

Inbreeding and its Impact on Design of Breeding Programs

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Inbreeding = mating of individuals that are related by ancestry

→ may carry alleles that are identical by descent (ibd) (vs. by state)

→ increases probability that progeny will be homozygous

Inbreeding coefficient = probability individual's pair of alleles at a locus are ibd
= coefficient of coancestry of parents

Coefficient of coancestry individuals x and y

= prob(a random allele from x (at a given locus) is ibd to
a random allele from y)

Additive genetic relationship $x,y = 2 \times$ coefficient of coancestry between x and y

Effects of inbreeding → increased homozygosity

- Increased incidence of recessive disorders
- Inbreeding depression → reduced phenotypic performance
- Loss of genetic variance → reduction in rates of genetic improvement

Genotypic frequencies and mean performance in a population with inbreeding coefficient F for a single gene with 2 alleles with inbreeding coefficient F

$p = \text{freq}(A_1)$ $q = \text{freq}(A_2)$

Genotype	Frequency	Value	Frequency x value
A_1A_1	$p^2 + pqF$	$+a$	$p^2a + pqaF$
A_1A_2	$2pq - 2pqF$	d	$2pqd - 2pqdF$
A_2A_2	$q^2 + pqF$	$-a$	$-q^2a - pqaF$
		Sum = M_F	$= a(p-q) + 2dpq - 2dpqF$ $= a(p-q) + 2dpq(1-F)$

Without inbreeding: mean = $M_0 = a(p-q) + 2dpq$

Inbreeding depression = $M_0 - M_F = -2dpqF$

Summed over loci (no epistasis): $M_0 - M_F = -2F \sum dpq$

Impact of inbreeding on genetic variance:

Infinitesimal genetic model

No inbreeding: $\sigma_{g(t+1)}^2 = \frac{1}{4}(1 - k_s r_{s(t)}^2) \sigma_{g(t)}^2 + \frac{1}{4}(1 - k_d r_{d(t)}^2) \sigma_{g(t)}^2 + \frac{1}{2} \sigma_{g(o)}^2$ $\sigma_{g(o)}^2 = \text{base pop. var.}$

With inbreeding: Mendelian sampling variance = $(1 - \bar{F}_{s(t)}) \frac{1}{4} \sigma_{g(o)}^2 + (1 - \bar{F}_{d(t)}) \frac{1}{4} \sigma_{g(o)}^2$
 $= (1 - \frac{1}{2}(\bar{F}_{s(t)} + \bar{F}_{d(t)})) \frac{1}{2} \sigma_{g(o)}^2$

$$\sigma_{g(t+1)}^2 = \frac{1}{4}(1 - k_s r_{s(t)}^2) \sigma_{g(t)}^2 + \frac{1}{4}(1 - k_d r_{d(t)}^2) \sigma_{g(t)}^2 + (1 - \frac{1}{2}(\bar{F}_{s(t)} + \bar{F}_{d(t)})) \frac{1}{2} \sigma_{g(o)}^2$$

Only Mendelian sampling variance is affected by inbreeding, depending on inbreeding coefficient of parents, rather than inbreeding of the progeny

PREDICTION OF RATES OF INBREEDING

$$\Delta F = \frac{F_{t+1} - F_t}{1 - F_t} = \frac{1}{2N_e} \quad N_e = \frac{1}{2\Delta F}$$

N_e = Effective population size = number of individuals that would give rise to a rate of inbreeding ΔF if bred as an idealized population

Idealized population

- Random mating (incl. selfing), No selection
- Discrete (non-overlapping) generations
- Random distribution of family size – each individual has equal probability to contribute a progeny

Factors affecting rate of inbreeding in a closed non-idealized population

In a population that is not under selection:

- # males (N_m) and females (N_f) used for breeding

↔ population size

↔ selection

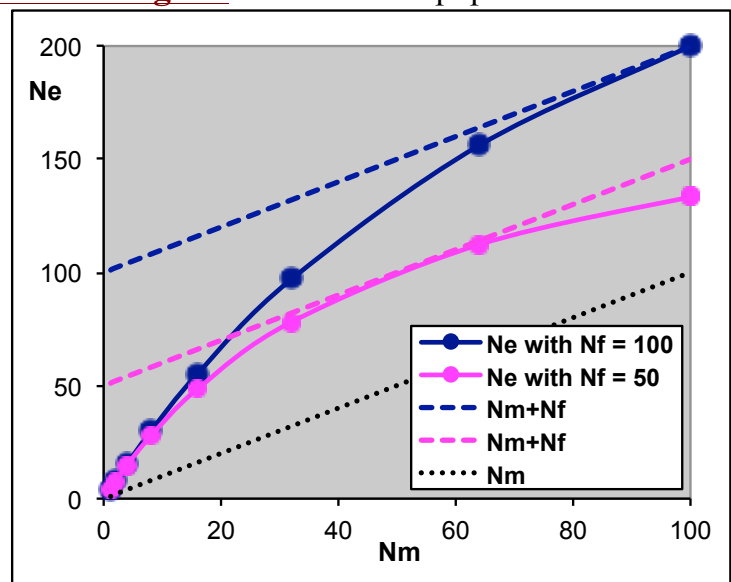
intensity

$$\frac{1}{N_e} = \frac{1}{4N_m} + \frac{1}{4N_f} \quad (\text{Wright, 1922})$$

$$\Delta F = \frac{1}{8N_m} + \frac{1}{8N_f}$$

→ N_e is less than the # parents; $\leq N_m + N_f$

→ N_e is driven primarily by the smaller of N_m and N_f



- **Variance of family size** \leftrightarrow unequal use of parents (and their progeny)
 - family size = number of progeny that become breeding parents
(Hill, 1979 Genetics 92:317)

$$N_e \approx \frac{8N}{V_{km} + V_{kf} + 4} \quad \rightarrow \quad \Delta F = \frac{1}{2N_e} = \frac{V_{km} + V_{kf} + 4}{16N}$$

N = Total population size ($\frac{1}{2}N$ males, $\frac{1}{2}N$ females)

V_{km} = Var(# progeny per male)

V_{kf} = Var(# progeny per female)

V_{km} and V_{kf} affected by unequal use of individuals for breeding

- selection
- differential use of selected individuals

Mean family size = 2 (each parent \rightarrow 2 progeny to maintain population size)

Idealized population: distribution of family size = Binomial \approx Poisson

$$\rightarrow V_{km} = V_{kf} = \text{mean family size} = 2 \quad \rightarrow \quad N_e = \frac{8N}{2 + 2 + 4} = N$$

Variance of family size can be reduced (by the breeder) by ensuring that all selected parents equally contribute breeders for the next generation

- within family selection – select best male and best female from each fullsib family $\rightarrow V_k = 0 \rightarrow N_e \approx 2N$

- **Generation Interval** \leftrightarrow shorter \rightarrow greater rate of inbreeding per year

$$N_e \approx \frac{8N_c L}{V_{km} + V_{kf} + 4} \quad \rightarrow \quad \Delta F/\text{yr} = \frac{1}{2N_e} / L = \frac{V_{km} + V_{kf} + 4}{16N_c L^2}$$

N_c = total # progeny per year

L = average generation interval (across males and females)

Selection increases inbreeding through: (Verrier et al. 1990)

- **Probability of co-selection of relatives** \leftrightarrow correlation of the selection criterion between relatives
- **Inheritance of selective advantage** – progeny of good parents are more likely to be selected themselves, as are their descendants \rightarrow increased variance of family size

More accurate methods to predict rates of inbreeding in populations under selection

In part based on notes from Bijma and van Arendonk
See Wray and Thompson (1990 Genet. Res. 55:41), Verrier et al. (1990)

Previous methods are 'single generation' methods

- account for differential contributions of ancestors to future generations through differential numbers of progeny that become breeding parents
- do not account for additional differences in an ancestral contributions through differential numbers of grand progeny that become breeding parents

$\Delta F \sim$ variance of long-term genetic contributions among ancestors (Wray&Thompson '90)

Theory of long-term genetic contributions

Wray and Thompson 1990. Genet. Res. 55:41 Woolliams et al. 1999 Genetics 153:1009
Woolliams and Bijma 2000 Genetics 154:1851 Bijma and Woolliams 2000 Genetics 156:361
Bijma et al. 2000 Genetics 156:361 Bijma et al. 2001 J.Anim.Sci. 79:840

$r_{i,t_1}(j, t_2)$ = **Genetic contribution** of ancestor i born at generation t_1 to an individual j born at generation t_2 ($t_2 > t_1$)
= proportion of genes of j expected to derive by descent from ancestor i .

Note: Full-sibs share $\frac{1}{2}$ of their genes but make no genetic contribution to each other.

$r_{i,t_1}(t_2)$ = **Mean genetic contribution** of ancestor i born at generation t_1 to generation t_2
= the average proportion of genes among individuals in generation t_2 contributed by ancestor i

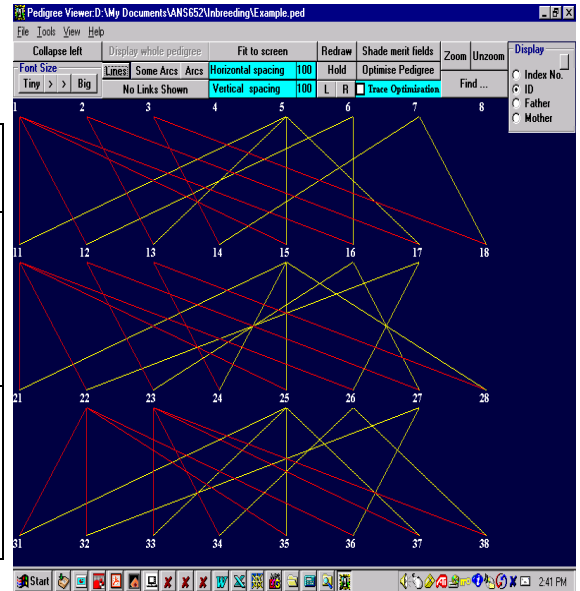
- $E(r_{i,t_1}(t_2)) = \frac{1}{2N_m}$ for male ancestors ($N_m = \#$ male ancestors)
= $\frac{1}{2N_f}$ for female ancestors
- $r_{i,t_1}(t_2)$ differ between ancestors due to differences in # **progeny**
and differences in the **selective advantage** of descendents
$$\sum_i r_{i,t_1}(t_2) = 1$$
- as $t_2 - t_1$ increases, contributions from a given ancestor stabilize and become similar across individuals in generation $t_2 \rightarrow \text{Var}_j(r_{i,t_1}(j, t_2)) \rightarrow 0$
- $t_2 - t_1 \rightarrow$ infinity, genetic contributions from a given ancestor are the same for all individuals in time t_2
= **long-term genetic contribution** of ancestor $i = r_i$

Pedigree to illustrate concept of genetic contributions

Each generation contains 4 males and 4 females.

Base population: 1-4=males ; 5-8=females

sex	Generation 1			Generation 2			Generation 3		
	ind	sire	dam	ind	sire	dam	ind	sire	dam
Male	11	1	5	21	11	15	31	22	25
	12	1	6	22	11	17	32	22	27
	13	2	5	23	12	16	33	23	25
	14	3	7	24	13	15	34	23	26
Female	15	1	5	25	11	15	35	22	25
	16	1	6	26	11	17	36	22	27
	17	2	5	27	12	16	37	23	25
	18	3	7	28	13	15	38	23	26



Contribution of each ancestors to each offspring: $r_{i,t_1}(j, t_2)$
and mean contribution of each ancestor: $r_{i,t_1}(t_2)$

<i>Offspring¹</i>	Ancestors							
	1	2	3	4	5	6	7	8
Generation 1								
11/15	0.5	0	0	0	0.5	0	0	0
12/16	0.5	0	0	0	0	0.5	0	0
13/17	0	0.5	0	0	0.5	0	0	0
14/18	0	0	0.5	0	0	0	0.5	0
Mean contribution	0.25	0.125	0.125	0	0.25	0.125	0.125	0
Generation 2								
21/25	0.5	0	0	0	0.5	0	0	0
22/26	0.25	0.25	0	0	0.5	0	0	0
23/27	0.5	0	0	0	0	0.5	0	0
24/28	0.25	0.25	0	0	0.5	0	0	0
Mean contribution	0.375	0.125	0	0	0.375	0.125	0	0
Generation 3								
31/35	0.375	0.125	0	0	0.5	0	0	0
32/36	0.375	0.125	0	0	0.25	0.25	0	0
33/37	0.5	0	0	0	0.25	0.25	0	0
34/38	0.375	0.125	0	0	0.25	0.25	0	0
Mean contribution	0.406	0.104	0	0	0.313	0.187	0	0

¹ Each generation consisted of a full sib male and female, which have equal contributions. Contributions can be derived from pedigree. Contributions across ancestors sum to 1. Contributions of a given ancestor to descendants become less variable over time.

Use of long-term genetic contribution theory to predict ΔF

Rate of inbreeding is related to the variance of long-term contributions among ancestors

- Asymptotic $\Delta F = \frac{1}{4} * \text{sum of squares of long-term contributions}$

$$\Delta F = \frac{1}{4} \sum r_i^2$$

Example: 20 selected parents per generation (ignoring that there are two sexes).

Pedigree analysis quantifies the contribution of each parent to a particular generation.

Their contribution will sum to 1; genetic contributions always sum to 1 per generation.

Consider two extreme cases:

1) the contribution of each individual is the same, $r = 0.05$ for all individuals

$$\rightarrow \Delta F = \frac{1}{4}(0.05^2 + 0.05^2 + \dots 0.05^2) = 0.0125 = 1.25\% \text{ per generation}$$

2) contributions differ between individuals: $r = 0.25$ for 4 best parents $r = 0$ for rest

$$\rightarrow \Delta F = \frac{1}{4}(0.25^2 + 0.25^2 + \dots 0^2) = 0.0625 = 6.25\% \text{ per generation.}$$

\rightarrow variance in the contributions of ancestors \rightarrow higher inbreeding

Example: If there were 2 male and 2 female ancestors in a generation with contributions $\frac{3}{8}$, $\frac{1}{8}$, $\frac{5}{16}$ and $\frac{3}{16}$ (note the 2 males sum to $\frac{1}{2}$ and the two females sum to $\frac{1}{2}$) then the estimate of ΔF attributed to that generation is

$$\Delta F = \frac{1}{4} \left\{ \left(\frac{3}{8} \right)^2 + \left(\frac{1}{8} \right)^2 + \left(\frac{3}{16} \right)^2 + \left(\frac{5}{16} \right)^2 \right\} = 0.072$$

If the population were in a steady state we would expect approximately the same answer every generation and the average over generations would be the expected ΔF .

The importance of relationship $\Delta F = \frac{1}{4} \sum r_i^2$ is:

- It is general and applies to both selected and unselected populations.
- It relates ΔF to terms that can be found in the relationship (A) matrix.
- Predictive forms can be developed from the relationship.
- Strictly it is an approximation, but the proportional error (an underestimate) is of the same order as those previously developed for unselected populations.
- Its form will lead to insights into how optimal selection schemes work.

A problem for prediction of ΔF is that it requires estimation of the variance of long term contributions

Use of long-term contributions to predict rates of inbreeding (Woolliams and Bijma, 2000):

$$E(\Delta F) = E\{\frac{1}{4}\sum r_i^2\} = \frac{1}{4}T^*E[r_i^2] \quad T = \# \text{ selection candidates}$$

$E[r_i^2]$ = expectation of square of contributions across all candidates

- Requires mean and variance of long-term contributions

BUT: Woolliams et al. ('99) showed: $\Delta F \sim$ square of *expected* long-term genetic contributions of selected parents

$$\Delta F = \frac{1}{4}\sum r_i^2 \quad \rightarrow \quad \Delta F = \frac{1}{2}NE(r)^2$$

→ prediction of the *variance* of long term genetic contributions not needed

Following Woolliams et al. (1999), the (long-term) genetic contribution of an ancestor can be predicted by regression on its breeding value, using the model:

$$E(r_i | g_i) = r_i = \alpha + \beta g_i$$

r_i = expected genetic contribution of ancestor i

α = expected genetic contribution for an average ancestor

β = regression coefficient of the genetic contribution on the BV (g_i) of the ancestor

For discrete generations: α is determined by the number of parents:

For male ancestors, $\alpha = \frac{1}{2}N_s$

For female ancestors $\alpha = \frac{1}{2}N_d$

β describes that:

- selective advantage influences the selection decisions in offspring generation
- selective advantage is inherited → has an influence beyond offspring generation

→ Two mechanisms must be described to enable the prediction:

- 1) better parents have on average more offspring that are selected as parents.
- 2) the selected offspring of better parents are on average better, which also affects the genetic contributions.

In short, the procedure (implemented in SelAction) is as follows:

1) A regression model is used to predict the long-term contribution of selected parents,

$$E(r) = \alpha + \beta(g - \bar{g})$$

$E(r)$ = expected contribution given the true BV of an individual

α = the contribution of an individual with an average BV

β = increase of the contribution of parents with a higher BV.

The second term accounts for parents with high BV having more selected offspring.

α and β can be derived mathematically (see Woolliams et al. 1999).

2) Calculate the square of the expected contributions of selected parents:

$$E(r)^2 = \alpha^2 + \beta^2 \sigma_A^2 (1 - k\rho^2) \quad (\text{Woolliams et al. 1999})$$

$\sigma_A^2(1 - k\rho^2)$ = genetic variance of selected parents; ρ = accuracy

The above gives $E(r)^2$, but in fact we need to calculate $E(r^2)$:

$E(r)^2$ = square of the expected contributions of selected parents.

$E(r^2)$ = expectation of the squared (actual) contribution of selected parents.

Under certain conditions $E(r^2) = 2[E(r)]^2$, leading to the following result to predict ΔF :

$$\Delta F = \frac{1}{2} N E(r)^2$$

N = # parents $E(r)^2$ = square of the expected contributions of selected parents,
predicted as given above

Note: $\frac{1}{4}$ in $\Delta F = \frac{1}{4} \Sigma r_i^2$ is replaced by $\frac{1}{2}$ because we have replaced the square of the actual contributions Σr^2 by the square of the expected contributions, $N E(r)^2$.

Woolliams et al. (1998) extended the method to overlapping generations.

Design of breeding programs with controls on inbreeding

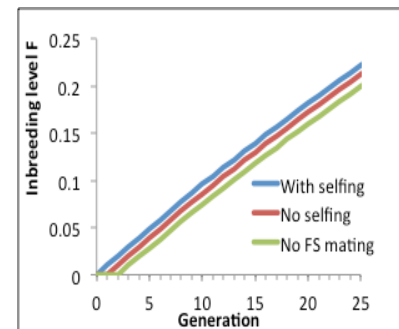
Short-term response is maximized by (based on $\Delta G = i r \sigma_g$):

- selection on BLUP EBV – i.e. maximize accuracy r
- select only the best individuals – i.e. maximize intensity i - given repro rates

But this may not maximize long(er)-term response because it leads to higher ΔF .

Strategies to control inbreeding

- (Mate selected parents such that inbreeding of progeny is minimized)
 - limited effect on long-term rates of inbreeding
- Select more animals - increase population size → increased costs
 - reduce selection intensity → reduced (short-term) response
- Reduce probability of co-selection of relatives
 - impose restrictions on selection of relatives (e.g. 1/full-sib family)
 - increase h^2 in genetic evaluation (affects both pedigree and progeny info)
 - decrease weight on pedigree information
 - control the average relationship among selected parents
 - cost factor on average relationship (Brisbane and Gibson 1994)
 - constraint on average relationship (optimal contribution selection) (Meuwissen 1997, JAS 75:934)
- Introduce outside genetics



Toro & Perez-Enciso 1990, GSE:

Optimal weight given to family information

Table I. Expected and observed cumulative selection response, R_E and R_o , and inbreeding coefficient (%), F_E and F_o , after 5 generations of selection, as a function of the weight given to family information, λ . The initial additive variance was 50.

Standard errors ranged from 0.24 to 0.28 (R_o), and from 0.16 to 0.43 (F_o).

	λ	R_E	R_o	F_E	F_o
$h^2 = 0.10$	0 w/in family	6.64	6.26	12.86	10.65
	1	13.80	11.74	13.63	14.65
	2	17.22	13.79	19.32	21.45
	3	18.45	15.27	23.81	26.28
	4	18.80	14.97	26.87	30.03
	5	18.88	14.89	28.98	32.39
	6	18.85	14.88	30.48	34.37
	7	18.77	14.46	31.55	35.06
	6.33 Optimal	18.83	15.00	30.85	34.52
$h^2 = 0.30$	0.0 w/in family	12.16	11.81	12.86	10.06
	1.0	23.72	16.87	15.38	12.97
	1.5	26.14	19.62	19.08	17.22
	2.0	27.27	21.62	22.24	25.06
	2.5	27.65	21.50	24.71	26.90
	3.0	27.73	21.73	26.64	29.06
	3.5	27.68	21.70	28.14	30.08
	4.0	27.57	21.36	29.36	31.94
	3.73 Optimal	27.64	21.09	28.71	31.92

Restriction on the distribution of family size

Table II. Expected and observed cumulative selection response, R_E and R_o , and inbreeding coefficient (%), F_E and F_o , after 5 generations of selection, as a function of family size. The initial additive variance was 50, $h^2 = 0.10$.

Standard errors ranged from 0.21 to 0.32 (R_o), and from 0.16 to 0.43 (F_o).

Case	Distribution of family size	R_E	R_o	F_E	F_o
1	4 4 0 0 0 0 0 0	17.42	12.77	42.76	41.40
2	4 3 1 0 0 0 0 0	18.17	13.94	35.81	35.88
3	4 2 2 0 0 0 0 0	17.87	13.85	33.26	33.88
4	4 2 1 1 0 0 0 0	17.78	14.85	30.59	31.94
5	3 3 2 0 0 0 0 0	17.30	13.72	30.59	31.17
6	3 3 1 1 0 0 0 0	17.21	14.34	27.80	28.60
7	4 1 1 1 1 0 0 0	16.38	13.48	27.80	28.62
8	3 2 2 1 0 0 0 0	16.91	14.99	24.87	26.56
9	3 2 1 1 1 0 0 0	16.24	14.32	21.79	24.06
10	2 2 2 2 0 0 0 0	14.91	12.66	21.79	22.89
11	2 2 2 1 1 0 0 0	14.85	13.18	18.57	20.24
12	3 1 1 1 1 1 0 0	14.23	12.78	18.57	20.17
13	2 2 1 1 1 1 0 0	13.56	12.22	15.20	16.81
14	2 1 1 1 1 1 1 0	10.83	9.65	11.66	13.27
15	1 1 1 1 1 1 1 1	5.90	5.54	7.96	9.18
Opt.		18.83	15.00	30.85	34.52

Table III. Expected and observed cumulative selection response, R_E and R_o , and inbreeding coefficient (%), F_E and F_o , after 5 generations of selection, as a function of family size. The initial additive variance was 50, $h^2 = 0.30$.

Standard errors ranged from 0.17 to 0.27 (R_o), and from 0.16 to 0.43 (F_o).				
Case	R_E	R_o	F_E	F_o
1	24.48	18.85	42.76	40.61
2	26.17	20.17	35.81	35.06
3	25.93	20.77	33.26	32.75
4	26.03	20.38	30.59	31.77
5	25.35	20.53	30.59	30.79
6	25.45	20.84	27.80	28.48
7	24.29	19.95	27.80	29.31
8	25.21	20.42	24.87	26.26
9	24.49	20.66	21.79	24.19
10	22.27	18.86	21.79	21.74
11	22.71	19.21	18.57	20.15
12	21.89	18.86	18.57	20.47
13	21.13	19.08	15.20	17.89
14	17.51	16.28	11.66	13.44
15	10.81	10.56	7.96	9.23
Opt.	27.64	21.09	28.71	31.92

Minimum coancestry matings

The observed genetic progress attained during the first 5 generations of selection, both with random, R_R , and minimum coancestry matings, R_{MC} , together with the corresponding inbreeding coefficients, F_R and F_{MC} , are shown in Table IV (λ_{op} was used). The selection response obtained was similar in both cases, as expected in a strictly additive model. However, minimum coancestry matings dramatically reduced inbreeding, compared with random mating. Nevertheless, it should be noted that this reduction was mainly due the one generation delay in the initial appearance of consanguinity.

Table IV. Observed cumulative selection response after 5 generations of selection with random mating, R_R , minimum coancestry mating, R_{MC} , and mate selection, R_{MS} , together with their respective inbreeding coefficient (%) F_R , F_{MC} and F_{MS} . The initial additive variance was 50.

Generation	R_R	R_{MC}	R_{MS}	F_R	F_{MC}	F_{MS}
$h^2 = 0.10$						
1	3.71	3.86	2.76	8.49	0.00	3.01
2	6.58	6.53	5.74	15.89	8.54	7.87
3	9.48	9.08	8.53	22.54	14.10	13.56
4	12.27	11.98	11.64	28.88	19.08	18.73
5	15.00	14.10	14.45	34.52	24.08	23.77
$h^2 = 0.30$						
1	5.26	5.65	4.96	7.87	0.00	3.03
2	9.54	9.64	9.90	14.44	7.21	8.00
3	14.51	16.68	14.38	21.01	12.48	13.19
4	17.43	17.79	18.49	26.43	17.03	17.81
5	21.09	21.34	22.31	31.92	21.78	22.92

Standard errors in the fifth generation ranged from 0.23 to 0.28 (R_R and R_{MC}), 0.80 (R_{MS}) and 0.40 (F_R , F_{MC} and F_{MS}).

Mates selection

Table IV shows the observed response, R_{MS} , and the inbreeding coefficient, F_{MS} . It can be seen that, while conforming with inbreeding restrictions, response was not smaller than that attained under the optimum unrestricted scheme, R_R .

Quinton, Smith, Goddard. 1992. Comparison of selection methods at the same level of inbreeding. J. Anim. Sci. 70: 1060.

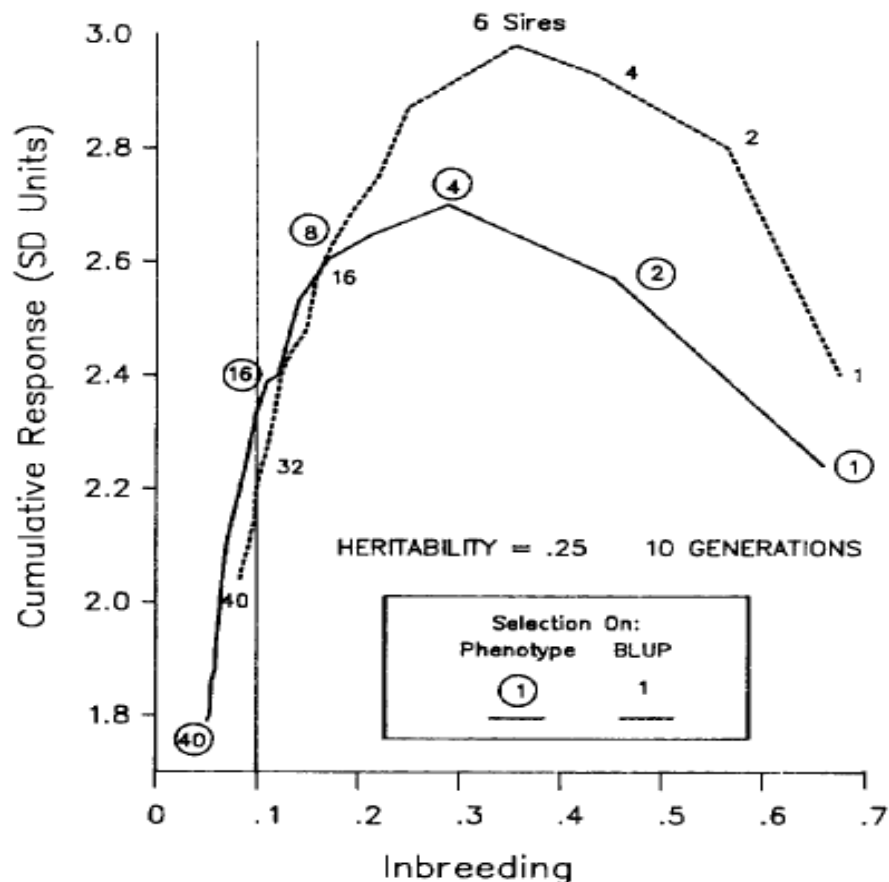


Figure 1. The average (100 replicates) simulated cumulative genetic response and inbreeding after 10 generations of phenotypic and best linear unbiased prediction (BLUP) selection for a range [1 to 40] in the number (S) of sires selected (heritability .25, S/100 males selected, 50/100 females selected). Numerical results are given in Table 2.

ABSTRACT: Animal geneticists predict higher genetic responses to selection by increasing the accuracy of selection using BLUP with information on relatives. Comparison of different selection methods is usually made with the same total number tested and with the same number of parents and mating structure so as to give some acceptable (low) level of inbreeding. Use of family information by BLUP results in the individuals selected being more closely related, and the levels of inbreeding are increased, thereby breaking the original restriction on inbreeding. An alternative is to compare methods at the same level of inbreeding. This would allow more intense selection (fewer males selected) with the less accurate

methods. Stochastic simulation shows that, at the same level of inbreeding, differences between the methods are much smaller than if inbreeding is unrestricted. If low to moderate inbreeding levels are targeted, as in a closed line of limited size, then selection on phenotype can yield higher genetic responses than selection on BLUP. Extra responses by BLUP are at the expense of extra inbreeding. The results derived here show that selection on BLUP of breeding values may not be optimal in all cases. Thus, current theory and teaching on selection methods are queried. Revision of the methodology and a reappraisal of the optimization results of selection theory are required.

Villaneuva and Woolliams (1997). Optimization of breeding programmes under index selection and constrained inbreeding. Genet. Res. Camb. 69:145

Objective = maximize response (over planning horizon) with constraint on ΔF

Parameters to optimize:

- Population size
- # sires and dams to select
- Selection criterion to use (emphasis on family info)
- Mating strategy

Population size = 200

Maximize average response from 5 - 20 generations by optimizing

- # sires selected
- # dams/sire
- weight on family vs. own performance

Table 1. An example of the maximization procedure for $N = 200$, $h^2_{(0)} = 0.3$ and $\Phi_{(5,20)} = \Delta G_{(5,20)} - \lambda \Delta F$. Hence, for a restriction of $\Delta F \leq 1\%$, the scheme for $\lambda = 7.4$ would be expected to give the greatest value of $\Delta G_{(5,20)}$ by using 30 sires (N_s) with a mating ratio (d) of 1 and a relative weight ($b_2 = b_3$) of 1.04 for the family means

λ	$\Phi_{(5,20)}$	$\Delta G_{(5,20)}$	ΔF	N_s	d	$b_2 = b_3$
0.0	0.322	0.322	0.03179	16	1	1.63
1.0	0.295	0.318	0.02336	19	1	1.47
2.0	0.274	0.312	0.01910	21	1	1.33
3.0	0.256	0.304	0.01612	23	1	1.25
7.3	0.201	0.276	0.01020	29	1	1.01
7.4	0.200	0.273	0.00986	30	1	1.04
55.6	-0.009	0.132	0.00253	67	1	0.74
55.7	-0.009	0.130	0.00249	68	1	0.76

	$h^2=0.1$			$h^2=0.3$		
	Constraint on Inbreeding			Constraint on Inbreeding		
	None	$\Delta F \leq 1\%$	$\Delta F \leq 0.25\%$	None	$\Delta F \leq 1\%$	$\Delta F \leq 0.25\%$
$\Delta F/\text{generation}$	2.09	1.00	0.25	2.00	1.00	0.25
ΔG in generation 20	0.109	0.100	0.047	0.278	0.258	0.128
# sires	22	32	69	21	30	68
# dams/sire	1	1	1	1	1	1
Relative weight on family info	2.12	1.60	1.07	1.43	1.06	0.76
Optimal weight based on sel. index	9.6					