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Presentation of "Incorporation of Competitive Effects in Forest Tree or Animal Breeding Programs" by Muir in Genetics (2005)

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► To cite this version:

Timothée Flutre. Presentation of "Incorporation of Competitive Effects in Forest Tree or Animal Breeding Programs" by Muir in Genetics (2005). Doctoral. Journal club of WP4 in the MoBiDiv project, France. 2023, pp.41. hal-04099164

HAL Id: hal-04099164

<https://hal.inrae.fr/hal-04099164>

Submitted on 16 May 2023

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”Incorporation of Competitive Effects in Forest
Tree or Animal Breeding Programs”
Muir, Genetics (2005)

Timothée Flutre

16/05/2023

Outline

Introduction

Theory

Experimental validation

Discussion

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Theory

Experimental validation

Discussion

IGEs not used in breeding

- ▶ the impacts of the genes of one individual on the performance of other individuals are generally ignored
- ▶ relative efficiency of BLUP-based selection index compared to mass selection: theoretical advantages not confirmed, or even worse, possibly because competition is ignored

Case of animals: breeding vs housing

- ▶ limit or ban suffering or injury to animals in breeding
- ▶ change management practices or update selection schemes

Objectives

- ▶ examine and compare alternative methods of incorporating competitive interactions in plant and animal breeding programs
- ▶ theory, simulations, and a biological experimentation

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Griffing (1967)

Group of n unrelated individuals:

$$\begin{aligned} P_i &= P_{D,i} + \sum_{j \neq i}^{n-1} P_{S,j} \\ &= A_{D,i} + E_{D,i} + \sum_{j \neq i}^{n-1} (A_{S,j} + E_{S,j}) \end{aligned}$$

- ▶ P_i : observed phenotypic value of individual i
- ▶ $A_{D,i}$: heritable direct effect (breeding value) of i
- ▶ $E_{D,i}$: nonheritable direct effect of i
- ▶ $A_{S,j}$: heritable social/indirect effect (breeding value) of j
- ▶ $E_{S,j}$: nonheritable indirect effect of j

Griffing (1967)

Expected change in the mean from selection on individual records:

$$\Delta\mu = \frac{\bar{i}}{\sigma_P} (\sigma_{A_D}^2 + (n - 1)\sigma_{A_{DS}})$$

where \bar{i} is the standardized selection differential (selection intensity)

Competition for a limited resource:

- ▶ $\sigma_{A,DS} < 0$
- ▶ positive selection can reduce rather than increase the mean

Griffing (1967)

Expected change in the mean from selection on groups:

$$\Delta\mu = \frac{1}{n} \frac{\bar{I}_{gr}}{\sigma_{\bar{P}_{gr}}} (\sigma_{A_D}^2 + 2(n-1)\sigma_{A_{DS}} + (n-1)^2\sigma_{A_S}^2)$$

- ▶ always positive

About group selection

the term group selection is used henceforth to refer to selection among groups, with the group as the unit of selection

Concretely, each group is selected based on its mean:

$$\bar{P}_{gr} = \frac{1}{n} \sum_{i=1}^n P_i$$

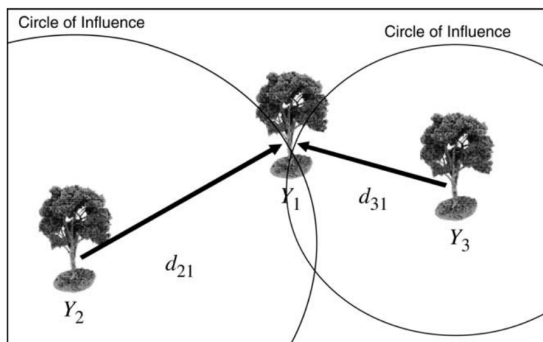
More theory and experiments

- ▶ exp.: Wade on randomly formed groups
- ▶ exp.: Goodnight comparing individual vs group selection
- ▶ theory: Griffing: group selection becomes more efficient as the average relationship within groups increases
- ▶ exp.: Muir, Craig and Muir

Needed improvements

Group selection is based entirely on between-group variation and ignores within-group variation. The optimal index would separate the direct and associative effects and weight each according to the variance-covariance structure of the genetic parameters.

Competition by distance (trees)



Influence of tree i on j : $c_{i \rightarrow j} \propto \left(\frac{1}{d_{ij}}\right)^2 a_{p,i}$

► phenotypic associative effect of tree i : $p_{,i} = a_{g,i} + a_{e,i}$

Competition within a pen (animals)

Assume all animals interact equally:

- ▶ same as above with distance set to 1 within a pen and zero between pens

Parameter estimation and BLUPs

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_D\mathbf{d}_g + \mathbf{Z}_A\mathbf{a}_g + \mathbf{Z}_{A^e}\mathbf{a}_e + \boldsymbol{\epsilon}$$

$$\mathbf{V} \begin{bmatrix} \mathbf{D} \\ \mathbf{A}^g \\ \mathbf{A}^e \\ \boldsymbol{\epsilon} \end{bmatrix} = \begin{bmatrix} \mathbf{G}\boldsymbol{\sigma}_D^2 & \mathbf{G}\boldsymbol{\sigma}_{A^g,D} & 0 & 0 \\ \mathbf{G}\boldsymbol{\sigma}_{A^g,D} & \mathbf{G}\boldsymbol{\sigma}_{A^g}^2 & 0 & 0 \\ 0 & 0 & \mathbf{I}\boldsymbol{\sigma}_{A^e}^2 & 0 \\ 0 & 0 & 0 & \mathbf{I}\boldsymbol{\sigma}_{\boldsymbol{\epsilon}}^2 \end{bmatrix}.$$

ReML algorithm to estimate the parameters and mixed-model equations to compute the BLUPs

Optimal index

$$I_i = eBLUP(d_{g,i}) + (n - 1) eBLUP(a_{g,i})$$

Relative efficiency of group vs index-based selection

Simulations with 512 individuals in 32 groups of size 16.

Four methods:

1. (K) group selection with groups composed of full sibs
2. (R) group selection with groups composed of random individuals
3. (D) individual selection using a model with only direct effects
4. (C) individual selection with a model with associative genetic effects

Relative efficiency of group vs index-based selection

Magnitude of associative effects	Method ^a	Response per generation	SE	Relative efficiency ^b
Large ^c	C	0.721	0.021	3.03
	D	-0.229	0.004	-0.96
	K	0.509	0.011	2.13
	R	0.238	0.002	1.00
Small ^d	C	0.098	0.002	3.69
	D	0.054	0.001	2.00
	K	0.078	0.002	2.88
	R	0.027	0.001	1.00

^a C, competitive effects BLUP, two random effects model; D, animal model with direct effects only; K, group selection composed of kin; R, group selection composed of random individuals.

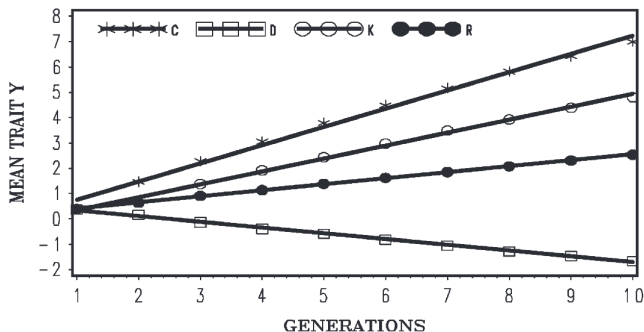
^b Relative to R.

^c $\sigma_D^2 = 69$, $\sigma_{A^g,D} = -30$, $\sigma_{A^g}^2 = 45.5$, $\sigma_\epsilon^2 = 69$.

^d $\sigma_D^2 = 68$, $\sigma_{A^g,D} = -5$, $\sigma_{A^g}^2 = 1.3$, $\sigma_\epsilon^2 = 68$.

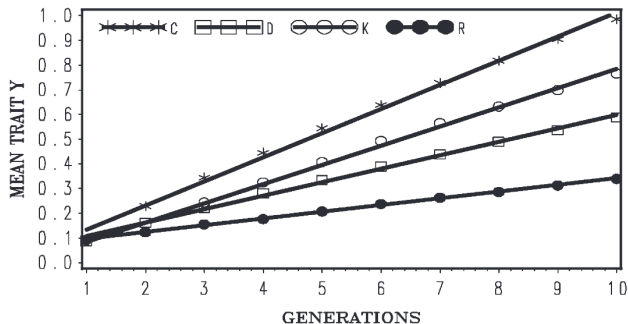
Relative efficiency of group vs index-based selection

- ▶ $\rho_{D,A} = -0.54$
- ▶ $\sigma_D^2 / (\sigma_D^2 + \sigma_A^2 + \sigma_\epsilon^2) = 0.38$
- ▶ $(\sigma_D^2 + \sigma_A^2) / (\sigma_D^2 + \sigma_A^2 + \sigma_\epsilon^2) = 0.62$



Relative efficiency of group vs index-based selection

- ▶ $\rho_{D,A} = -0.53$
- ▶ $\sigma_D^2 / (\sigma_D^2 + \sigma_A^2 + \sigma_\epsilon^2) = 0.495$
- ▶ $(\sigma_D^2 + \sigma_A^2) / (\sigma_D^2 + \sigma_A^2 + \sigma_\epsilon^2) = 0.505$



Relative efficiency of group vs index-based selection

- ▶ individual selection with DGEs and IGEs (C) always best
- ▶ 2nd best is group selection composed of full-sibs (K)
- ▶ group selection in random groups (R) always positive but inefficient when $\sigma_{A_g}^2$ small
- ▶ individual selection with only DGEs (D) always sub-optimal and even detrimental when $\sigma_{A_g}^2$ high

Impact of group size

Simulations with groups of size 16 versus 4 (for the same progeny size: 256).

Correlations between estimated and true genetic effects.

- ▶ both direct and associative effects were estimated more precisely in small groups than in large, but the difference was small

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Material

Japanese quail:

- ▶ short generation time (6 weeks)
- ▶ can be individually tagged (pedigree)
- ▶ very aggressive and cannibalistic (IGE)

Experimental design

- ▶ 3 rooms: 1 for brooding and 2 for growing and breeding
- ▶ each room has 6 rows
- ▶ each row has 12 cages (61x61cm)

Competition for resources

Restrict access to food:

- ▶ 15.2 cm per cage
- ▶ once a day

⇒ 240 g / day

- ▶ adequate to meet all nutritional requirements provided the birds did not waste feed
- ▶ in some cages, some birds dominating the social order restricted access to the feeder

G1: choice of the optimal density

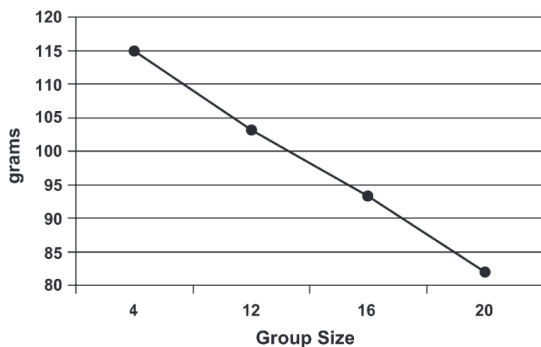


FIGURE 6.—Mean body weight at 42 days by group (pen) size.

Choice of 16 birds.

G1: choice of the optimal density

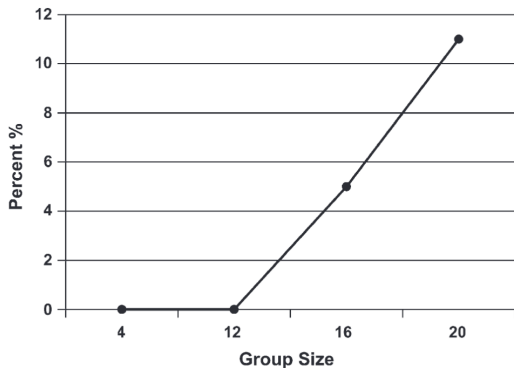


FIGURE 7.—Mean percentage of mortality by group size.

Choice of 16 birds.

G2 and G3

The next two generations were devoted to parameter estimation. In each of two rooms, 24 sires were each mated to two dams at random. Females were placed in individual mating cages and a male was placed with each female and was rotated between the two females twice a week. Eggs were marked and collected for 2 weeks and kept in a cooler. After 2 weeks, they were incubated as a group. Upon hatching chicks within a sire family were toe clipped, left or right, to distinguish the dam families, moved to the brooding room, and caged by sire half-sib family. At 2 weeks of age the chicks were wing banded and randomly allocated to grow-out cages, 16 per cage, and up to 12 cages, depending on numbers hatched. If not enough birds were available to fill an additional cage, those extra birds were discarded. At 6 weeks of age, the birds were sexed and weights were recorded. This process was replicated three times. As birds reached 12 weeks of age, random males and females were selected to replace the breeders and data for the second generation were collected.

Parameter estimation

$$\begin{bmatrix} \hat{\sigma}_D^2 & \hat{\sigma}_{A^g, D} \\ \hat{\sigma}_{A^g, D} & \hat{\sigma}_{A^g}^2 \end{bmatrix} = \begin{bmatrix} 33.7 & -5.5 \\ -5.5 & 2.87 \end{bmatrix}$$

$$\hat{\sigma}_\varepsilon^2 = 124.5.$$

- ▶ $\rho_{D,A} = -0.56$
- ▶ $\sigma_D^2 / (\sigma_D^2 + \sigma_A^2 + \sigma_\varepsilon^2) = 0.21$
- ▶ $(\sigma_D^2 + \sigma_A^2) / (\sigma_D^2 + \sigma_A^2 + \sigma_\varepsilon^2) = 0.23$

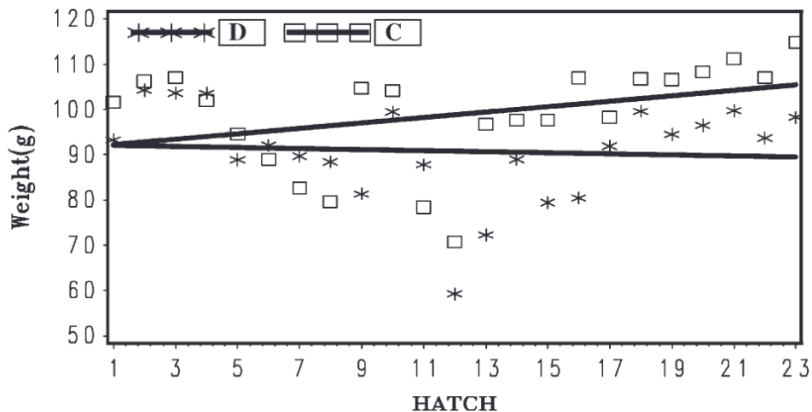
Selection scheme for weight

to large and negative (-0.56). Using these estimates of the genetics parameters, and starting with the adults of the second generation, birds in each room were selected on the basis of solutions from a model that included an index with either direct and associative effects (C-BLUP) or only direct effects (D-BLUP). Within a selection method, sires and dams were kept for breeding until replaced with an animal with a higher breeding value. Selected birds were kept in holding cages for another 4 weeks to become fully sexual mature, *i.e.*, 10 weeks of age, before being used as replacements. Mating was therefore with overlapping generations. Matings between full- and half-sibs were avoided. The experiment was continued for 23 hatches, approximately six generations.

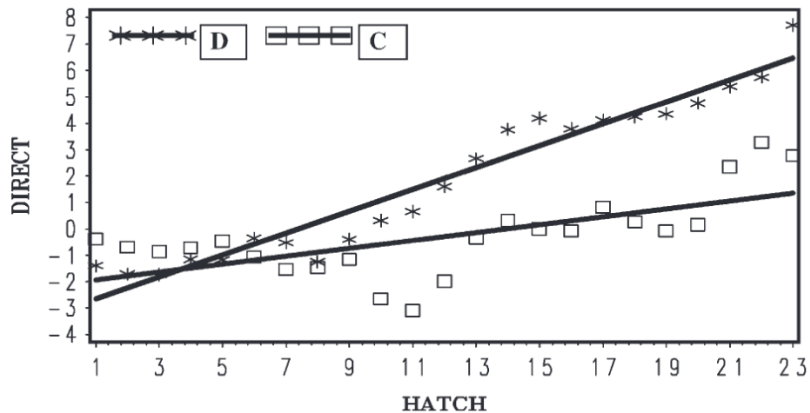
Selection outcome

At the termination of the experiment, feed efficiency was measured with the feed restrictors removed. At 2 weeks of age, 60 birds from each line were randomly chosen, weighed, and placed in five cages (12 per cage). Feed was weighed into each trough and birds were allowed to feed continuously. Feed was replaced when the feeders were almost empty. At 6 weeks of age, food was removed 24 hr prior to the birds being weighed. The entire experiment was replicated three times.

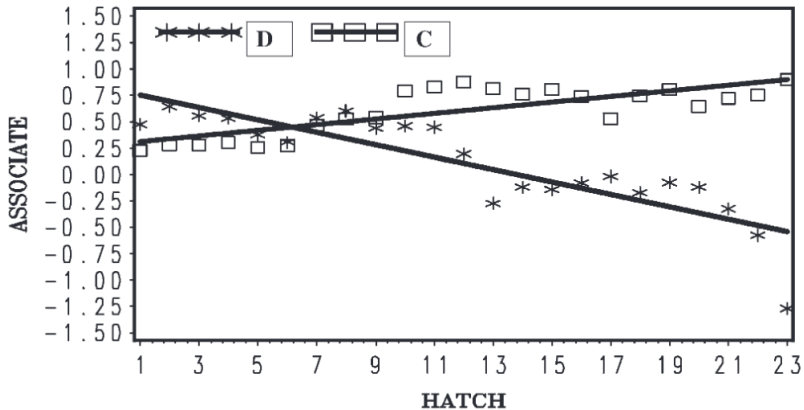
Change in weight along hatches per scheme



Change in DGEs along hatches per scheme



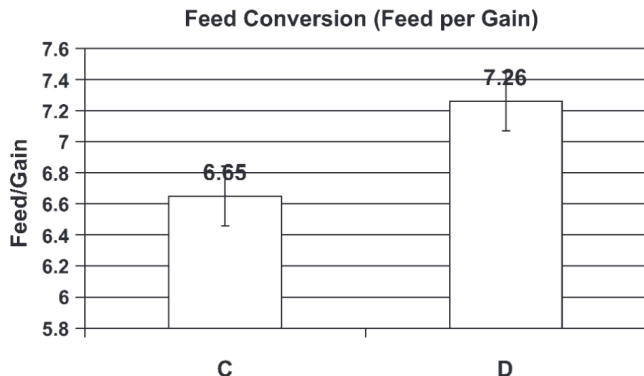
Change in IGEs along hatches per scheme



Change in mortality per scheme

Mortality was highly variable and the regression of percentage of mortality on hatch number showed a slight reduction in mortality with C-BLUP ($b = -0.06 \pm 0.15$ deaths/hatch) while mortality increased with D-BLUP ($b = 0.32 \pm 0.15$ deaths/hatch). The difference between regression coefficients was tested by the interaction of method by hatch and was found to be significant ($P < 0.05$). These results are consistent with the above findings that the associative effects were made worse with selection using D-BLUP and better with selection on the index from C-BLUP.

Final efficiency



6.65g of food to get 1g (?) of weight: the lower, the better

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- ▶ even if variation due to associative effects is small relative to the environmental variance, the impact of associative effects on group performance can be dramatic, particularly if group size is large
- ▶ with D-BLUP feed conversion efficiency can be improved only if feed efficiency is included in the selection program
- ▶ because of the biology of most traits, it is difficult to envision a situation in which the genetic correlation between direct and associative effects would be positive
 - ▶ cases of complementarity, altruism?

See also

Among many others:

- ▶ Bijma P, Muir WM, Van Arendonk JAM. 2006. Multilevel Selection 1: Quantitative Genetics of Inheritance and Response to Selection. *Genetics*. 175(1):277–288. doi:10.1534/genetics.106.062711.
- ▶ Ellen ED, Muir WM, Teuscher F, Bijma P. 2007. Genetic Improvement of Traits Affected by Interactions Among Individuals: Sib Selection Schemes. *Genetics*. 176(1):489–499. doi:10.1534/genetics.106.069542.