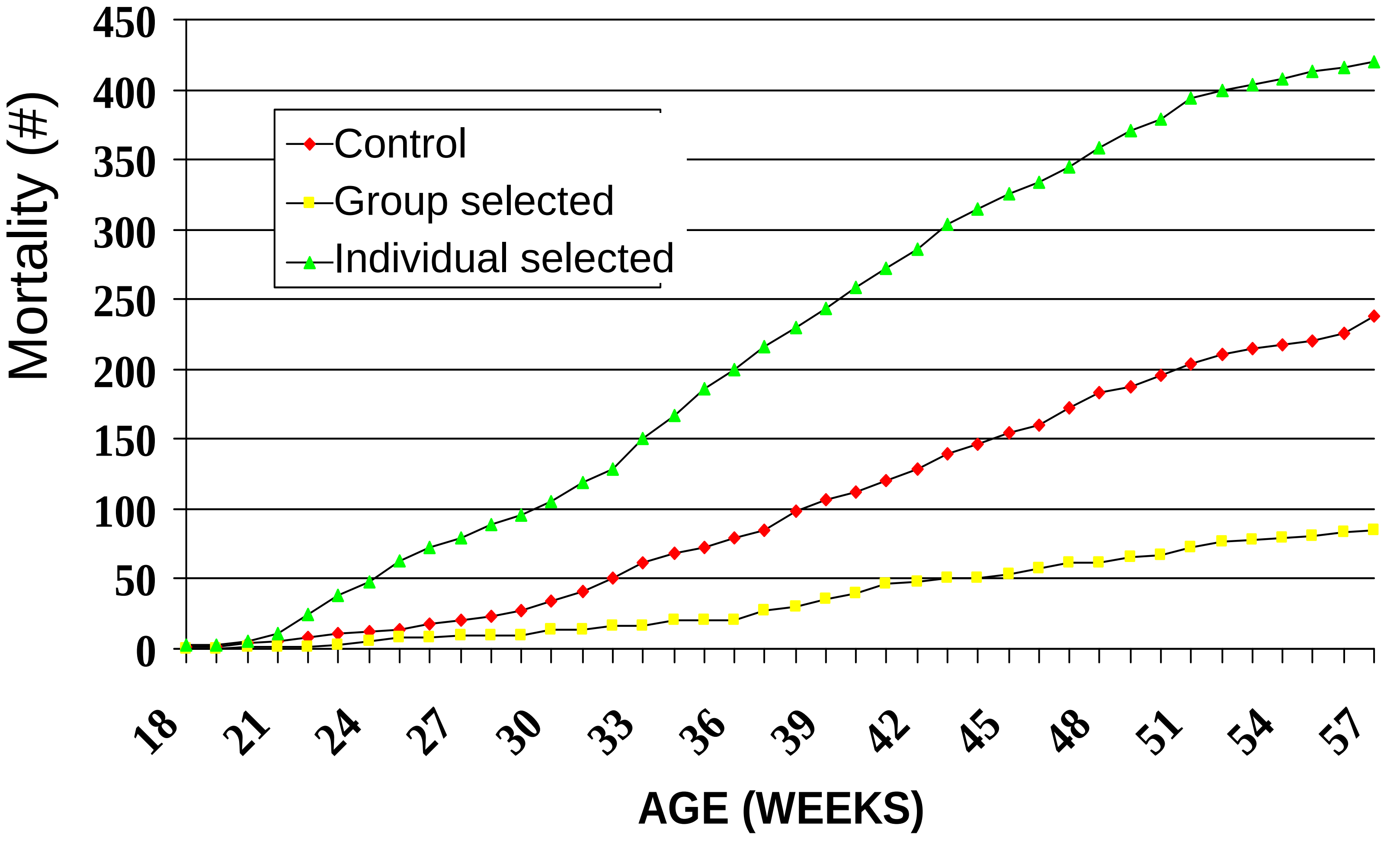
2. Results from selection experiments

Results of selection experiments

- Some experiments show positive response when the selection methods specifically targets social effects

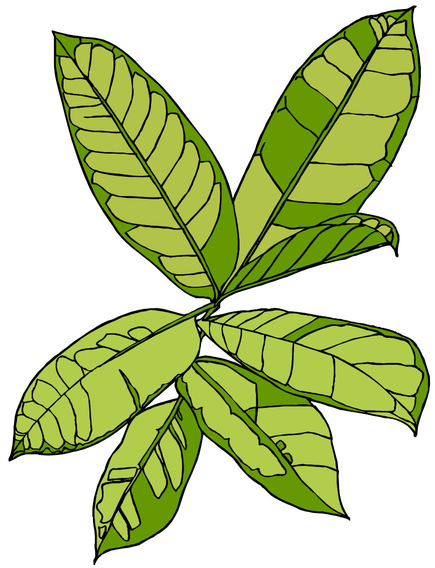
- Two examples comparing individual to group selection

Group vs individual selection against mortality in laying hens (Muir)



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
  - Probably due to correlated response in competitiveness



Conclusions

- Still limited evidence for heritable social effects
  - Selection experiments are convincing in my opinion
- Not all data is suitable
  - Group composition and number of groups is important
- Often estimated T^2 is rather large, but unnoticed
- Often $\mathrm{Cov}(A_D, A_S) > 0$, indicating "cooperation", nevertheless studies refer to "competitive effects"