

## Effect of population structure and underlying magnitude of dominance genetic effects on the estimation of additive and dominance genetic variances

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### Abstract

Five populations with varying percentages of animals in full-sib families were simulated. For each population, three combinations of additive and dominance genetic variances of different relative magnitudes were considered, thereby creating fifteen sub-populations. Constant residual variance was used in all populations. Variance components were estimated using the tilde-hat approximation to REML based on sire-dam model. Populations with few full-sibs (2% and 10%) and small magnitude of dominance variance (50), resulted in inaccurate estimation of dominance genetic variance. In populations with a large number of animals having dominance genetic relationships (20% or greater), estimates of dominance genetic variances can be obtained with improved accuracy even when the dominance genetic effect in the population is of small magnitude. Overestimation of additive genetic variance increased as both the number of full-sibs and the magnitude of dominance effects increased.

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### Introduction

The sustained ability to improve phenotypic performance of livestock with respect to economically important traits is partially dependent upon accurate evaluation of an animal's genetic merit. Knowledge of genetic variance and its distribution in the population structure can lead to the design of optimum breeding plans (Miller *et al.*, 1963; Willham & Pollak, 1985).

Genetic evaluation in any livestock species has been for the prediction of transmitting ability, or additive genetic effects only. Dominance and other nonadditive genetic effects have not been commonly considered. The use of linear mixed model, or animal model, for genetic evaluations could be expanded to include prediction of genetic merit and estimation of genetic variances for dominance, epistatic and cytoplasmic effects.

Recent developments in statistical methods and computing algorithms especially for the inverted nonadditive genetic relationship matrices allow the use of animal models to evaluate nonadditive genetic effects for large data sets (Hoeschele & VanRaden, 1991; Misztal *et al.*, 1995). These developments have triggered many recent studies for dairy cattle and fish in identifying traits that have significant dominance genetic effects. Evidence of dominance effects though inconsistent is reported in several studies (Tempelman & Burnside, 1990; Lawlor *et al.*, 1992; VanRaden *et al.*, 1992; Wei & Van der Werf, 1993; Miglior *et al.*, 1995; Rodriguez-Almeida *et al.*, 1995; Misztal *et al.*, 1995; 1998; Misztal, 1997; Varona *et al.*, 1997; Culbertson *et al.*, 1998; Rye & Mao, 1998). The differences in magnitude of dominance effects in these studies could be partly attributed to the differences in the data structure (Rye & Mao, 1996; Misztal, 1997).

Accuracy of genetic evaluations could be increased when dominance effects are considered in animal models (Henderson, 1989; De Boer & van Arendonk, 1992; VanRaden *et al.*, 1992; Johansson *et al.*, 1993; Misztal, 1997). It is expected that changes in breeding values would be pronounced in animals with many dominance relationships (Misztal, 1997; Varona *et al.*, 1997). The objectives of this study were: a) to investigate the effect of ignoring versus considering dominance genetic effects in the model on the estimation of additive genetic variance, b) to test the hypothesis that the ability to detect and the accuracy of detecting the magnitude of dominance genetic variance depends on the density and size of full-sib families in the data.

## Materials and Methods

Five populations with varying percentages of animals in full-sib families were simulated (Table 1). Percentages of animals in full-sib families were 100, 50, 20, 10 and 2 percent. The number of animals in each population was 10 000 and each full-sib family had 25 animals. For each population, combinations of additive variance,  $V_A$  and dominance variance,  $V_D$  were considered:  $V_A = 950$  and  $V_D = 50$ ,  $V_A = 800$  and  $V_D = 200$ ,  $V_A = 500$  and  $V_D = 500$ , thereby creating a total of 15 sub-populations, each with 10 000 animals. The residual variance was constant at 2000 in all populations. Each sub-population was simulated for 50 replicates.

**Table 1** Percentage of full-sib animals in different populations

Number of animals	Number of full-sib families	% of animals in full-sib families
10 000	400	100
10 000	200	50
10 000	80	20
10 000	40	10
10 000	8	2

Records were simulated and analyzed according to the following sire and dam model:

$$y_{ijk} = \mu + s_i + m_j + sm_{ij} + e_{ijk}$$

where  $\mu$  is the population mean,

$s_i$  is the additive effect of sire  $\sim N(0, 1/4\sigma_a^2)$

$m_j$  is the additive effect of dam  $\sim N(0, 1/4\sigma_a^2)$

$sm_{ij}$  is the dominance effect due to interaction of sire and dam  $\sim N(0, 1/4\sigma_d^2)$

$e_{ijk}$  is the residual effect  $\sim N(0, \sigma_e^2 + 1/2\sigma_a^2 + 3/4\sigma_d^2)$

Derivation of additive (a) and dominance (d) genetic values Hoeschele & VanRaden, 1991):

$$a = .5a_s + .5a_d + m_a$$

$$d = fd_{s,d} + m_d$$

Where  $a_s$  and  $a_d$  are the additive genetic effects of sire and dam, respectively.  $fd_{s,d}$  is combination of sire with dam due to interaction of genes from the sire with genes from the dam.  $m_a$  and  $m_d$  are the respective additive and dominance genetic effects due to mendelian sampling.

$$\text{Var}(m_a) = 0.5 \sigma_a^2; \text{Var}(m_d) = 0.75 \sigma_d^2$$

The above sire-dam model can be written in matrix notation on an individual animal basis as :

$$y = Za + Zd + e$$

where,

$y$  is the data vector;

$a$  is the vector of random additive effects for sire and dam;

$d$  is the vector of random dominance effects;

$e$  is the vector of residuals;

$Z$  are known matrices corresponding to, respectively, to  $a$  and  $d$ .

Sires and dams were all unrelated and as a consequence, the  $sm_{ij}$  interactions are not correlated.

Another sire-dam model (reduced model) which did not include dominance genetic effects was used to analyze the same data as analyzed under the full model to assess the impact on additive genetic variance when dominance genetic effects are ignored in the evaluation:

Variance components were estimated using the tilde-hat approximation to REML (VanRaden & Jung, 1988). The inverse relationship matrices,  $A^{-1}$  and  $D^{-1}$  were computed directly by algorithms described by Henderson (1976) and Hoeschele & VanRaden (1991). Computations were done using FORTRAN programs INVERS and NONAD2 written by Hoeschele (1991).

## Results and Discussion

Presented in Tables 2 are the estimates of additive genetic variances under reduced and full models in populations with 2% of animals in full-sib families.

**Table 2** Additive genetic variances in population with 2% animals in full-sib families

Model	$V_A$	Additive variance	s.e.	Dominance variance	s.e.	Residual variance	s.e.
Reduced	950	980	48	-		2034	12
Full	950	949	47	185	35	1918	12
Reduced	800	830	32	-		2195	8
Full	800	801	31	188	43	2077	12
Reduced	500	557	27	-		2459	9
Full	500	497	22	444	49	2071	8

$V_A$  - Simulated (true) additive variance; s.e. – standard error

In the population shown in Table 2 above for the simulated genetic variance,  $V_A = 950$ , the estimate of additive genetic variance obtained in this population under the reduced model was 980 which seems slightly higher than the  $V_A$ . However, this was not different ( $P > 0.05$ ) from  $V_A$ . Under the full model, the estimate of the additive variance is similar ( $P > 0.01$ ) to the simulated value of 950. For the population with a simulated additive genetic effect of 800, the estimate of additive genetic variance under the reduced model was 830 and this estimate under the full model was 800. These estimates were not different ( $P > 0.01$ ). Under a full model, the estimated variance and the simulated value were also similar. Estimates of additive genetic variance under a population with simulated additive genetic effects of 500, was 557 and the estimate under the full model was 497. The estimate under the reduced model is different ( $P < 0.05$ ) from the simulated value while under the full model the estimated additive variance is the same as the simulated value. Under populations with a small number of animals in full-sib families (2%) and smaller magnitude of the dominance genetic effect, the estimates of additive genetic variance are slightly higher than the true simulated additive values though the difference is not significant. However, with a large (500) dominance value, the estimate of the additive variance is biased upwards under the reduced model.

Presented in Table 3 are the estimates of additive genetic variances under reduced and full models in populations with 10% of animals in full-sib families. The estimate of additive genetic variance obtained in the population with a simulated additive genetic value of 950, was 1048 under the reduced model which is higher ( $P < 0.05$ ) than the simulated true value. Under the full model, the estimate of the additive genetic variance corresponds well with the simulated additive genetic value. In a population with simulated additive genetic effects of 800, the estimate of additive genetic variance obtained in this population under the reduced model was 920, which is greater ( $P < 0.01$ ) than the simulated true value. Under the full model, the estimate is similar to the simulated value. In the population with a simulated genetic variance of 500, the estimate of additive genetic variance obtained in this population under the reduced model was 652, which is higher ( $P < 0.01$ ) than the simulated true value. Under the full model, the estimate of the additive genetic variance corresponds well with the simulated additive genetic variance.

**Table 3** Additive genetic variances in population with 10% animals in full-sib families

Model	$V_A$	Additive Variance	s.e.	Dominance Variance	s.e.	Residual Variance	s.e.
Reduced	950	1048	33	-		1973	8
Full	950	959	33	158	28	1923	8
Reduced	800	920	33	-		2107	11
Full	800	837	36	188	31	2036	11
Reduced	500	652	21	-		2386	8
Full	500	485	23	386	40	2227	10

$V_A$  - Simulated (true) additive variance; s.e. – standard error

Presented in Tables 4 are the estimates of additive genetic variances under reduced and full models in populations with 20% of animals in full-sib families.

**Table 4** Additive genetic variances in population with 20% animals in full-sib families

Model	$V_A$	Additive Variance	s.e.	Dominance Variance	s.e.	Residual Variance	s.e.
Reduced	950	995	21	-		2018	7
Full	950	945	23	97	21	2006	7
Reduced	800	921	23	-		2081	21
Full	800	785	31	231	35	2036	6
Reduced	500	826	24	-		2246	7
Full	500	474	25	543	44	2111	8

$V_A$  - Simulated (true) additive variance; s.e. – standard error

For the population with  $V_A = 950$ , the estimate of additive genetic variance obtained in this population under the reduced model was 995 which is higher ( $P < 0.05$ ) than the simulated true value. In a population with simulated additive genetic value of 800, the estimate of additive genetic variance under the reduced model was 921 and this estimate was higher ( $P < 0.01$ ) than the simulated true value. With simulated additive genetic value of 500, the estimate of additive genetic variance under the reduced model was 826 and the estimate under the full model was 474. Under the full model, an accurate estimate is obtained.

Presented in Table 5 are the estimates of additive genetic variances under reduced and full models in populations with 50% of animals in full-sib families.

In the population with a  $V_A = 950$ , the estimate of additive genetic variance obtained in this population under the reduced model was 1012 which is higher ( $P < 0.01$ ) than the simulated true value. Under the full model, the estimate of the additive genetic variance corresponds well with the simulated additive genetic value. In a population with simulated additive genetic value of 800, the estimate of additive genetic variance obtained in this population under the reduced model was 955, which is higher ( $P < 0.01$ ) than the simulated true value. With  $V_A$  set at 500, the estimate of additive genetic variance obtained in this population under the reduced model was 896, which is higher ( $P < 0.01$ ) than the simulated true value. A similar pattern of results, which is even more dramatic, is shown in populations with all animals in full-sib families (Tables 6).

**Table 5** Additive genetic variances in population with 50% animals in full-sib families

Model	$V_A$	Additive Variance	s.e.	Dominance Variance	s.e.	Residual Variance	s.e.
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Reduced	950	1012	17	-		1996	6
Full	950	943	24	86	22	1984	6
Reduced	800	955	15	-		2079	6
Full	800	788	32	214	33	2049	6
Reduced	500	896	17	-		2174	6
Full	500	481	26	523	29	2125	6

$V_A$  - Simulated (true) additive variance; s.e. – standard error

**Table 6** Additive genetic variances in population with 100% animals in full-sib families

Model	$V_A$	Additive Variance	s.e.	Dominance Variance	s.e.	Residual Variance	s.e.
Reduced	950	1010	15	-		2010	5
Full	950	948	17	67	16	2006	5
Reduced	800	993	14	-		2052	5
Full	800	809	28	217	28	2034	5
Reduced	500	905	14	-		2181	5
Full	500	477	24	501	27	2141	5

$V_A$  - Simulated (true) additive variance; s.e. – standard error

The estimate of additive genetic variance obtained for a simulated value of 950 was 1010 under the reduced model, which is higher ( $P < 0.01$ ) than the simulated true value. The estimate of additive genetic variance in a population with simulated additive genetic value of 800 was 993 under the reduced model, which is higher ( $P < 0.01$ ) than the simulated true value. In the population with a simulated value of 500, the estimate of additive genetic variance obtained in this population under the reduced model was 905, which is greater ( $P < 0.01$ ) than the simulated true value. Almost all of the dominance genetic variance becomes part of the additive genetic variance and there is a very small decline in the error variances.

The dominance genetic variance fades into both the additive and residual genetic variances under the reduced model. This is supported by Misztal (1997), where he showed that in an animal model, with no permanent environment, the dominance genetic effects become part of both the additive and residual effects when dominance effects are not included in the model.

Results show that as the number of animals in full-sib families increases and the magnitude of dominance effects increases, the estimates of additive genetic variance under reduced models become increasingly biased upwards. Under the full model, the estimates of additive genetic effects are estimated with increased accuracy. It is also apparent that as the number of animals in full-sib families increases, most of the dominance genetic variance become part of the additive variance and there is marginal decline in the error variances. Rye & Mao (1998) found similar results in the study of non-additive genetic effects in fish. Considering dominance genetic effects in animal models, increases the accuracy of genetic evaluations (Henderson, 1989; De Boer & Van Arendonk, 1992; Johansson *et al.*, 1993). This is particularly true for populations with a large number of animals with dominance genetic relationships (Misztal, 1997). However, accounting for nonadditive genetic effects in dairy and beef cattle has led to a less dramatic effect on the estimation of genetic variances (Templeman & Burnside, 1990; Miglior *et al.*, 1995; Rodriguez-Almeida *et al.*, 1995). This may be an indication of the general effect of the population structure.

It becomes obvious that when the additive genetic variance is overestimated in situations where there are many animals with nonadditive relationships in the population, the heritabilities should follow suit. The estimates of heritability would be estimated with greater accuracy under a full model. This phenomenon would also occur when the magnitude of dominance genetic effects is large. The overestimation of

heritability in the narrow sense when only additive genetic effects are included in the model, suggests that simultaneous inclusion of nonadditive genetic effects explained part of the genetic variance that would otherwise be allocated with the additive genetic component (Fuerst & Solkner, 1994; Miglior *et al.*, 1995)

Estimates of dominance genetic variance under various population structures and magnitudes of dominance genetic effects are summarised in Table 7 for greater clarity.

**Table 7** Estimates of dominance genetic variances under different population structures and magnitude of dominance genetic effect

% Full-sib families	Dominance Genetic Variances					
	s.e.		s.e.		s.e.	
2	185.39	34.8	188.03	43.7	444.52	49.1
10	158.37	28.8	187.78	31.4	386.27	39.8
20	97.30	21.3	231.19	34.8	543.19	43.6
50	85.58	22.0	214.08	32.7	523.30	29.2
100	66.81	16	216.98	28.3	501.42	26.5
$V_D$	50		200		500	

s.e. – standard error

Dominance genetic variance estimate was biased upwards for a simulated true value of 50 in a population with 2% of animals in full-sib families. VanRaden *et al.* (1992) pointed out that estimates of genetic variances are most precise if the data contains large numbers of several types of close relatives and the number of family types must equal or exceed the number of genetic variances to estimate. The population with 2% animals in full-sib families has only 8 full-sib families. This small number of dominance relationships could have led to inaccurate estimates of dominance genetic variance. With  $V_D$  simulated at 200, the estimate of dominance genetic variance in this case was 188 and this was not different ( $P > 0.05$ ) from the simulated variance. This seems to contradict the earlier assertion that the incorrect estimate of dominance genetic variance is due to the fact that there were few animals with dominance genetic relationships. However, this may be an indication that the magnitude of dominance genetic variance in the population is important in the estimation of this parameter. This seems to be supported with a simulated value of 500 as the estimate of dominance genetic variance is close to what was simulated. Though the number of full-sibs in the population was small, the higher magnitude of dominance genetic variance resulted in more accurate estimates of dominance genetic variance.

The same pattern as seen in 2% full-sibs emerges in population with 10% animals in full-sib families. With  $V_D = 50$ , the resultant estimate of dominance genetic variance is 158.37 which is a gross overestimation ( $P < 0.01$ ) of what was simulated. With  $V_D$  simulated at 200, the estimate of dominance genetic variance in this case was 187.78 and this was not different ( $P > 0.05$ ) from the simulated variance. However, at a simulated dominance value of 500, the estimate is much lower than what was expected given the pattern that is emerging.

In the population with 20% animals in full-sib families, the estimate of dominance genetic variance was 97 for  $V_D$  set at 50. This seems to be an improvement over the estimates obtained in 2% and 10% full-sibs. The estimate of dominance genetic variance for a simulated value of 200 was 231 while for a simulated dominance value of 500 estimate of dominance genetic variance obtained was 543. The results in these populations follow the pattern of results found in populations with 2% and 10% full-sibs except that in this case (20 % animals in full-sib families), there is a general improvement in the estimation of dominance genetic variance. This is especially the case for simulated dominance value of 50.

For 50% of animals in full-sib families, the estimate of dominance genetic variance in which  $V_D$  was 50 is 85. Though the values are still different ( $P < 0.05$ ), there is an improvement trend showing. The dominance genetic variance estimate, 214 is similar ( $P > 0.01$ ) to the simulated value of 200. The estimates are also the same for simulated value of 500.

The dominance genetic variance of 66.81 is similar ( $P > 0.05$ ) to the simulated dominance genetic value of 50 in the population with all animals in full-sib families. Estimates of dominance genetic variances are also similar ( $P > 0.05$ ) to the simulated dominance genetic values of 200 and 500.

Estimation of nonadditive dominance genetic variance requires large data sets (Chang, 1988; Misztal, 1997). The size of each population in this study is 10 000 though each population was replicated 50 times. Misztal *et al.* (1998) pointed out that accurate estimates of dominance variance require them to be derived from data sets with at least 30 000 to 100 000 animals for populations with many full-sibs. However, results suggest that even when the number of animals with dominance genetic relationships is small, as long as the magnitude of dominance genetic variance is large, dominance genetic variances can be estimated with relatively good accuracy.

Results from populations with 50% and 100% show that when the number of full-sibs is large, dominance genetic variance can be estimated with improved accuracy even if the magnitude of the dominance genetic value in the population is small (50). It was observed that in populations with a small number of full-sibs (2% and 10%), dominance genetic variance estimates could be obtained with relatively good accuracy when the magnitude of the dominance genetic variance is large. However, the estimates are not as accurately estimated as those estimated in populations with a higher number of full-sib families.

The general conclusion that can be made is that in populations with small number of full-sibs in the population (2% and 10%), accurate estimates of dominance genetic variance would be difficult to obtain unless the magnitude of dominance variance is large. In populations with a large number of animals having dominance genetic relationships, estimates of dominance genetic effects can be obtained with improved accuracy even when the effect in the population is of small magnitude.

Models with fewer nonadditive effects produce smaller standard errors of variance estimates (VanRaden *et al.*, 1992). In this study, the magnitude of standard errors seems to increase as the magnitude of dominance genetic variances increases irrespective of the number of animals in full-sib families. On the same note, the standard errors seem to decrease in magnitude as the number of animals with dominance genetic relationships increases. Higher standard errors are likely to occur for estimates of dominance genetic variation as compared to additive variation and generally the precision of dominance genetic effects is expected to be much less than for estimation of additive genetic variance (Tempelman, 1989). This is also the case in this study, the size of standard errors for dominance genetic variance was higher than the standard errors for additive genetic variances. It must be pointed out that the method used in the analysis does not generate standard errors. The standard errors in this study were estimated from the empirical standard errors of the differences between the observed values and the simulated values.

Dominance genetic variation has been found to be important for several traits of economic importance. Culbertson *et al.* (1998) found dominance effects to be important for reproductive and growth traits in swine. Wei & Van der Werf (1993) observed large estimates of dominance variance for most of the traits they studied in poultry. Rye & Mao (1996) also found dominance genetic effects to be important for growth in Atlantic Salmon. In all these studies, the species were of high fecundity.

The study considered the dominance effects due to full-sibs, however in real populations, other relationships such as 3/4 sibs exist. It must be noted that the Tilde-hat Approximation to REML method used in this study may have reduced efficiency compared to REML or Bayesian methods.

## Conclusions

The widespread use of Best Linear Unbiased Prediction (BLUP) for genetic evaluation in livestock has led to significant improvement in many traits of economic importance. This improvement can further be enhanced by increasing the accuracy of genetic evaluations through inclusions of nonadditive genetic effects in the genetic evaluation models. This would be particularly important in populations with a large number of nonadditive relationships and in traits where nonadditive genetic variance is important. Further study is necessary to determine if the rankings of animals based on breeding values would be changed when dominance genetic effects were considered.

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