

MIXED MODEL METHODOLOGY TO ESTIMATE ADDITIVE AND DOMINANCE GENETIC VALUES
UNDER COMPLETE DOMINANCE AND INBREEDING

Pekka Uimari¹ and B.W. Kennedy
Department of Animal and Poultry Science, University of Guelph
Guelph, Ontario, Canada N1G 2W1

SUMMARY

Four different mixed models were used to estimate additive and dominance genetic values of animals from simulated data. Five generations were produced allowing inbreeding using a genetic model with a large number of loci (64) and two different gene frequencies (0.5 and 0.8). There was complete dominance at all loci. Population size at each generation was 40 and 5 males were either randomly selected or selected on phenotype and mated to 20 females. In generation 5, average inbreeding was 0.08. A model with an additive relationship matrix (A), dominance relationship matrix (D) and inbreeding coefficient (F) as a covariate gave unbiased prediction of additive and dominance values and unbiased estimation of inbreeding depression under random as well as phenotypic selection. A model which included A but ignored D and F underestimated predictors of additive genetic values under both random and phenotypic selection and a model that included A and F but ignored D overestimated additive genetic values with phenotypic selection. A model which ignored A and D and included only F seriously underestimated inbreeding depression when phenotypic selection was practised.

INTRODUCTION

Mixed model methodology is widely used in animal breeding, but most applications are restricted to handling additive gene effects only. Henderson (1985) presented methods for obtaining best linear unbiased predictions (BLUP) of nonadditive genetic merits in non-inbred populations. However, if the model includes dominance gene action with inbreeding, predictions of additive genetic value are biased (Maki-Tanila & Kennedy, 1986). Smith and Maki-Tanila (1990) have extended a method of Smith and Allaire (1985) which uses a genomic table to compute the relationship matrix and its inverse based on the theory of the genetic covariances between inbred relatives as given by Gillois (1964) and Harris (1964). However, the method is computationally very difficult. Kennedy et al. (1988) proposed including F as a covariate in the model, in addition to additive (A) and dominance (D) relationship matrices, as a simple expedient to account for inbreeding depression. This study examines this proposal through computer simulation.

MATERIALS AND METHODS

Forty animals were sampled from a base population in Hardy-Weinberg and linkage equilibrium for a trait controlled by 64 loci with complete dominance at each locus. Each locus had two alleles and gene frequency of the favourable allele was 0.5 or 0.8. Heritability, in the narrow sense, was 0.3 in the base population in both cases. To produce the next generation, five males were selected either randomly or on the animal's phenotypic value and were bred to 20 females. This breeding structure was carried over five generations.

The simulation was based on a FORTRAN program (M. Quinton, personal communication) which was tested by using full sib-matings and computing variances and covariances between family members. These were then compared with values implied by the genetic theory of Gillois (1964) and Harris (1964).

¹ Present address: Department of Animal Breeding, University of Helsinki, SF-00710 Helsinki, Finland.

Using data over all generations, four different mixed models were used to evaluate animals:

$$\begin{aligned}
 [1] \quad & y_i = \mu + a_i + e_i \\
 [2] \quad & y_i = \mu + bF_i + a_i + e_i \\
 [3] \quad & y_i = \mu + bF_i + a_i + d_i + e_i \\
 [4] \quad & y_i = \mu + bF_i
 \end{aligned}$$

where y_i is the phenotypic value of the i th animal, μ is the population mean, a_i is the additive genetic (breeding) value of the i th animal $\sim(0, A\sigma_a^2)$, d_i is the dominance genetic value of the i th animal $\sim(0, D\sigma_d^2)$, b is the regression of y_i on F_i , the inbreeding coefficient of the i th animal and e_i is the random error of the i th animal $\sim(0, I\sigma_e^2)$. D was computed from the elements of A ignoring inbreeding (Henderson, 1985). Estimates of additive effect under models [1] to [3] were compared to true (simulated) additive effects computed relative to the base population. Dominance effects under [3] were estimated as $d_i + bF_i$ and were compared with true (simulated) dominance values using base population parameters. The last model [4] was used to show the bias in estimates of inbreeding depression when covariances between relatives in selected populations are ignored. All 16 alternative cases consisted of 100 replicates.

RESULTS

Average inbreeding was 0.03 in generation three and 0.08 in generation five. Table 1 shows the amount of the bias between true (simulated) and estimated additive and dominance genetic value for generations 1, 3 and 5. The evaluations were done at the end of generation five.

Model [1] underestimated the additive genetic value because it did not account for inbreeding depression. Underestimation was greater in case of random selection than with phenotypic selection because with selection there is a reduction in inbreeding depression (Falconer, 1981). Model [2] gave unbiased predictions of additive genetic value, when selection was random, but biased when animals were selected on their phenotypic value. Model [3] gave unbiased estimates of additive and dominance genetic values under both random and phenotypic selection (see figures 1 and 2 for phenotypic selection).

Table 1. Average predicted minus true additive and dominance genetic values in generation 1, 3 and 5 for models [1], [2] and [3] under random (r) and phenotypic (ph) selection. Estimates of dominance genetic value are $d_i + bF_i$ using the model [3]. Standard errors are in brackets.

Sel.	Gene freq.	Gen.	Additive			Dominance
			[1]	[2]	[3]	[3]
r	.5	1	0.00 (.08)	0.00 (.08)	0.00 (.08)	0.04 (.06)
		3	-0.59 (.13)	0.16 (.14)	0.15 (.14)	-0.06 (.08)
		5	-1.61 (.17)	0.15 (.18)	0.11 (.18)	-0.14 (.13)
r	.8	1	-0.02 (.02)	-0.02 (.02)	-0.02 (.02)	0.03 (.03)
		3	-0.62 (.05)	-0.07 (.05)	-0.01 (.04)	0.04 (.03)
		5	-1.46 (.07)	-0.06 (.07)	-0.04 (.06)	0.06 (.04)
ph	.5	1	0.00 (.08)	0.00 (.08)	0.00 (.08)	0.04 (.06)
		3	-0.41 (.14)	0.31 (.15)	0.04 (.15)	0.10 (.07)
		5	-1.11 (.17)	0.51 (.20)	-0.05 (.20)	0.20 (.15)
ph	.8	1	-0.02 (.02)	-0.02 (.02)	-0.02 (.02)	0.02 (.03)
		3	-0.20 (.05)	0.33 (.05)	0.00 (.04)	0.02 (.03)
		5	-0.41 (.06)	0.76 (.07)	-0.02 (.06)	0.03 (.04)

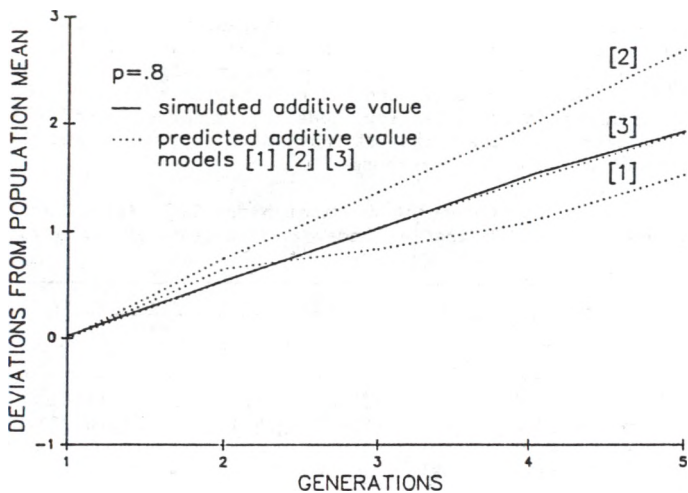


Figure 1. Simulated (true) and estimated additive genetic value according to models [1], [2] and [3] under phenotypic selection.

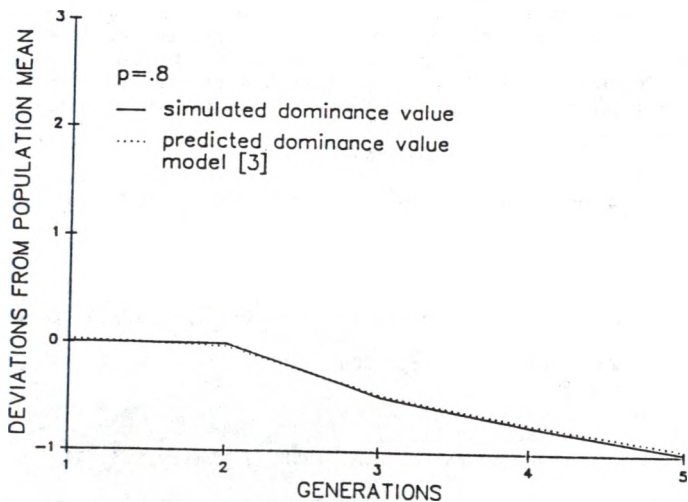


Figure 2. Simulated (true) and estimated dominance genetic value according to model [3] under phenotypic selection.

Estimates of inbreeding depression for 100% inbred animals, i.e. the estimated regression coefficient for F from models [2], [3] and [4], are listed in table 2. The expected values for b under random selection were computed from $-2p(1-p)dF$ times number of loci (Falconer, 1981). Models [2] and [3] gave better estimates of b under random selection than with phenotypic selection. Model [4] underestimated b, because selection response runs counter to the effect of inbreeding depression and the model [4] does not take account of selection response.

Table 2. Expected and estimated inbreeding depression for 100% inbred animals in generation five for models [2], [3] and [4] under random (r) and phenotypic (ph) selection.

Sel.	Gene freq.	Expected	Models		
			[2]	[3]	[4]
r	.5	-32.00	-33.43 (1.28)	-33.32 (1.29)	-33.17 (1.62)
	.8	-20.48	-20.24 (0.54)	-20.25 (0.53)	-20.78 (0.73)
ph	.5		-31.13 (1.39)	-30.00 (1.39)	-4.34 (1.65)
	.8		-17.77 (0.47)	-14.84 (0.45)	-6.44 (0.53)

DISCUSSION

The model $y_i = \mu + bF_i + a_i + d_i + e_i$ gave unbiased estimates of additive and dominance genetic values and of inbreeding depression under selection and inbreeding. An advantage of this model is that there is need to specify only two genetic parameters, the additive and dominance genetic variances of the population, instead of five required to build a complete relationship matrix under dominance and inbreeding (Gillois, 1964; Harris, 1964). A disadvantage of the method is that there are no simple rules for computing the inverse of D as there are for A (Henderson, 1976). The usefulness of this method for practical purposes with large data sets is dependent, therefore, upon ability to invert D. Many D matrixes, however, will be amenable to inversion using block diagonal and sparse matrix inversion techniques.

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