South African Journal of Animal Science 2006, 36 (4)

Genetic parameters for weaning weight of Kenyan Boran cattle accounting for direct-maternal genetic covariances

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Abstract

Genetic parameters were estimated for weaning weight (WW) in Kenya Boran cattle using animal models that assumed non-zero direct-maternal genetic covariance. In addition to the direct and maternal genetic effects, maternal permanent environmental and sire by herd-year interaction effects were tested. Two datasets were used. Dataset 1 (DS1) included all animals while dataset 2 (DS2) constituted only records of animals with known paternity. Estimates of direct and maternal heritabilities from DS1 ranged from 0.61 to 0.64 and 0.25 to 0.27, respectively. Estimates of direct and maternal heritabilities from DS2 ranged from 0.07 to 0.31 and 0.16 to 0.23. Direct-maternal genetic correlations were large and negative but were lower in the analyses of DS2 than in DS1. Similarly, estimates of direct and maternal heritability were lower in the analyses of DS2 than in DS1 especially when the effect of sire by herd-year effect was fitted in the model. This study shows that WW is highly heritable and under the influence of maternal effects. Estimates of genetic parameters and direct-maternal genetic covariance are dependent on data size and structure and how direct and maternal effects have been accounted for.

Keywords: Parameter estimates; data structure; sire by herd-year interaction
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Introduction

Genetic parameter estimates are needed for implementation of breeding programmes and assessment of progress of ongoing programmes. Therefore, accuracy in their estimation is paramount. Estimation of genetic parameters for growth traits is always considered problematic mainly due to confounding of direct and maternal effects (Baker, 1980). However, several methods of estimation of genetic parameters have been suggested to overcome this problem (Meyer, 1997; Quintanilla *et al.*, 1999). Nonetheless, problems associated with precision of estimates and high sampling correlations between estimates still remain, especially in field data.

The Kenya Boran cattle are extensively managed and therefore use of field data in the estimation of genetic parameters is inevitable. Generally, field data are highly unbalanced with missing records and poor linkage between generations due to inconsistent recording resulting in high estimates of negative direct-maternal covariance. This situation is further aggravated by the small herd sizes of indigenous tropical beef cattle (Lobo *et al.*, 2000). These fairly high negative estimates imply an antagonistic relationship between direct genetic and maternal effects (Meyer, 1992), indicating slow response to selection in the traits concerned.

Genetic parameter estimates for indigenous African beef breeds have been estimated considering mainly direct genetic effects and to some extent maternal effects. However, in most studies where maternal effects were considered, the covariance between direct and maternal genetic effects was ignored. In a few studies of genetic evaluation of growth performance where they were considered, highly negative direct-maternal genetic covariance estimates were reported (Haile-Mariam & Kassa-Mersha, 1995; Khombe *et al.*, 1995; Maiwashe *et al.*, 2002; Demeke *et al.*, 2003; Nephawe, 2004; Norris *et al.*, 2004). Meyer (1997) attributed the highly negative estimates of direct-maternal genetic covariance in Hereford, Angus and Limousine to unaccounted for sources of variation such as management groups. This implies that the negative covariance was partly genetic and partly environmental. However, no attempt has been made to explain the possible causes of these highly negative estimates in indigenous African beef breeds. The objective of this paper was to estimate genetic parameters for weaning weight (WW) of Kenya Boran cattle accounting for direct-maternal genetic covariance and explain the causes of the magnitude of the direct-maternal genetic covariance.

Material and Methods

Data on WW of Kenya Boran cattle were made available by a large scale commercial ranch and the National Beef Research Centre of the Kenya Agricultural Research Institute (KARI) - Lanet, located in Agro Ecological Zones (AEZ) 4 and the inter phase of AEZ 3 and 4, respectively. Cattle on both farms were raised on natural pastures composed of mainly *Themeda triandra.* A continuous mating and cow-calf systems were practiced on both farms. Calves were weaned at seven months on the research station and at nine months on the ranch.

Selection of breeding animals was done at weaning and at 18 and 24 months, based on physical appraisal of growth performance and conformation. On the ranch initial culling of animals was done at weaning where all animals with conformation contrary to Boran Cattle Breeders Society of Kenya standards were culled. Selection and voluntary culling was more stringent on the ranch than on the research station. Heifers that showed excellent growth and conformation attributes were put in stud herds on both farms as replacements while those with good growth and conformation were put in the commercial herds to breed stock for sale and slaughter. Once in the breeding herds, heifers that did not calve down within two years were culled on both farms. Culling of cows was determined by their reproduction efficiency rather than age. On the ranch, breeding bulls for the stud and commercial herds were sourced from other Kenya Boran breeders and within the stud herds, respectively. On the other hand, bulls used in the research station were sourced from within the farm and occasionally from other Kenya Boran breeders. Breeding bulls were replaced when their daughters attained breeding age.

A complete animal record consisted of its identity, pedigree information, dates of birth and weaning, sex, herd of origin and WW. Data were edited for consistency of pedigree information and correct dates of birth and weighing. Records with anomalies in pedigree information and dates were discarded. Also discarded were records of animals with unknown or incorrect sexuality. A final data set (Dataset 1, DS1) for analyses comprised of 4496 records of animals born between 1989 and 2003 and sired by 93 bulls. The data spanned three generations from the grandparent generation. From DS1, a second data set (DS2) was extracted that constituted only of records of animals with known paternity. This was for the purpose of investigating the effect of incomplete pedigrees on estimates of direct-maternal genetic covariance. The structure and summary statistics for both data sets are shown in Table 1.

Table 1 Characteristics of the data structure and summary statistics

	Dataset 1 (DS1)	Dataset 2 (DS2)
Number of records	4496	2026
Number of animals[a]	5389	2638
Number of dams	1487	849
Number of sires	93	93
Weaning age, days	243.05	243.74
Weaning weight, kg	184.56	176.86
SD	41.59	47.82
CV %	22.54	27.04

[a] All animals in the pedigree including those without records

Estimates of (co)variance components were obtained using the ASREML programme (Gilmour *et al*., 2001). An animal model was used throughout, incorporating all pedigree information available and assuming non-zero direct-maternal genetic covariance. In addition to the direct and maternal genetic effects, maternal permanent environmental and sire by herd-year interaction effects were tested by fitting four alternative models. Fixed effects fitted included sex (two classes), parity of the dam (five classes) and the herd-year-season of birth (52 classes). Two seasons were described in each year based on rainfall which influenced the availability of pastures as wet (high rainfall and more pasture) and dry season (low rainfall and scarce pasture); the wet season which comprised the months of March - June and September- October and the dry season comprised of January- February, July- August and November - December. This mode of contemporary grouping was preferred to the commonly used herd x weigh date x user's defined management group because of the continuous mating system which would result in few animals per contemporary group if the latter was used. Each contemporary group had at least two sires. Parity effect was grouped into five classes, with any calving recorded in parity five and above being grouped under parity five due to receding number of records in later parities. Age of the calf at weaning was fitted as a linear covariable. The following four models were fitted:

Model 1
$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z_1a} + \mathbf{Z_2m} + \mathbf{e} \quad (1)$$
$$\text{with cov}(\mathbf{a}, \mathbf{m}) = \mathbf{A}\sigma_{am},\ \text{var}(\mathbf{e}) = \mathbf{I}_n\sigma^2_e$$

Model 2
$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z_1a} + \mathbf{Z_2m} + \mathbf{Z_3s} + \mathbf{e} \quad (2)$$
$$\text{with cov }(\mathbf{a}, \mathbf{m}) = \mathbf{A}\sigma_{am},\ \text{var}(\mathbf{s}) = \mathbf{I}_{NS}\sigma^2_s \text{ and var}(\mathbf{e}) = \mathbf{I}_n\sigma^2_e$$

Model 3
$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z_1a} + \mathbf{Z_2m} + \mathbf{Z_4c} + \mathbf{e} \quad (3)$$
$$\text{with cov}(\mathbf{a}, \mathbf{m}) = \mathbf{A}\sigma_{am},\ \text{var}(\mathbf{c}) = \mathbf{I}_{NC}\sigma^2_c \text{ and var}(\mathbf{e}) = \mathbf{I}_n\sigma^2_e$$

Model 4
$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z_1a} + \mathbf{Z_2m} + \mathbf{Z_3s} + \mathbf{Z_4c} + \mathbf{e} \quad (4)$$
$$\text{with cov }(\mathbf{a}, \mathbf{m}) = \mathbf{A}\sigma_{am},\ \text{var}(\mathbf{s}) = \mathbf{I}_{NS}\sigma^2_s,\ \text{var}(\mathbf{c}) = \mathbf{I}_{NC}\sigma^2_c \text{ and var}(\mathbf{e}) = \mathbf{I}_n\sigma^2_e$$

where **y** is a vector of observations on the animal, **b, a, m, s** and **c** are vectors of fixed effects including covariables, direct additive genetic effects, maternal additive genetic effects, sire by herd-year interaction and maternal permanent environmental effects, respectively, $\mathbf{X}$, $\mathbf{Z_1}$, $\mathbf{Z_2}$, $\mathbf{Z_3}$ and $\mathbf{Z_4}$ are corresponding incidence matrices relating the effects to **y**, **e** is the vector of residual error, **A** is the numerator relationship matrix, **I** is the identity matrix, NS is the number of sires, NC is the number of dams, n is the number of animals in the analysis including parents without records, σ_{am} is the direct-maternal genetic covariance and σ^2_s, σ^2_c and σ^2_e are the variances due to sire by herd-year interaction, maternal permanent environmental and residual error effects, respectively.

Convergence was assumed when the change in the Euclidian norm of the vector of the first derivatives was less than 10^{-4}. Each analysis was restarted using the resultant (co)variance component estimates as new priors until changes in the function value and estimates in the scaled parameters were less than 0.01. At convergence, phenotypic variance (σ^2_p) was calculated as the sum of direct additive genetic variance (σ^2_a), maternal additive genetic variance (σ^2_m), σ_{am}, σ^2_s, σ^2_c and σ^2_e, appropriately. Comparison of models was done using likelihood ratio test with reference to model 1.

Results and Discussion

Table 2 presents estimates of (co)variance components and genetic parameters for WW from DS1. Estimates of additive genetic variance were highest in model 4 and lowest in model 1. Model 4 had the lowest estimates of residual error variance and the highest log-likelihood. Based on log likelihood ratio tests, models 2 and 4 were not significantly different but were different from models 1 and 3. This implies that models fitting sire x herd effect better fitted the data by accounting for possible environmental sources of variation that were lumped in the residual variance when models 1 and 3 were used. Estimates of maternal genetic variance were highest in model 2 and lowest in model 3 because of partitioning of maternal effects into genetic and permanent environmental effects. Phenotypic variance increased with increase in the number of effects in the model. Meyer (1992) and Meyer *et al*. (2004) observed this trend and attributed it to compounded cross substitution effect in partitioning of the phenotypic variance when estimating highly correlated components following the inclusion of the effect of sire by herd-year interaction without improvement in the data structure, particularly when the data size is small.

Direct heritability estimates ranged from 0.61 to 0.64. These estimates were higher those reported by Meyer (1992; 1997) and Haile-Mariam & Kassa-Mersha (1995) in Australian beef cattle and Boran cattle in Ethiopia, respectively. The high estimates in the present study are attributable to the high variances, which imply a high genetic variability in the population considered thus presenting a wide scope of genetic selection for improvement. Maternal heritability estimates ranged from 0.25 to 0.27. This falls within the range reported by Meyer (1997). Estimate of maternal environmental variance as a proportion of phenotypic variance was 0.02 while sire by herd-year variance as a proportion of phenotypic variance was 0.09.

A comparison between models (models 2 and 4) that fitted sire by herd-year interaction as an additional random effect and those that only fitted maternal effects (models 1 and 3) indicates that estimates of direct and maternal heritability were generally higher in the former. This is contrary to the results of Meyer (1997) who noted a decline in estimates of direct and maternal heritability when sire by herd-year interaction was fitted. The high parameter estimates in models 2 and 4 could be as a result of compounded cross substitution alluded to earlier, given the size of the data. Maternal permanent environmental variance as a proportion of phenotypic variance and the variance of sire by herd-year interaction as a proportion of phenotypic variance were not significantly different across the models. These estimates fell within the range reported in the literature (Haile-Mariam & Kassa-Mersha, 1995; Meyer, 1997; Meyer *et al.*, 2004).

Table 2 Estimates of (co)variance components and genetic parameters for weaning weight from dataset 1 (DS1)

	Model[b]			
Estimates[a]	1	2	3	4
σ^2_a	398.22	447.91	402.90	452.86
σ^2_m	177.35	192.98	166.01	182.83
σ^2_c			13.69	12.11
σ^2_s		65.47		65.44
σ^2_e	293.25	240.51	288.11	235.37
σ^2_p	655.70	706.80	656.40	707.30
σ_{am}	-212.60	-241.08	-214.66	-241.71
h^2	0.61	0.63	0.61	0.64
m^2	0.27	0.27	0.25	0.26
c^2			0.02	0.02
s^2		0.09		0.09
r_{am}	-0.80	-0.82	-0.83	-0.84
Log L	0.00	-14.10	-0.10	-14.20

[a] σ^2_a - direct additive genetic variance; σ^2_m - maternal additive genetic variance; σ^2_c - maternal permanent environmental variance; σ^2_s - variance due to sire by herd-year interaction; σ^2_e - residual error variance; σ^2_P - phenotypic variance; σ_{am} - direct-maternal genetic covariance; h^2 - direct heritability; m^2 - maternal heritability; c^2 - maternal environmental variance as a proportion of phenotypic variance; s^2 - variance due to sire by herd-year interaction as a proportion of phenotypic variance; r_{am} - direct-maternal genetic correlation. Standard errors for direct heritability, maternal heritability, variance due to sire by herd-year interaction as a proportion of phenotypic variance and maternal environmental variance as a proportion of phenotypic variance was 0.08, ranged from 0.05 to 0.06, was 0.03 and 0.04, respectively. Log likelihood expressed as a deviation from model 1

[b] See text for description of the models

Estimates of direct-maternal genetic correlation were highly negative across the models. These estimates were higher than -0.54 and -0.57 reported by Maiwashe *et al.* (2002) for South African Bonsmara and Haile-Mariam & Kassa-Mersha, (1995) for Ethiopian Boran. The estimates were slightly higher in models 2 and 4 with sire by herd-year effect than in models 1 and 3. However, inclusion of sire by herd-year effects in the model has been shown to reduce the direct-maternal correlation in Wokalup cattle (Meyer, 1997) and Suffolk sheep population (Maniatis, 2000). Despite this, the reduction in the error variance and improvement of the log-likelihood in models 2 and 4 indicate that fitting sire by herd-year interaction effect provided a better fit to the data.

Estimates of (co)variance components and genetic parameters for WW from DS2 are presented in Table 3. Estimates of (co)variance components and genetic parameters were higher in models 1 and 3 than in models 2 and 4. Residual error and phenotypic variances were, however, higher in models 2 and 4. The high estimates of error variance in model 4 could be due to high sampling variance as a result of additional random effects in the model. This indicates that the models were fairly over-parameterised given the size of the data being analysed. Meyer (1997) also reported higher estimates of variance components and genetic parameters in models that only fitted maternal effects as an additional random effect. Estimates of direct heritability were lower than maternal heritability when sire by herd-year effect was fitted (0.07 *vs*. 0.18 and 0.07 *vs*. 0.16 in models 2 and 4, respectively). The fall in parameter estimates could be due to further partitioning of direct and maternal variances as a result of reduction in covariance between paternal sibs in the contemporary groups when sire by herd-year effect was fitted (Meyer, 1997). The reduction in estimates of direct heritability in models 1 and 3 between DS1 and DS2 could be attributed to more genetic connectedness in DS2 following the removal of animals with unknown sires that were otherwise included in the analysis of DS1.

Table 3 Estimates of (co)variance components and genetic parameters for weaning weight from dataset 2 (DS2)

	Model[b]			
Estimates[a]	1	2	3	4
σ^2_a	194.01	45.62	194.39	47.33
σ^2_m	144.42	110.97	125.59	101.38
σ^2_c			18.77	9.96
σ^2_s		74.85		74.31
σ^2_e	390.28	446.80	386.71	444.06
σ^2_p	619.30	631.90	618.80	631.50
σ_{am}	-108.80	-46.25	-106.25	-45.72
h^2	0.31	0.07	0.31	0.07
m^2	0.23	0.18	0.20	0.16
c^2			0.03	0.02
s^2		0.12		0.12
r_{am}	-0.65	-0.65	-0.68	-0.66
Log L	0.00	-15.75	-0.18	-14.84

[a]See Table 2 for description of variance components and genetic parameters. Standard errors for direct heritability, maternal heritability, variance due to sire by herd-year interaction as a proportion of phenotypic variance and maternal environmental variance as a proportion of phenotypic variance was 0.09, ranged from 0.06 to 0.08, was 0.03 and 0.05, respectively. Log likelihood expressed as a deviation from model 1

[b]See text for description of the models

Estimates of direct-maternal correlation were highly negative across the models although the magnitude was lower in models 2 and 4. These estimates were lower than those obtained when DS1 was analysed. This reduction in estimates of direct-maternal correlation when DS2 was analysed suggest that high estimates obtained from analysis of DS1 may have been caused by some unaccounted for sources of variation especially those associated with data structure rather than true biological relationship between direct and maternal genetic effects. Dodenhoff *et al*. (1998), Maniatis & Pollott (2002) and Phocas & Laloe (2004) reached a similar conclusion in their study with Hereford cattle. Meyer (1997) attributed large negative direct-maternal genetic correlation estimates to sources of variation such as management groups and heterogeneous variance. Several attempts have been made to explain the covariance structure of maternal effects and reduce the magnitude of the negative direct-maternal genetic correlation. Meyer (1997) and Dodenhoff *et al.* (1999) observed a decline in the magnitude of direct-maternal correlation by fitting models with regression of offspring performance on maternal phenotype and sire by herd-year interaction effects. The presence and increase in estimates of variance due to sire by herd-year effect in the present study when data structure is improved (DS2) accompanied by decline in estimates of direct maternal correlation confirm their findings. It is thus evident that there are high possibilities of bias in estimates of maternal effects, if direct-maternal covariance is not accurately modelled, given the intricacies of performance recording and resultant data size in the developing tropical Africa. The high estimates of error and phenotypic variances in this study could be attributed to problems of sampling variation encountered during partitioning of the total phenotypic variance into its components (Meyer, 1992).

Generally, estimates obtained from analyses of DS1 were higher than obtained from DS2 across the models except for the error variance. Meyer (1997) and Maniatis (2000) observed a similar pattern in analyses of WW in Polled Hereford and Suffolk sheep populations, respectively. They attributed the lower estimates to enhanced uniformity as a result of increased connectedness in data structure in experimental datasets relative to field datasets, a scenario that was simulated in this study by considering only animals with known paternity in DS2. In studies where a covariance between direct and maternal effects was considered, covariances ranging from slightly positive in datasets from animals under experimental setting to highly negative estimates in field datasets have been reported (Maniatis, 2000).

Conclusions

This study has shown that WW is highly heritable and under the influence of maternal effects. This study has also shown the possibility of overestimation of genetic parameter estimates when models accounting for direct maternal genetic covariance are used in less uniform datasets (DS1). Estimates of direct-maternal genetic correlation were high and negative. This is probably due to some other unaccounted for sources of variation other than the true biological relationship which were partly explained by sire by herd-year interaction effect in analysis of a more uniform dataset (DS2). Selection programmes for genetic improvement of growth performance should therefore be based on genetic models where direct-maternal genetic correlation has been well taken care of, if high and sustainable genetic progress is anticipated. Reliable estimation of direct and maternal genetic parameters accounting for direct maternal genetic covariance requires data with a sufficient amount of reliable records and good pedigree information. This was, however, a major limitation in this study. This paper sheds light on the possibility of inflation of direct-maternal genetic correlation estimates due to non-genetic sources of variation; as more data is availed on growth performance of the Kenya Boran cattle, the highly negative estimates of direct-maternal genetic correlation should be further investigated to establish the true estimate of covariance that could be attributed to a biological relationship between the direct and maternal effects.

Acknowledgements

We appreciate the kind support of the staff of the farms during the collection of data and the Department of Animal Sciences, Egerton University, Njoro, Kenya, for provision of facilities.

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